

Accounting for detectability improves estimates of species richness in tropical bat surveys

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Summary

1. Species richness is a state variable of some interest in monitoring programmes but raw species counts are often biased due to imperfect species detectability. Therefore, monitoring programmes should quantify detectability for target taxa to assess whether it varies over temporal or spatial scales. We assessed the potential for tropical bat monitoring programmes to reliably estimate trends in species richness.
2. Using data from 25 bat assemblages from the Old and New World tropics, we estimated detectability for all species in an assemblage (mean proportion of species detected per sampling plot) and for individual species (species-specific detectability). We further assessed how these estimates of detectability were affected by external sources of variation relating to time, space, survey effort and biological traits.
3. The mean proportion of species detected across 96 sampling plots was estimated at 0·76 (range 0·57–1·00) and was significantly greater for phytophagous than for animalivorous species. Species-

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averaged detectability for phytophagous species was influenced by the number of surveys and season, whereas the number of surveys and sampling methods [ground- or canopy-level mist nets, harp traps and acoustic sampling (AS)] most strongly affected estimates of detectability for animalivorous bats. Species-specific detectability averaged 0·4 and was highly heterogeneous across 232 species, with estimates ranging from 0·03 to 0·84. Species-level detectability was influenced by a range of external factors such as location, season, or sampling method, suggesting that raw species counts may sometimes be strongly biased.

4. Synthesis and applications. Due to generally high species-specific detection probabilities, Neotropical aerial insectivorous bats proved to be well suited for monitoring using AS. However, for species with low detectability, such as most gleaning animalivores or nectarivores, count data obtained in bat monitoring surveys must be corrected for detection bias. Our results indicate that species-averaged detection probabilities will rarely approach 1 unless many surveys are conducted. Consequently, long-term bat monitoring programmes need to adopt an estimation scheme that corrects for variation in detectability when comparing species richness over time and when making regional comparisons. Similar corrections will be needed for other species-rich tropical taxa.

Key-words: bats, biodiversity monitoring, Chiroptera, community ecology, detection probability, jackknife estimator, species richness

Introduction

Species richness is an important state variable in the majority of biodiversity monitoring programmes (Yoccoz, Nichols & Boulanger 2001; Pollock *et al.* 2002). Studies investigating spatial or temporal trends in species richness or the effects of different environmental factors on local species occurrence are generally faced with the problem of imperfect and variable species detectability. Especially for species-rich taxa, it is unlikely that all species present at a particular place and time will be recorded during a typical survey, leading to a bias in species counts. Thus, comparisons of species richness over temporal or spatial scales will be distorted if based on simple counts of species (Boulanger *et al.* 1998; Pollock *et al.* 2002; Kéry & Royle 2008). Unbiased estimates of the relative difference in observed species richness require that mean species detectabilities are equal across assemblages (Kéry & Schmid 2006). Consequently, whenever species counts are used as a proxy for true species richness, tests of whether the expectation of the average species detection probability is constant over space and time are essential (Kéry & Plattner 2007; Kéry & Royle 2008). Knowledge about differences in detectability prior to implementation of a particular survey design may prove crucial. Moreover, the suitability of a taxon for a long-term monitoring programme depends on the baseline temporal and spatial variation in the state variables selected and how this inherent variability is influenced by extrinsic factors relating to options for survey design, sampling methodology or species traits.

Bats, with a cosmopolitan distribution and at least 1,232 extant species (N.B. Simmons, pers. comm.), are major contributors to mammalian biodiversity, comprising about 20% of mammalian species globally (IUCN 2009). Variation in bat species richness parallels that of mammals in general, showing

a strong increase towards the equator (Patterson, Willig & Stevens 2003). In tropical forests, bats are important components of local mammal assemblages as they occupy a large variety of trophic niches and are often the most species-rich and abundant taxa (Kingston, Boo Liat & Zubaid 2006; Rex *et al.* 2008; Fahr & Kalko 2010). Tropical bats provide critical ecosystem services with respect to pollination, seed dispersal and control of arthropod populations (Patterson, Willig & Stevens 2003; Kalko, Smith & Kalko 2008; Lobova, Geiselman & Mori 2009). Bats are considered excellent bioindicators because they respond to a wide range of human-induced changes in habitat quality and climate, including urbanization, agricultural intensification, logging, habitat loss and fragmentation, global climate change and overhunting (Clarke, Rostant & Racey 2005; reviewed in Jones *et al.* 2009). Moreover, bats are reservoirs of a wide range of emerging infectious diseases whose spread may be related to habitat deterioration and climate change (Jones *et al.* 2009).

Globally, almost a quarter of all bat species are considered threatened (Schipper *et al.* 2008). Largely as a consequence of habitat loss, fragmentation, and degradation, bat populations have experienced world-wide declines in recent decades. In both the Neotropics and Paleotropics, bats have been projected to undergo considerable future declines as a result of continuing rampant deforestation and habitat fragmentation (Lane, Kingston & Lee 2006; IUCN 2009). Although the potential of bats as bioindicators and the urgent need for the implementation of a global network for monitoring bat populations have been recognized (Jones *et al.* 2009), existing monitoring programmes are largely limited to temperate regions (O'Shea & Bogan 2003). Long-term monitoring programmes for tropical bats are currently lacking, and so far bats have not been considered in established long-term monitoring programmes in the tropics [e.g. Conservation Interna-

tional's Tropical Ecology, Assessment and Monitoring (TEAM) network, <http://www.teamnetwork.org>].

A standardized sampling scheme as part of a tropical bat monitoring programme should allow for consistent estimation of species richness at selected study sites so that robust conclusions can be made about temporal trends. Our primary objectives in the present study were to quantify detectability in tropical bat surveys and to identify important determinants of species detectability. Access to numerous empirical data sets from 25 locations across the Neotropics and Paleotropics constituted the basis for our assessment, providing us with the necessary reference data against which to calibrate a possible bat monitoring programme. Our analysis considered data from multiple sampling methods [ground and canopy mist nets, harp traps and acoustic sampling (AS)] as many bat species are usually missed in species inventories that employ only a single method (MacSwiney, Clarke & Racey 2008; Kunz & Parsons 2009; Fahr & Kalko 2010), and thus we judged sampling method to be a major factor affecting estimates of detectability.

Estimation of species richness as part of a bat monitoring programme would typically be based on repeated surveys conducted at various sampling plots at selected locations. Capture–recapture models permit estimation of species richness based on the pattern of detection/nondetection of species in replicated surveys. We employed the jackknife estimator associated with model M_h , which explicitly assumes heterogeneity in species encounter rates (Burnham & Overton 1979), and has been widely used for estimating species richness (Boulinier *et al.* 1998; Kéry & Schmid 2006; Husté & Boulinier 2007; Kéry & Plattner 2007; Rex *et al.* 2008). Using this analytical framework, we first estimated mean species detectability for each data set as the mean proportion of species detected for each plot-year combination (mean species inventory completeness). Following the approach of Kéry & Plattner (2007), we then modelled species-specific detectability as the probability of detecting a particular species during two successive surveys. We subsequently used the resulting estimates to assess how detectability varies in relation to potentially important sources of heterogeneity, particularly temporal and spatial variation and survey effort. We made the following predictions: (i) detection probability varies widely among bat species and between trophic groups or ensembles; (ii) sampling method is a strong determinant of detectability as suggested by a large body of empirical evidence; (iii) detectability is influenced by sampling interval, with higher detection probability for sampling on nonconsecutive vs. consecutive nights as a result of trap shyness of bats; (iv) we did not *a priori* expect detectability to vary between sampling years; however, several studies have noted seasonal differences in bat abundance (e.g. Stoner 2005; Meyer & Kalko 2008), and thus we predicted detection probability to differ among seasons; (v) mean species detectability is affected by sampling locality due to structural and compositional differences among local assemblages or habitat effects.

