



# Risky business or simple solution – Relative abundance indices from camera-trapping



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## ABSTRACT

Camera-traps are a widely applied to monitor wildlife populations. For individually marked species, capture–recapture models provide robust population estimates, but for unmarked species, inference is often based on relative abundance indices (RAI, number of records per trap effort), although these do not account for imperfect and variable detection. We use a simulation study and empirical camera-trapping data to illustrate how ecological and sampling-related factors can bias RAIs. Our simulations showed that (1) differences in detection between species led to bias in RAI ratios toward the more detectable species, especially at low detection levels, (2) species with larger home ranges were photographed more often, inflating RAIs, (3) species specific responses to different types of trap setup biased RAI ratios, and (4) changes in detection over time blurred true population trends inferred from RAIs. Empirical data for leopard cats *Prionailurus bengalensis* and common palm civets *Paradoxurus hermaphroditus* showed that traps set up along roads led to higher RAIs than off-road traps, but targeting roads increased detection more for leopard cats than for common palm civets. Comparing RAIs of Sunda clouded leopards *Neofelis diardi* and leopard cats with spatial capture–recapture based density estimates across sites, RAIs did not reflect differences in density. Analytical options for estimating density from camera-trapping data of unmarked populations are limited. Consequently, we fear that RAIs will continue to be applied. This is alarming, since these measures often form the basis for conservation and management decisions. We suggest considering alternative analytical and survey methods, especially when dealing with threatened species.

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## 1. Introduction

Estimating the abundance of populations is of central importance in wildlife conservation. Camera traps are a popular tool for surveying wildlife, with a steep increase in studies applying this technique over the past decades (Kays and Slauson, 2008; O'Connell et al., 2011). Their non-invasive character and their ability to quickly accumulate data over large areas with relatively little effort make them an ideal tool for wildlife monitoring and biodiversity assessments. Particularly in the context of sustainable forest management, such as Forest Stewardship Council (FSC) certifications, or in projects to measure the co-benefits of Reduced Emissions from Deforestation and Degradation (REDD+), camera-trapping is increasingly discussed as a general biodiversity monitoring tool (e.g., Waldon et al., 2011), without much attention to its limitations.

For individually marked species, camera trapping data can be analyzed with capture–recapture models, both spatial and non-spatial to derive statistically sound abundance estimates (Link and Karanth, 1994; Karanth and Nichols, 1998). These models, however, require that individuals can be uniquely identified from photographs and thus cannot be applied to species that do not have conspicuous individual markings, which represent the majority among the medium to large sized mammals targeted by camera traps.

For species that cannot be individually identified from photographs, indices are often used to make inference about differences in abundance across time, space and species (O'Brien et al., 2003; O'Brien, 2011). An index of abundance or density can be any measure that correlates with these quantities (Caughley, 1977). While indices rarely be used for inference about absolute population size (they need to be calibrated to do so), under certain conditions they can provide information on relative differences in abundance or density (Williams et al., 2002; O'Brien, 2011). The most widely used index for camera-trapping data is the number of photographs

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of the focal species per trap day (O'Brien, 2011), also often referred to as relative abundance index (RAI; referring to RAI2 of O'Brien et al., 2003). The use of such indices as a measure of (relative) abundance is controversial. The fundamental problem is that to provide valid comparison across time, space, species, or other dimensions of interest, we have to make the assumption that our ability to detect animals is constant across this dimension. Unfortunately, this assumption is rarely ever tested in studies that base their inference on indices (Williams et al., 2002). Further, when detection probabilities can be estimated within studies, they generally vary across time, space and species (e.g., Link and Sauer, 1998; Yoccoz et al., 2001; Pollock et al., 2002). Under these conditions, differences in an index cannot be unambiguously attributed to actual differences in abundance, but may have arisen from differences in detection (Pollock et al., 2002; Archaux et al., 2012).

In spite of these shortcomings, RAIs are still published as part of camera trapping studies and are found even more frequently in wildlife monitoring reports and biodiversity assessments. As the number of these programs applying camera-trapping increases it is likely that abundance indices will become even more popular in the upcoming years. Considering that such monitoring and assessment programs often form the basis for conservation and management decisions, a better understanding of the pitfalls of RAIs is needed.

While 'detection probability' may seem like an abstract concept to program managers with little or no biological and statistical training, differences in detection can arise from very tangible factors, including changes in sampling design, differences in species ecology, for example, home range size and use, or changes in behavior. Here, rather than dealing with the underlying statistical concepts of detectability and abundance modeling (discussed extensively in, e.g., Seber, 1992; Williams et al., 2002), we illustrate how RAIs can be biased in response to ecological characteristics of animals and sampling related factors. For this purpose we use both simulations and empirical field data from three forest reserves in the tropical rainforest of Sabah, Malaysian Borneo. We believe that linking the concept of detection probability to 'real life' scenarios will help field researchers and managers better understand the possibilities and especially limitations of their data and of camera-trapping as a monitoring tool.