Materials and methods

ESTIMATION OF THE PROPORTION OF SPECIES DETECTED

To assess inventory completeness [i.e. the proportion of species detected (P)], we calculated the ratio of observed to estimated species richness for each plot-year combination (Boulinier *et al.* 1998; Kéry & Schmid 2006).

Observed species richness was derived from capture or AS data from 96 sampling plots in 25 different study locations (see Table S1, Supporting information). For data sets originating from fragmented or otherwise disturbed areas, data only from control plots in unfragmented or mostly undisturbed forest were used for analysis. Across the 25 study locations, the number of sampling sites (plots/transects) averaged 3.8 ± 2.9 (SD, range 1–10), with a mean of 2.8 ± 2.1 surveys conducted per site (range 2–20) for an average of 2.0 ± 0.8 sampling years per location (range 1–4).

In the case of most data sets, encounter histories were in the form of a species-by-plot-by-replicate matrix. For the few data sets for which replicated surveys were conducted on the same single plot, the capture-history matrix was comprised only of species and temporal replicates. In all cases, data sets were then partitioned according to sampling plot/transect, year and season (dry and wet season where applicable). For each combination of plot, year and season, the capture/AS data were summarized in a two-dimensional matrix, with rows denoting the species detected and columns denoting the visits on a particular plot (cf. Kéry & Schmid 2006). This matrix formed the basis for subsequent estimation of species richness.

We estimated species richness using the first-order jackknife estimator (Jack1; Burnham & Overton 1979), which was originally developed in the context of capture–recapture models for closed populations. The heterogeneity model M_h underlying the jackknife estimator allows for heterogeneity among species in their probability of detection but assumes constant detectability across surveys and a closed species pool for the duration of the study, i.e. that all species are present for the entire survey duration (Burnham & Overton 1979). For the data sets used in this study, we assumed that any changes in assemblage composition between sampling periods are negligible and, if present, that violations of the closure assumption are only mild. Although several tropical bat species show seasonal fluctuations in abundance and a few species migrate (Fleming & Eby 2003; Stoner 2005), closure violation is less likely for tropical bat assemblages than for avian assemblages, which often contain many migrant species with staggered arrival times (Kéry & Schmid 2006). Moreover, minor violations of the closure assumption do not always introduce a measurable bias into estimates of species richness (Kéry & Schmid 2006). Thus, we are confident that temporal closure is a reasonable assumption for our study and that any minor violations of this assumption will not noticeably bias estimates of species richness.

The Jack1 estimator has performed consistently well in comparisons of various estimators of species richness, and is widely used for estimating species richness and detectability (Burnham & Overton 1979; Boulinier *et al.* 1998; Walther & Moore 2005; Kéry & Schmid 2006; Husté & Boulinier 2007). Moreover, the Jack1 estimator provides reliable estimates of local species richness even when habitats are heterogeneous within sampling units (Jiguet, Renault & Petiau 2005). Calculations were performed using EstimateS software (Colwell 2006).

PREDICTORS OF THE AVERAGE PROPORTION OF SPECIES DETECTED

The proportion of species detected (i.e. the ratio of observed to estimated species richness for each plot-year combination) was treated as the response variable (log-transformed) in a linear mixed-effects model (LMM) (Zuur *et al.* 2009) designed to assess the importance of a suite of factors related to spatial and temporal variation and to variation in survey effort that might potentially affect P . To account for the relative uncertainty in species richness estimates, we included the inverse of the standard deviation of the estimates for species richness as weights in the LMMs. Thus, more precise estimates were weighted more heavily in the model. Covariates included in the model as fixed effects were year, season (dry, wet), region (Neotropics, Paleotropics), number of surveys per plot, sampling interval (consecutive vs. nonconsecutive nights), sampling method (ground nets – GN, canopy nets – CN, harp traps – HT, AS), spatial configuration (line transect, sampling plot – same net locations, sampling plot – varying net locations) and trophic group [phytophagous (frugivores and nectarivores), animalivorous (insectivores, carnivores, piscivores, sanguivores) Patterson, Willig & Stevens 2003]. Sampling plot nested within location was specified as a random effect in the model. Although it also would have been desirable to examine interactions, we could only consider additive effects, as we did not have enough observations for all combinations of fixed effects to fit more complex models. This was mostly due to the scarcity of data sets available from the Paleotropics. The significance of the fixed and random effects was determined by sequentially dropping terms and comparing models based on likelihood (L-) ratio tests and changes in Akaike's Information Criterion (AIC) scores, with the model with the lower AIC indicating the model with the better fit (Zuur *et al.* 2009). Models were initially fitted using maximum likelihood estimation; however, estimates of model parameters in the minimum adequate model (MAM) were subsequently obtained by re-fitting the model using restricted maximum likelihood estimation (REML). Parameter estimates based on REML are generally preferable, because they avoid or reduce the biases of maximum likelihood estimates (Zuur *et al.* 2009). Following model simplification, we tested the remaining fixed effects using Wald tests. Models were fitted using the nlme package (Pinheiro *et al.* 2008) in R version 2.6.2 (R Development Core Team 2008).

Phytophagous and animalivorous species differ in the way they move and acquire resources and therefore can be expected to differ in their detectability. Thus, we first estimated the proportion of species detected for all species pooled and included trophic group as a covariate in the model, and subsequently estimated completeness separately for each trophic group.

DETERMINANTS OF SPECIES-LEVEL DETECTABILITY

The jackknife estimate of species richness is an estimate of all species in the assemblage, which includes those that were not detected, but it does not retain individual species identity and thus cannot provide species-specific estimates of detectability. To obtain detectability estimates at the species level, we followed the approach of Kéry & Plattner (2007), and restricted analysis to species that were captured during survey i , and modelled the probability that a species was also detected in the subsequent survey $i + 1$. Data used for this analysis comprised 232 bat species sampled across 25 locations and included for each location data from two successive surveys per sampling site (plot/transect), season and year. We fitted a GLMM with a logit link and binomial error distribution to the binary species presence-absence data. Plot (nested within location) and species

were included as random factors in a partially crossed design to account for possible correlations of species detections due to shared sampling plots and species. Fixed effects evaluated in the model were year, season, interval between sampling nights, sampling method, bat ensemble (frugivores, nectarivores, aerial insectivores, gleaning animalivores) and region (Neotropics vs. Paleotropics, see below). The significance of individual model terms was assessed using likelihood ratio tests, sequentially removing nonsignificant terms to determine the MAM (Zuur *et al.* 2009). After model simplification, we tested fixed effects retained in the MAM using Wald tests. Because the initial model with region as a fixed effect suggested significant differences in species detectability between the Neotropics and Paleotropics, we also performed separate GLMMs for Neotropical (once including both acoustic and capture data and again using only the latter) and Paleotropical data sets. Model fitting was conducted using the lme4 package (Bates 2007) in R 2.6.2 (R Development Core Team 2008).