## 2. Material and methods

### 2.1. Simulation study

To illustrate how differences in detection probability among species, in space and time affect relative abundance indices (RAIs), we carried out a simulation study in which we generated detection data on an array of  $20 \times 20$  traps spaced regularly at 1-unit intervals. We simulated data by adopting a bivariate normal movement model, which is also the underlying movement model in spatial capture–recapture modeling (e.g., Efford, 2004; Royle and Young, 2008): Each individual has an activity center and the expected number of times the individual encounters a given trap (the trap encounter rate) decreases with increasing distance to this activity center following a half-normal function. The encounter rate at a hypothetical trap located at the activity center is called baseline trap encounter rate,  $\lambda_0$ . The spread of locations around the activity center is governed by the parameter  $\sigma$ , which can be translated into an estimate of home range radius (Reppucci et al., 2011). With this model we generated individual encounter histories for each trap across 10 sampling occasions, determined the total number of photographs per trap and used the average over all 400 traps as RAI. While in reality the number of pictures is divided by the number of trap days to correct for differences in sampling effort,

in a simulation study, effort is constant and there is no need to account for it.

We simulated data for two species A and B, under four scenarios. Unless stated otherwise, there are 50 and 100 individuals of species A and B, respectively and individuals move over areas of 10 units<sup>2</sup> (corresponding to a home range radius of 1.78 units). Thus, in order to adequately reflect relative species abundance, the ratio in RAI of species B to A should be 2. Details on implementation of the simulations can be found in online [Supplementary Material S1](#).

While there are many factors (that are not mutually exclusive) that can influence detection rates of individuals by camera traps, we chose to investigate four scenarios, which we believe are commonly encountered in the field. The first three scenarios address comparisons between species (although they are also applicable to comparisons between groups of individuals, such as males and females, within a single species), while the last scenario looks at the comparison of RAIs of one species across repeated surveys.

#### 2.1.1. Scenario 1: Encounter Rates

Species A has a higher baseline trap encounter rate  $\lambda_0$  than species B. Motivation: You may compare a ground-dwelling species (here, species A) with a partially arboreal species (B); the latter is less often available for sampling. We ran six different combinations of  $\lambda_0$ : low (0.1) and high (0.4) for species B and for both cases, +0.1, +0.2 and +0.3 for species A.

#### 2.1.2. Scenario 2: home ranges

Both species have the same  $\lambda_0$  (0.3), but A moves over larger areas than B. Motivation: You may compare species with different home range sizes, or the same species at two sites where home ranges differ due to different ecological conditions. Making  $\lambda_0$  the same for both species entails the assumption that movement rates increase with increasing home range size; otherwise, an individual with a larger home range would be exposed to more cameras but encounter each camera less frequently. While this assumption is likely not true for all situations, a positive correlation between home range size and movement rates has been shown for a variety of mammals (e.g., Phillips et al., 1973; Sunquist et al., 1987; Jedrzejewski et al., 2002; Gehring and Swihart, 2004). In our simulation, home range size for species A is constant at 20 units<sup>2</sup> (corresponding to a home range radius of 2.52 units<sup>2</sup>), with ranges for species B = 5, 10 and 15 units<sup>2</sup> (corresponding to radii of 1.26, 1.78 and 2.19 units).

#### 2.1.3. Scenario 3: trap setup

There are two types of trap setups. Species A has a constant  $\lambda_0$  across both setup types; species B has a lower  $\lambda_0$  at setup type 2. Motivation: Some species exhibit a tendency to walk on roads (here, type 1) and consequently have lower encounter rates with traps set at off-road locations (type 2), but this response to trap placement is species-specific. For both species we chose  $\lambda_0$  at setup type 1 as 0.3 and for species B, we simulated a low ( $\lambda_0$  type 2 = 0.15), medium ( $\lambda_0$  type 2 = 0.1) and strong ( $\lambda_0$  type 2 = 0.05) response in  $\lambda_0$  to setup type 2. For each scenario we simulated a low (20%) and a medium (50%) percentage of randomly chosen traps of setup type 2.

#### 2.1.4. Scenario 4: repeated surveys

$\lambda_0$  of species B increases across five surveys while abundance N decreases linearly at a rate of 8% from 100 (survey 1) to 68 (survey 5). Motivation: a pattern of increasing trap visitation rates with decreasing population density has been observed for several species (Sargeant et al., 2003; Matthews et al., 2011). We looked at four different situations in which (a) there is no increase in  $\lambda_0$ , (b) the increase in  $\lambda_0$  is half the decrease in N, (c) the increase in

$\lambda_0$  matches the decrease in  $N$ , and (d) the increase in  $\lambda_0$  is twice the decrease in  $N$ .