Results

MEAN PROPORTION OF SPECIES DETECTED

Based on jackknife estimates of species richness an average proportion of 0.76 ± 0.08 SD (range 0.57–1.00, Fig. 1) of all

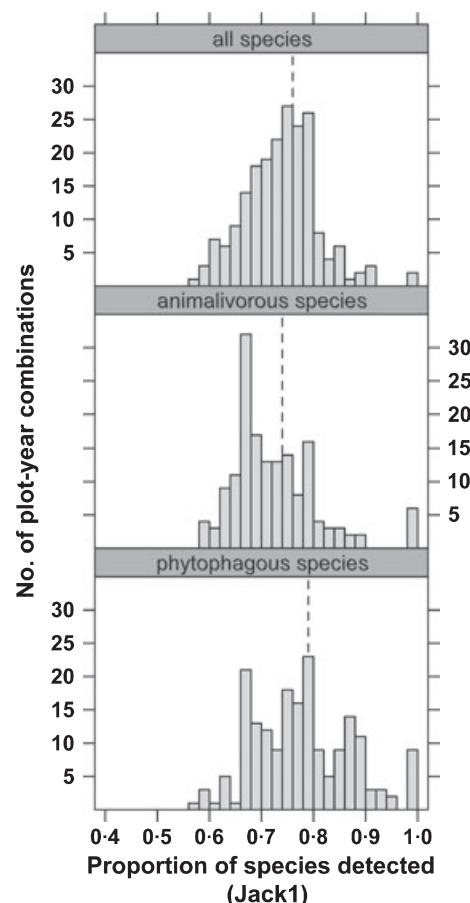


Fig. 1. Frequency distributions of estimates of bat species inventory completeness based on Jack1. Results shown are based on 550 plot-year combinations and include capture data from ground-level mist nets. The dotted line indicates the mean.

Table 1. Factors associated with the proportion of species detected based on a LMM that included all species, with trophic group as a covariate

Source of variation	L-ratio χ^2	d.f.	P
Random effects			
Location	14.86	1	<0.001
Plot (Location)	<0.001	1	0.999
Fixed effects			
Spatial configuration	4.044	2	0.132
Season	1.957	1	0.162
No. of surveys	1.236	1	0.266
Region	0.159	1	0.690
Year	2.259	3	0.521
Sampling interval	1.812	1	0.178
Method	29.43	1	<0.001
Trophic group	89.67	1	<0.001
	Estimate (SE)	t	P
Intercept	-0.182 (0.028)	-6.545	0.000
Trophic group_Phytophagous	0.093 (0.009)	10.09	0.000
Method_Canopy nets	-0.197 (0.033)	-5.988	0.000
Method_Ground nets	-0.177 (0.030)	-5.920	0.000
Method_Harp traps	-0.192 (0.052)	-3.689	<0.001

The analysis includes data from all sampling methods. Significant effects are boldfaced. Parameter estimates given are for the fixed effects retained in the minimum adequate model.

bat species was detected across the 96 sampling plots. Mixed-effects modelling revealed that the mean proportion of species detected was significantly higher for phytophagous species (0.79 ± 0.10 , range 0.57–1.00, Fig. 1) than for animalivores (0.74 ± 0.09 , range 0.60–1.00, Fig. 1) and indicated an additional effect of sampling method when all methods (GN, CN, HT & AS) were considered, with lower mean species detectability for capture methods compared to AS (Table 1). The latter effect is attributable to Neotropical aerial insectivores, as this analysis only involved AS data from this region. When acoustic data were omitted from the analysis, trophic group retained the strongest effect on mean species detectability, whereas capture method was no longer significant (Table S2). Interestingly, in neither of these cases was there a discernible effect of year, season or the number of sampling nights on a plot's estimated inventory completeness.

Analysing phytophagous and animalivorous species separately yielded partly contrasting results relative to when all species were pooled in the analysis. The model for phytophagous species identified the number of repeat surveys as the best predictor. Although only marginally significant, this analysis further suggested that a larger proportion of plant-visiting bat species may be detected in the wet compared to the dry season (Table 2).

For animalivorous species, mean species detectability was significantly affected by sampling method and the LMM indicated that the proportion of animalivorous species detected on a particular plot may be maximized by using acoustic techniques rather than any of the capture methods. Moreover, as for phytophagous species, the model suggested an influence of

Table 2. Factors associated with the proportion of phytophagous bat species detected based on a LMM

Source of variation	L-ratio χ^2	d.f.	P
Random effects			
Location	21.01	1	<0.001
Plot (Location)	0.041	1	0.839
Fixed effects			
Spatial configuration	4.009	2	0.135
Season	3.516	1	0.061
No. of surveys	9.307	1	0.002
Region	0.012	1	0.913
Year	0.730	3	0.866
Sampling interval	1.392	1	0.238
Method	0.001	1	0.978
	Estimate (SE)	t	P
Intercept	-0.319 (0.020)	-16.31	0.000
No. of surveys	0.008 (0.003)	3.099	0.002
Season_Wet	0.021 (0.011)	1.864	0.064

The analysis is based on mist net captures (GN, CN). Significant or marginally significant effects are boldfaced. Parameter estimates are provided for the fixed effects retained in the minimum adequate model.

GN = ground nets; CN = canopy nets.

Table 3. Factors associated with the proportion of animalivorous bat species detected based on a LMM

Source of variation	L-ratio χ^2	d.f.	P
Random effects			
Location	0.735	1	0.391
Plot (Location)	0.328	1	0.567
Fixed effects			
Spatial configuration	0.802	2	0.700
Season	2.159	1	0.142
No. of surveys	3.694	1	0.055
Region	0.258	1	0.612
Year	4.125	3	0.127
Sampling interval	0.316	1	0.574
Method	30.97	3	<0.001
	Estimate (SE)	t	P
Intercept	-0.170 (0.023)	-7.353	0.000
Method_Canopy nets	-0.194 (0.031)	-6.334	0.000
Method_Ground nets	-0.157 (0.024)	-6.583	0.000
Method_Harp traps	-0.153 (0.049)	-3.103	0.002
No. of surveys	-0.006 (0.003)	-1.843	0.068

Significant or marginally significant effects are boldfaced. Parameter estimates are given for the fixed effects retained in the minimum adequate model.

the number of surveys per plot (Table 3); however, as its estimated effect was negative, this is likely a statistical artefact.

In all models, there was no significant effect of sampling plot on the proportion of species detected; however, the variance component for location was significant in the analyses pertaining to all species and phytophagous bats, respectively.

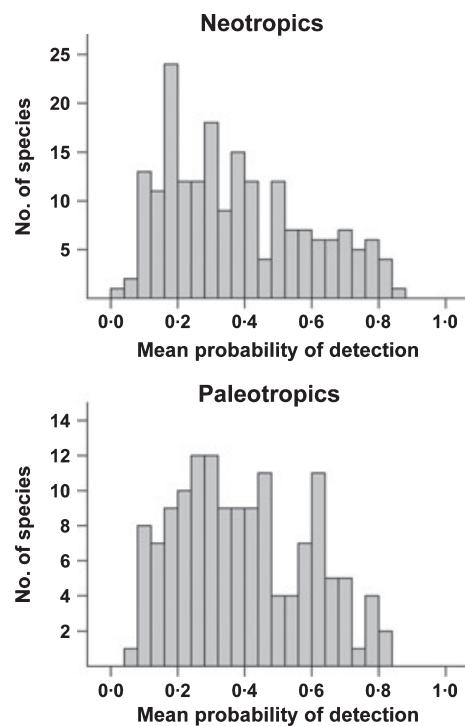


Fig. 2. Distribution of the mean probability of detection for 128 Neotropical and 104 Paleotropical bat species, respectively, based on generalized mixed-effects modelling.

Table 4. GLMM assessing the influence of a set of predictors on species-specific detection probability in two successive surveys

Source of variation	L-ratio χ^2	d.f.	P
Random effects			
Location	25.94	1	<0.001
Plot (Location)	1.496	1	0.221
Species	120.16	1	<0.001
Fixed effects			
Season	0.569	1	0.451
Year	6.469	3	0.091
Sampling interval	9.059	1	0.003
Method	6.281	2	0.043
Ensemble	15.62	3	0.001
	Estimate	z	P
Intercept	-1.917 (0.444)	-4.317	0.000
Ensemble_Frugivores	1.03 (0.416)	2.474	0.013
Ensemble_Gleaning animalivores	-0.105 (0.469)	-0.224	0.823
Ensemble_Nectarivores	0.786 (0.511)	1.539	0.124
Method_Ground nets	0.482 (0.215)	2.240	0.025
Method_Harp traps	-0.144 (0.532)	-0.271	0.786
Year_2	-0.172 (0.148)	-1.159	0.247
Year_3	-0.384 (0.227)	-1.689	0.091
Year_4	-0.847 (0.437)	-1.937	0.053
Sampling interval	0.004 (0.002)	2.954	0.003

The analysis is based on 19 Neotropical capture data sets (GN, CN & HT). Parameter estimates are given for significant fixed effects retained in the minimum adequate model. Significant or marginally significant effects are boldfaced.

GN = ground nets; CN = canopy nets; HT = harp traps.

Table 5. GLMM assessing the influence of a set of predictors on species-specific detection probability in two successive surveys

Source of variation	L-ratio χ^2	d.f.	P
Random effects			
Location	<0.001	1	0.999
Plot (Location)	4.491	1	0.034
Species	22.98	1	<0.001
Fixed effects			
Season	5.558	1	0.018
Year	5.850	3	0.119
Sampling interval	0.954	1	0.329
Method	6.585	2	0.037
Ensemble	8.643	3	0.034
	Estimate	z	P
Intercept	-0.037 (0.361)	-0.104	0.917
Ensemble_Frugivores	0.97 (0.394)	2.465	0.014
Ensemble_Gleaning animalivores	-0.278 (0.593)	-0.470	0.639
Ensemble_Nectarivores	-0.619 (1.166)	-0.531	0.595
Method_Ground nets	-0.098 (0.272)	-0.360	0.719
Method_Harp traps	-1.004 (0.423)	-2.376	0.018
Season_Wet	-0.56 (0.250)	-2.234	0.026

The analysis is based on capture data (GN, CN & HT) from 6 Paleotropical locations. Parameter estimates are given for significant fixed effects in the minimum adequate model. Significant effects are boldfaced.

GN = ground nets; CN = canopy nets; HT = harp traps.

SPECIES-LEVEL DETECTABILITY

The 232 species included in the analysis were highly heterogeneous in their probabilities of detection during two successive surveys (Fig. 2). Based on the GLMM, mean detectability across 128 Neotropical bat species averaged 0.38 (SD 0.21, range 0.03–0.84). Similarly, for 104 Paleotropical species the mean detection probability under the GLMM was on average 0.39 (SD 0.19, range 0.06–0.82).

In all models, the variance component due to species identity was highly significant. In addition, mean species-specific detectability varied significantly among locations when all 25 data sets (Table S3) or only Neotropical studies were considered (Table 4). On the other hand, the random effect of sampling plot nested within location was significant for capture data from Paleotropical, but not from Neotropical localities (Tables 4 & 5); however, the plot effect in the latter case was significant when acoustic data were included in the analysis (results not shown).

The GLMM that included both Neotropical and Paleotropical data sets indicated that all fixed effects examined except season had a significant influence on the species-specific probability of detection and suggested higher detectability for Paleotropical than for Neotropical bat species (Table S3). This pattern remained when Neotropical data sets were analysed separately, although the effect of sampling year was only mar-

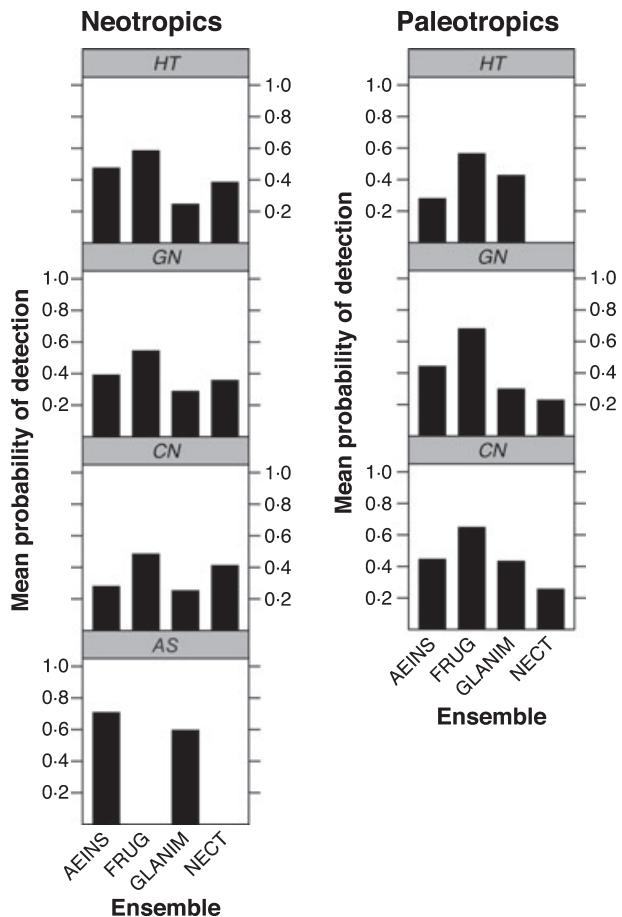


Fig. 3. Comparison of estimates of mean species detectability between ensembles and for different sampling methods based on the GLMM analysis. AEINS = aerial insectivores, FRUG = frugivores, GLANIM = gleaning animalivores, NECT = nectarivores; GN = ground nets, CN = canopy nets, HT = harp traps, AS = acoustic sampling.

ginally significant when the analysis was restricted to capture data (Table 4). In contrast, for the Paleotropics the GLMM lacked a positive effect of sampling interval; there was no significant difference in detectability between years but a negative effect of sampling during the wet season (Table 5).