For each scenario we generated 1000 data sets. Within each iteration we tested for differences in RAls between species using a Poisson regression, where the RAls at each camera represent the response variable and 'species' is a categorical covariate. Further, for each iteration we calculate the ratio of RAls of species  $B$  to species  $A$ , using the average RAls across the 400 cameras. For scenarios 1–3 we report the percentage of iterations where RAls were significantly different between species, indicated as a significant species coefficient in the Poisson regression, as well as the mean ratio of RAls of species  $B$  to species  $A$ . We analyzed data of scenario 4 using time (here, repeated survey) as a linear covariate in the Poisson regression. We report the number of iterations in which the model estimated a significant negative coefficient for 'time', corresponding to a significant decline in RAl.

To look at how RAls behave under a smaller camera trap setup, we extracted the same information as described above from the innermost 36 cameras of the trapping grid. Subsampling results can be found in online [Supplementary Material S2](#).

## 2.2. Empirical data

We present empirical data to further illustrate problems with comparing RAls both between different species, as well as within a single species but from different study setups. Data come from camera trapping studies carried out in three forest reserves in the Malaysian state of Sabah, on Borneo: Deramakot Forest Reserve (DFR), Tangkulap-Pinangah Forest Reserve (TFR) and Segaliud Lokan Forest Reserve (SLFR).

First, we compare RAls of leopard cats *Prionailurus bengalensis* and common palm civets *Paradoxurus hermaphroditus* from two studies, both of which were conducted in two of the three reserves, DFR and TFR. In study  $A$ , camera traps were placed at random off-road locations. In study  $B$ , pairs of camera traps were placed regularly at  $\sim 1.7$ -km intervals and predominantly along roads. For a more detailed description of the studies, see [Samejima et al. \(2012\)](#) (study  $A$ ), and [Wilting et al. \(2012\)](#) and [Mohamed et al. \(in press\)](#) (study  $B$ ). Due to the differences in study design (e.g., number of camera traps per sampling location) comparable subsets of data had to be extracted from the full data sets; the selection procedure is described in online [Supplementary Material S3](#). For each camera we calculated RAls as the number of pictures per 100 trap days ([O'Brien et al., 2003](#)), and tested for differences in average RAls between species and sites using a Wilcoxon rank-sum test. These comparisons resemble our simulation scenarios 1 and 3, with possible differences in species-specific trap encounter rates and comparison across different trap setups.

Second, we compared RAls and actual density estimates from spatial capture–recapture (SCR) models based on camera trapping data of leopard cats from DFR, TFR and SLFR ([Mohamed et al., in press](#)), and Sunda clouded leopards *Neofelis diardi* from TFR and SLFR ([Wilting et al., 2012](#)). Here, differences in trap Encounter Rates (scenario 1) or Home Ranges (scenario 2) across sites, which can be accounted for in SCR models, could lead to biases in RAls.

All analyses were performed in the software R ([R Development Core Team, 2011](#)).

## 3. Results

### 3.1. Simulation study

#### 3.1.1. Scenario 1: Encounter Rates

At overall high levels of  $\lambda_0$  (species  $A = 0.5$ – $0.7$ , species  $B = 0.4$ ) the more abundant species  $B$  had mostly higher average RAls than

$A$ . The  $B:A$  RAl ratio, however, shifted from the actual 2:1 to 1.6, 1.3 and 1.1 ([Fig. 1](#)). When  $\lambda_0$  for species  $A$  was 0.7, its RAls were sometimes significantly higher than for the more abundant species  $B$  ([Table 1](#)). At low levels of  $\lambda_0$  ( $A = 0.2$ – $0.4$ ,  $B = 0.1$ ), RAls for species  $A$  were either similar to or higher than RAls for species  $B$  ([Fig. 1](#)). For  $\lambda_0$  of species  $A = 0.3$  and  $0.4$  in virtually all cases (99.7% and 100%, respectively) RAls were significantly higher than for species  $B$  ([Table 1](#)).

#### 3.1.2. Scenario 2: Home Ranges

The RAl ratio of  $B:A$  decreased proportionally to the decrease in home range of the more abundant species  $B$ , with ratios ranging from 1.5:1 (home range of species  $B = 15$  units<sup>2</sup>) to 1:1 (10 units<sup>2</sup>) to 0.5:1 (5 units<sup>2</sup>) ([Fig. 1](#)). When range size for  $B$  was 15 units<sup>2</sup>, RAls for  $B$  remained significantly higher than for  $A$ . But when we decreased range size of species  $B$  to 5 units<sup>2</sup> RAls for  $A$  were always significantly higher than for species  $B$  ([Table 1](#)).