In all GLMMs detection probabilities varied significantly among ensembles and sampling methods (Fig. 3). For Neotropical aerial insectivores, detectability averaged 0.71 for AS compared to 0.28–0.47 for the other sampling methods. Similarly, detection probabilities for gleaning animalivores were on average higher with AS (0.60) than with any of the capture methods (0.25–0.29). It must be noted, however, that this result merely reflects the ease of detection of *Noctilio* with AS and that this pattern cannot be taken to represent the vast majority of species in this ensemble. Neotropical frugivores had rather similar detection probabilities across capture methods (0.48–0.58), as did nectarivores (0.36–0.41). For Paleotropical species, mean detectability varied somewhat between methods but was generally highest for frugivorous species (0.56–0.68), within the same low range for aerial insectivores (0.28–0.44) and gleaning animalivores (0.30–0.43), and lowest for nectarivores (0.23–0.26).

Discussion

ASSEMBLAGE-LEVEL DETECTABILITY

Similar to several avian monitoring programmes (Boulinier *et al.* 1998; Kéry & Schmid 2006), we found that heterogeneity in species detectability is prevalent in surveys of tropical bats. The mean proportion of species detected across 96 sampling plots was estimated at 0.76. In other words, on average, roughly 25% of the species estimated to be present in a particular sampling plot were missed during all visits to that plot. Estimates were generally highly variable among plots (Fig. 1). Our mean estimates of detectability compare well with what has been found for the North American Breeding Bird Survey (BBS, c. 76%; Boulinier *et al.* 1998), but are considerably lower than estimates obtained for the Swiss BBS (89%, Kéry & Schmid 2006). There are no comparable bat studies using a similar analytical approach.

In all models analysed, there was no significant effect of sampling plot on the average proportion of species detected; however, the variance component for location was significant in the model that included all species. Analysing phytophagous and animalivorous species separately suggested that this effect was mainly due to phytophagous species since the random effect for location was nonsignificant for animalivores alone. Differences in species composition, local species abundance, habitat types or landscape attributes may largely explain the observed variation in average detectability among localities. Evidence for a location effect on detectability highlights the challenge for implementing a large-scale bat monitoring programme consisting of a network of geographically disparate sampling localities. It shows the potential biases that may result from using simple species counts in comparisons among different survey locations in a monitoring programme and underscores the importance of correcting count data for detection error. This problem could be addressed by calibrating the monitoring programme based on location-specific estimates of species detectability and using these estimates when drawing inferences about spatial or temporal trends in species richness. The way in which detectability varies across locations along large-scale geographic or environmental gradients (e.g. in relation to species ranges) is relevant from a macroecological perspective. For example, based on geometric constraints models that predict peaks in richness at mid-domains (Colwell & Lees 2000), species with wide geographic ranges should, by chance alone, have higher detection probabilities at the middle of gradients where sampling localities are more often intersected, rather than at their edges, as has been demonstrated for birds (Doherty, Boulinier & Nichols 2003). Such an outcome would also be expected as range size in bats is positively associated with species abundances (Willig, Patterson & Stevens 2003) and hence species richness of local assemblages is influenced disproportionately by species with wide geographic ranges.

Detectability is known to vary between survey years, seasons and regions in large-scale bird monitoring programmes (Boulinier *et al.* 1998; Kéry & Schmid 2006). The ability to estimate

species richness of bats with the same detectability across years would be an essential attribute for a successful bat monitoring scheme. We found no evidence for mean species detectability to differ between sampling years, which is encouraging for long-term monitoring of bats. In this regard, our results agree with studies on birds that cover comparable time spans (*c.* 3 years; Kéry & Schmid 2006). However, Sauer, Peterjohn & Link (1994) documented increasing detectability over a time period of 26 years for birds in the BBS, which they found attributable to among-observer variability and a temporal increase in observer skills. While such observer effects are less likely to confound analyses from bat survey data, our results should nonetheless be interpreted with caution, because the lack of a significant year effect may simply reflect the limited temporal coverage of our data sets.

The model for phytophagous species suggested a marginally significant effect of season on estimated mean inventory completeness. A number of tropical plant-feeding bat species to some degree show seasonal fluctuations in abundance as a result of habitat shifts associated with seasonal changes in resource availability (e.g. Stoner 2005), which may explain the higher mean species detectability for the wet compared to the dry season. It is possible that this effect would even be stronger if a larger number of study sites with marked seasonality in rainfall, such as tropical dry forests, had been included in the analysis.

Sampling method was a significant predictor of the mean proportion of species detected only in models that included all species or only animalivorous species, and only when AS data were contrasted with capture data. Here, mean estimates of detectability based on capture data were significantly lower than for AS data. Because all acoustic data for our analysis were derived from studies in the Neotropics, this finding only pertains to aerial insectivores from this biogeographic region. In agreement with the few studies in the Neotropics that relied on AS (Rydell *et al.* 2002; Jung, Kalko & von Helversen 2007; Estrada Villegas, Meyer & Kalko 2010), our results indicate that acoustic surveys are the most effective method for sampling Neotropical aerial insectivorous bats, making species of this ensemble good candidates for long-term monitoring. This is further corroborated by recent studies in the Neotropics and Paleotropics which suggest that acoustic methods are indispensable for maximizing inventory completeness in tropical bat surveys (Kalko *et al.* 2008; MacSwiney, Clarke & Racey 2008; Furey, Mackie & Racey 2009). However, AS alone is inadequate for detecting many species sampled using traditional capture techniques (MacSwiney, Clarke & Racey 2008; Kunz & Parsons 2009). For example, captures are clearly preferable for the nonecholocating Paleotropical fruit bats, which have considerable monitoring potential. This highlights the fact that complete descriptions of tropical bat faunas will generally require the simultaneous use of multiple methods (Kalko *et al.* 2008; Kunz & Parsons 2009).

Trophic group was a strong determinant of mean inventory completeness, with generally lower estimates for animalivores compared to phytophagous species, which probably results to a large extent from general differences

in ecological characteristics among these groups. Our results generally imply that unless surveys are conducted frequently, species-averaged detection probabilities will only rarely approach 1 (Fig. 1). This highlights the need for employing appropriate statistical models that properly account for errors in species detection when analysing data from bat surveys, and new approaches are now available to do so (Kéry & Royle 2008; Kéry *et al.* 2009). Notwithstanding, because detection probabilities were reasonably high (*c.* 0.75 across species), it seems feasible to infer species presence with relatively few repeat visits per site. However, it must be noted that detection probabilities for individual species (see below) were often considerably lower than species-averaged estimates, indicating that many visits would be required to infer absence of rare species. Thus, financial and time constraints on monitoring programmes ultimately impose a limit on what can be achieved in terms of the number of repeat visits per plot. With some species having characteristically low detection probabilities and a limited number of visits per site, estimation-based approaches to monitoring are essential as they allow formal detectability corrections in species richness comparisons (Pellet & Schmidt 2005).

We used a traditional capture–recapture approach for estimating species richness, following several other studies (Boulinier *et al.* 1998; Doherty, Boulinier & Nichols 2003; Kéry & Schmid 2006; Husté & Boulinier 2007). Recently developed hierarchical multispecies site-occupancy models (Dorazio & Royle 2005; Kéry & Royle 2008; Kéry *et al.* 2009) provide a somewhat more versatile framework as they retain species identity across sites and thus allow for the simultaneous estimation of assemblage-wide and species-level detectability, thereby eliminating the need for a two-step analysis. Moreover, site- or survey-specific covariates that may influence detection (e.g. habitat variables) can be directly incorporated into the modelling process. This new analytical framework clearly offers great potential for the analysis and interpretation of data from a bat monitoring programme.

SPECIES-LEVEL DETECTABILITY

Species-level detectability for 128 Neotropical and 104 Paleotropical species averaged 0.38 and 0.39, respectively. Estimates were highly heterogeneous, ranging between 0.03 and 0.84 (Figs. 2 & 4). In the Neotropics, aerial insectivores seem well suited for monitoring using AS techniques, as their species-specific detection probabilities (mean 0.71) were comparatively high. In contrast, detectability for individual species of Neotropical gleaning animalivores based on captures was typically low (*c.* 0.3), implying that effective monitoring of most of these species will require substantial survey efforts. Based on capture techniques, frugivorous bat species from both the Neotropics and Paleotropics had probabilities of detection in the intermediate range (0.48–0.58), whereas detectability for the remainder of species was typically quite low (0.23–0.44). Large variation in detectability among species also has been reported for other taxa, including birds, butterflies and amphibians (Pellet &

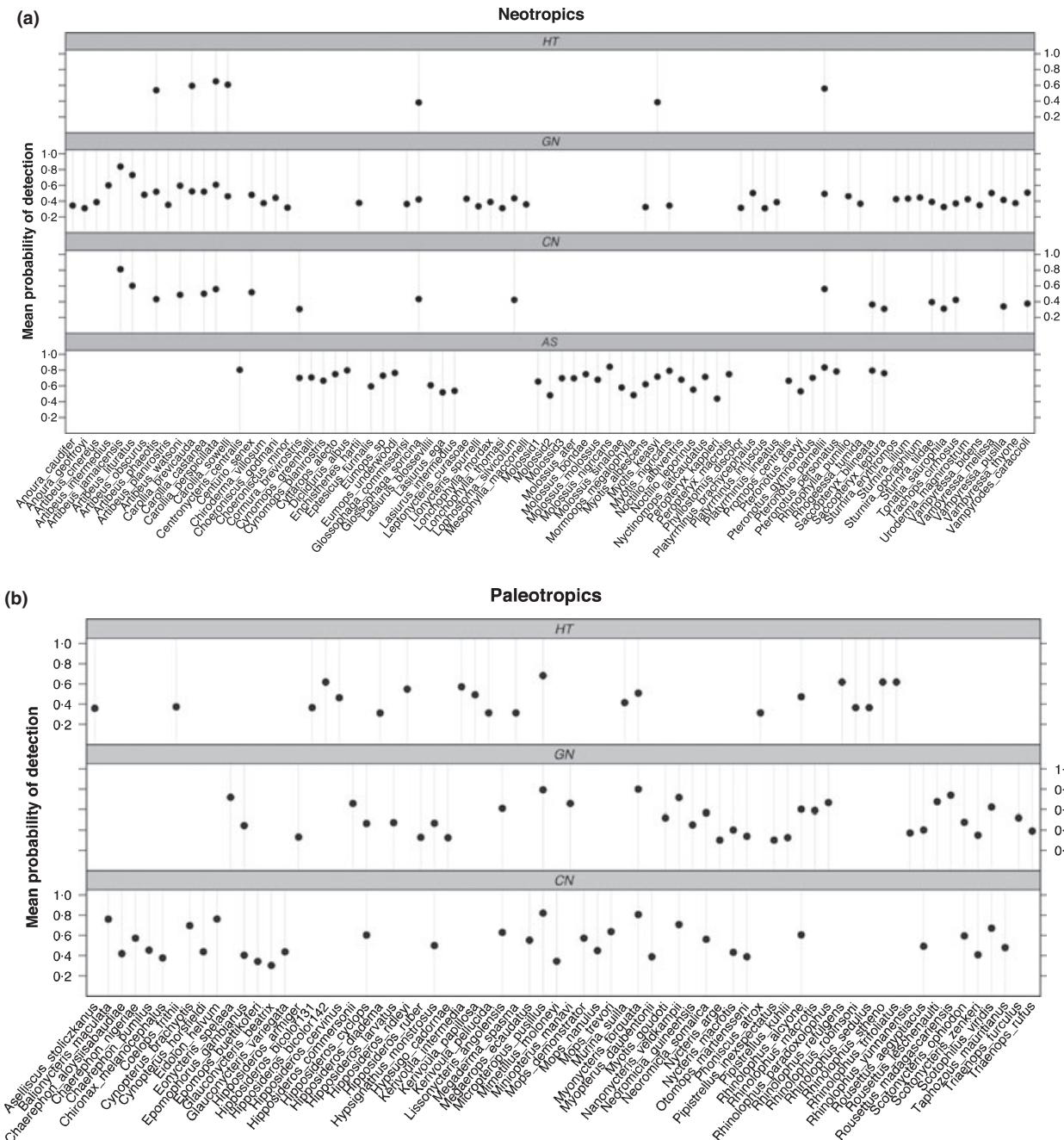


Fig. 4. Mean probability of detection for a range of (a) Neotropical and (b) Paleotropical bat species based on the GLMM analysis. Only species with detectability estimates ≥ 0.3 are shown. AS = acoustic sampling; CN = canopy nets; GN = ground nets; HT = harp traps.

Schmidt 2005; Kéry & Plattner 2007; Kéry & Royle 2008; Kéry *et al.* 2009). Studies estimating probabilities of detection for bats are scarce and focused either on one or a few species in the context of acoustic monitoring surveys (Duchamp *et al.* 2006; Gorresen *et al.* 2008). In the first study to estimate detection probabilities for multiple species at a regional scale, Weller (2008) reported estimates ranging between 0.24 and 0.53 for eight species of temperate-zone bats in the Pacific Northwest, USA. Although not directly comparable due to differences in the estimation methods employed, these estimates of detectability were similarly low compared to our estimates based on GLMM modelling.

Our results indicate that a substantial proportion of species may be missed when only two surveys are conducted per sampling unit. Moreover, in contrast to the approach using species richness estimators, nearly all covariates tested in the GLMMs had a significant influence on the probability of detecting a species in two successive surveys. Only season did not significantly influence detectability estimates in all models but the one that included only Paleotropical data sets. The fact that this analysis involved many species from different trophic groups probably makes it more difficult to detect a seasonal effect compared to the assemblage-level analysis where we examined seasonal variation in mean species detectability sepa-

rately for phytophagous and animalivorous bats (see above). Overall these results suggest that, unless surveys are conducted more frequently, raw counts of individual species may in some cases be strongly biased. This problem may be ameliorated by increasing the number of surveys because our estimates of species-specific detectability were based on only two successive surveys. With a reasonable number of visits (e.g. four repeat visits per sampling plot), bias may become smaller and more tolerable in cases where fairly high species-specific detectability amounts to an overall high level of average detection probability (> 0.8). However, species with very low detection probabilities will probably be missed altogether or else be prohibitively expensive to monitor as part of long-term initiatives. Given the large heterogeneity in species-specific detectability, it seems clear that a single design will be inefficient for all species in a bat monitoring programme and that survey protocols should be adapted to the programme's particular aims and constraints. For species with low detectability estimates ($< c. 0.3$, such as most gleaning animalivores or nectarivores), it will be essential to correct count data obtained in monitoring surveys for detection error.

Conclusions

From our results it seems clear that using raw species counts as a proxy for species richness in a tropical bat monitoring programme could lead to erroneous inferences about trends in species richness. Monitoring requires robust estimates, thus we strongly recommend that studies which seek to investigate trends in species richness over time or make regional comparisons statistically correct for variation in species detectability. Monitoring schemes that aim to reliably detect trends in species richness require a sufficient number of temporal replicate observations on the same monitoring plot. Our study demonstrated that species-level detectability is often low with only two replicated surveys. In view of what would also be practically feasible, we recommend conducting four replicate surveys per sampling unit within a given year, which should considerably reduce bias in estimates of species richness and ensure relatively high mean detection probability overall. It is important to stress that the detection of species presumed to be rare or uncommon can be increased by employing multiple methods, such as vertical arrays of canopy nets or acoustic detectors in addition to harp traps and ground-based mist nets and detectors (e.g. Furey, Mackie & Racey 2009; Kunz & Parsons 2009; Estrada Villegas, Meyer & Kalko 2010; Fahr & Kalko 2010). Finally, we advocate standardizing sampling as much as possible to largely eliminate *a priori*, i.e. at the design stage, any sources of variation in detectability that may be introduced by external factors related to sampling design.

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References

- Bates, D. (2007) *lme4: Linear Mixed-Effects Models Using S4 Classes*. R package version 0.99875-99879. <http://www.R-project.org>.
- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, **79**, 1018–1028.
- Burnham, K.P. & Overton, W.S. (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology*, **60**, 927–936.
- Clarke, F.M., Rostant, L.V. & Racey, P.A. (2005) Life after logging: post-logging recovery of a neotropical bat community. *Journal of Applied Ecology*, **42**, 409–420.
- Colwell, R.K. (2006) *EstimatesS: Statistical Estimation of Species Richness and Shared Species from Samples*. Version 8. <purl.oclc.org/estimates>.
- Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, **15**, 70–76.
- Doherty, P.F., Boulinier, T. & Nichols, J.D. (2003) Local extinction and turnover rates at the edge and interior of species' ranges. *Annales Zoologici Fennici*, **40**, 145–153.
- Dorazio, R.M. & Royle, J.A. (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, **100**, 389–398.
- Duchamp, J.E., Yates, M., Muzika, R.-M. & Swihart, R.K. (2006) Estimating probabilities of detection for bat echolocation calls: an application of the double-observer method. *Wildlife Society Bulletin*, **34**, 408–412.
- Estrada Villegas, S., Meyer, C.F.J. & Kalko, E.K.V. (2010) Effects of forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, **143**, 597–608.
- Fahr, J. & Kalko, E.K.V. (2010) Biome transitions as centres of diversity: habitat heterogeneity and diversity patterns of West African bat assemblages across spatial scales. *Ecography*. doi: 10.1111/j.1600-0587.2010.05510.x.
- Fleming, T.H. & Eby, P. (2003) Ecology of bat migration. *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 156–208. The University of Chicago Press, Chicago.
- Furey, N.M., Mackie, I.J. & Racey, P.A. (2009) The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. *Current Zoology*, **55**, 327–341.
- Gorresen, P.M., Miles, A.C., Todd, C.M., Bonaccorso, F.M. & Weller, T.J. (2008) Assessing bat detectability and occupancy with multiple automated echolocation detectors. *Journal of Mammalogy*, **89**, 11–17.
- Husté, A. & Boulinier, T. (2007) Determinants of local extinction and turnover rates in urban bird communities. *Ecological Applications*, **17**, 168–180.
- IUCN (2009) *IUCN Red List of Threatened Species. Version 2009.1*. <http://www.iucnredlist.org>. Accessed on 8 June 2009.
- Jiguet, F., Renault, O. & Petiau, A. (2005) Estimating species richness with capture-recapture models: choice of model when sampling in heterogeneous conditions. *Bird Study*, **52**, 180–187.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) *Carpe noctem*: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93–115.
- Jung, K., Kalko, E.K.V. & von Helversen, O. (2007) Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *Journal of Zoology*, **272**, 125–137.
- Kalko, M.B., Smith, A.R. & Kalko, E.K.V. (2008) Bats limit arthropods and herbivory in a tropical forest. *Science*, **320**, 71.
- Kalko, E.K.V., Estrada Villegas, S., Schmidt, M., Wegmann, M. & Meyer, C.F.J. (2008) Flying high – assessing the use of the aerosphere by bats. *Integrative and Comparative Biology*, **48**, 60–73.
- Kéry, M. & Plattner, M. (2007) Species richness estimation and determinants of species detectability in butterfly monitoring programmes. *Ecological Entomology*, **32**, 53–61.
- Kéry, M. & Royle, J.A. (2008) Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, **45**, 589–598.
- Kéry, M. & Schmid, H. (2006) Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology*, **43**, 101–110.
- Kéry, M., Royle, J.A., Plattner, M. & Dorazio, R.M. (2009) Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, **90**, 1279–1290.

- Kingston, T., Boo Liat, L. & Zubaid, A. (2006) *Bats of Krau Wildlife Reserve*. Penerbit Universiti Kebangsaan Malaysia Press, Bangi.
- Kunz, T.H. & Parsons, S. (2009) *Ecological and Behavioral Methods for the Study of Bats*, 2nd edn. Johns Hopkins University Press, Baltimore, Maryland.
- Lane, D.J.W., Kingston, T. & Lee, B.P.Y.H. (2006) Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. *Biological Conservation*, **131**, 584–593.
- Lobova, T.A., Geiselman, C.K. & Mori, S.A. (2009) *Seed Dispersal by Bats in the Neotropics*. New York Botanical Garden Press, New York.
- MacSwiney, M.C., Clarke, F.M. & Racey, P.A. (2008) What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology*, **45**, 1364–1371.
- Meyer, C.F.J. & Kalko, E.K.V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711–1726.
- O'Shea, T.J. & Bogan, M.A. (2003) *Monitoring Trends in Bat Populations of the United States and Territories: Problems and Prospects*. U. S. Geological Survey, Biological Resources Division, Information and Technology Report, USGS/BRD/ITR-2003-0003.
- Patterson, B.D., Willig, M.R. & Stevens, R.D. (2003) Trophic strategies, niche partitioning, and patterns of ecological organization. *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 536–579. University of Chicago Press, Chicago.
- Pellet, J. & Schmidt, B.R. (2005) Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. *Biological Conservation*, **123**, 27–35.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & the R Core Team (2008) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-89. <http://www.R-project.org>.
- Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L. & Sauer, J.R. (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics*, **13**, 105–119.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org>.
- Rex, K., Kelm, D.H., Wiesner, K., Kunz, T.H. & Voigt, C.C. (2008) Species richness and structure of three Neotropical bat assemblages. *Biological Journal of the Linnean Society*, **94**, 617–629.
- Rydell, J., Arita, H.T., Santos, M. & Granados, J. (2002) Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *Journal of Zoology*, **257**, 27–36.
- Sauer, J.R., Peterjohn, B.G. & Link, W.A. (1994) Observer differences in the North American breeding bird survey. *The Auk*, **111**, 50–62.
- Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V. et al. (2008) The status of the World's land and marine mammals: diversity, threat, and knowledge. *Science*, **322**, 225–230.
- Stoner, K.E. (2005) Phyllostomid bat community structure and abundance in two contrasting tropical dry forests. *Biotropica*, **37**, 591–599.
- Walther, B.A. & Moore, J.L. (2005) The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography*, **28**, 815–829.
- Weller, T.J. (2008) Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: bats in the Pacific Northwest. *Biological Conservation*, **141**, 2279–2289.
- Willig, M.R., Patterson, B.D. & Stevens, R.D. (2003) Patterns of range size, richness, and body size in the Chiroptera. *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 580–621. University of Chicago Press, Chicago.
- Yoccoz, N.G., Nichols, J.D. & Boulanger, T. (2001) Monitoring of biodiversity in space and time. *Trends in Ecology and Evolution*, **16**, 446–453.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology With R*. Springer, New York.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. List of data sets with sampling characteristics used in this study.

Table S2. Determinants of species-averaged detectability based on a LMM that included all species.

Table S3. Predictors of species-specific detection probability based on capture data from Neotropical and Paleotropical localities.

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Table S1 Data sets from tropical bat assemblages used for assessing mean species inventory completeness and individual species detectabilities. The list summarizes the sampling methods used in each study as well as the number of sampling years covered by each data set.

Country	Location ¹	Sampling method ²	No. sampling years
Neotropics	Mexico	Yucatan	GN, CN, HT, AM
	Mexico	Chamela ^{a)}	GN
	Costa Rica	Palo Verde ^{a)}	GN
	Costa Rica	La Selva	GN, CN
	Panama	Fort Sherman	GN
	Panama	Fort Sherman	AM
	Panama	BCNM	GN, CN
	Panama	BCNM	AM
	Panama	BCI	AM
	Panama	BCI	GN, CN
	Panama	BCI	GN
	Panama	Soberanía	GN
	Panama	Gamboa	AM
	Trinidad	Victoria-Mayaro	GN, CN, HT
	French Guiana	St. Eugène	GN
	French Guiana	Nouragues	GN
	Ecuador	Podocarpus	GN, CN
	Ecuador	Tiputini	GN, CN
	Peru	Manu	GN, CN
	Brazil	Una	GN
	Brazil	Roncador ^{b)}	GN
	Brazil	BDFFP	GN
	Bolivia	Yungas de La Paz	GN
Paleotropics	Malaysia	Lubuk Baung	HT
	Malaysia	Kuala Lompat	CN
	Vietnam	Kim Hy	GN, HT
	Ivory Coast	Comoé ^{c)}	GN, CN, HT
	Ivory Coast	Taï	GN, CN, HT
	Madagascar	Bemaraha ^{a)}	GN

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 monitoring

Table S2 Factors associated with the proportion of species detected based on a linear mixed-model analysis that includes all species, with trophic group (phytophagous and animalivorous bats) specified as a covariate. Parameter estimates for the fixed effects retained in the minimum adequate model are given. The analysis includes only capture data (GN, CN & HT), omitting acoustic monitoring data. Significant effects are bold-faced.

<i>Source of variation</i>	<i>L - ratio χ^2</i>	<i>df</i>	<i>P</i>
<i>Random effects</i>			
Location	12.27	1	0.0005
Plot (Location)	< 0.001	2	0.999
<i>Fixed effects</i>			
Spatial configuration	3.322	2	0.190
Season	0.899	1	0.343
No. of surveys	1.213	1	0.271
Region	0.208	1	0.648
Year	3.366	3	0.339
Sampling interval	2.018	1	0.156
Method	1.711	1	0.425
Trophic group	89.46	1	< 0.0001
	<i>Estimate (SE)</i>	<i>t</i>	<i>P</i>
Intercept	-0.362 (0.010)	-35.26	0.000
Trophic group_phytophagous	0.091 (0.009)	9.992	0.000

Table S3 Results of a generalized linear mixed model (GLMM) analysis assessing the influence of a set of predictors on the probability that a species detected during survey i was also detected during the subsequent survey $i+1$. The analysis was restricted to capture data (GN, CN & HT) and included 232 bat species from 25 Neotropical and Paleotropical localities. Parameter estimates are given for significant fixed effects retained in the minimum adequate model following model simplification. Significant or marginally significant effects are bold-faced. For ensemble abbreviations, see Methods.

<i>Source of variation</i>	<i>L - ratio χ^2</i>	<i>df</i>	<i>P</i>
<i>Random effects</i>			
Location	26.59	1	< 0.001
Plot (Location)	3.331	1	0.068
Species	148.79	1	< 0.001
<i>Fixed effects</i>			
Season	0.159	1	0.690
Region	9.693	1	0.002
Year	8.840	3	0.031
Sampling interval	5.285	1	0.022
Method	6.430	2	0.040
Ensemble	26.10	3	< 0.001
	<i>Estimate (SE)</i>	<i>z</i>	<i>P</i>
Intercept	-1.664 (0.348)	-4.774	0.000
Year_2	-0.101 (0.126)	-0.804	0.421
Year_3	-0.274 (0.191)	-1.435	0.151
Year_4	-0.754 (0.265)	-2.849	0.004
Sampling interval	0.003 (0.001)	2.265	0.024
Ensemble_FRUG	1.091 (0.276)	3.952	0.000
Ensemble_GLANIM	-0.121 (0.342)	-0.355	0.723
Ensemble_NECT	0.718 (0.425)	1.690	0.091
Method_GN	0.159 (0.166)	0.956	0.339
Method_HT	-0.559 (0.324)	-1.723	0.085
Region_Paleotropics	1.207 (0.408)	2.957	0.003

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