#### 3.1.3. Scenario 3: Trap Setup

For both 20% and 50% of traps of setup type 2 and all reduced baseline trap encounter rates  $\lambda_0$  for species  $B$  at those traps, RAls for the more abundant species  $B$  remained higher than for species  $A$  in 100% of all iterations ([Table 1](#)). The  $B:A$  RAl ratio, however, declined from 1.8:1 (species  $B \lambda_0$  at trap type 2 = 0.15, 20% type 2) to 1.2:1 (species  $B \lambda_0$  at trap type 2 = 0.05, 50% type 2) ([Fig. 1](#)). For this latter combination, RAls of species  $B$  were only significantly higher than RAls of species  $A$  in 64% of all iterations.

#### 3.1.4. Scenario 4: Repeated Surveys

When  $\lambda_0$  remained constant across repeated surveys while population size declined (a), the decrease in RAls over time was always significant. If  $\lambda_0$  increased at half the rate of the population decline (b) and at the same rate as the population decline (c), Poisson regressions on RAls estimated a significant decline in RAl for 100% and 77% of the iterations, respectively, but the estimated decline was lower than the true population decline. When  $\lambda_0$  increased at twice the rate of population decline (d), RAls increased significantly over time in 78% of the iterations ([Table 2](#), [Fig. 1](#)).

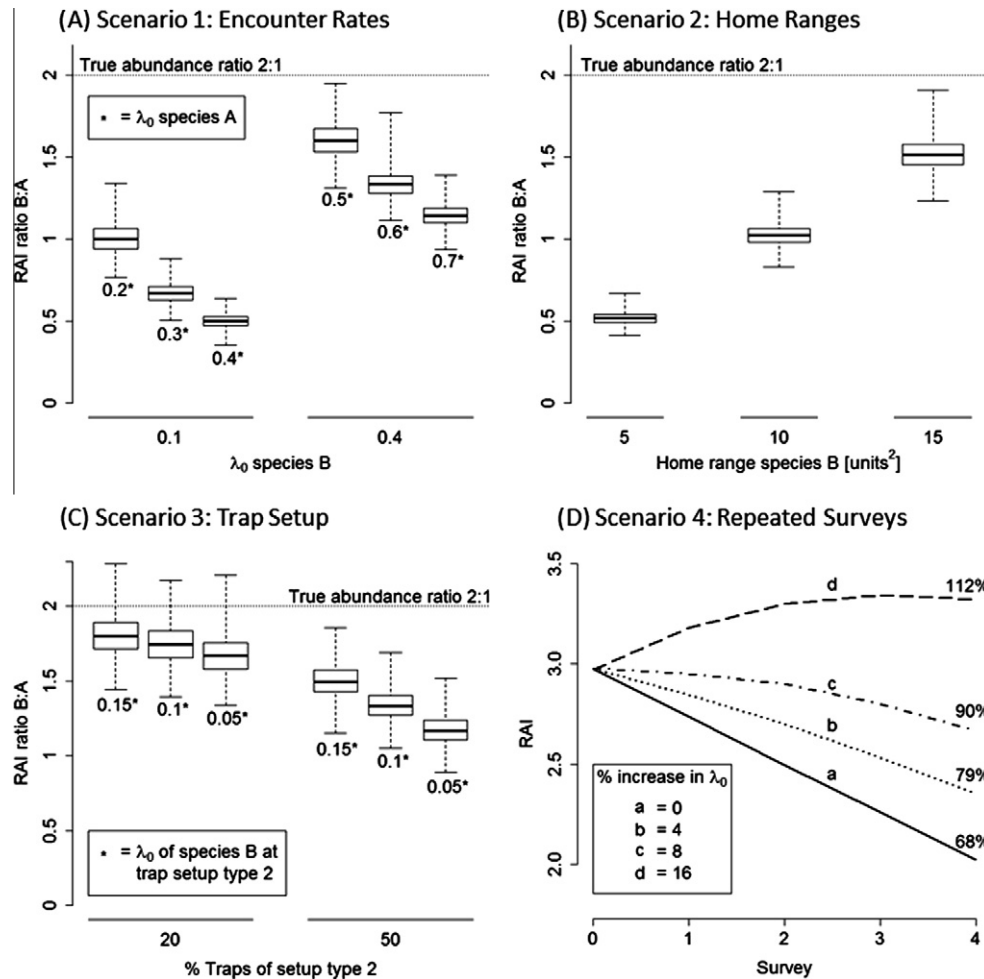
### 3.2. Empirical study

For both leopard cats and common palm civets, RAls from cameras set up along roads (study  $B$ ) were consistently 1–2 orders of magnitude larger than from cameras set up randomly (study  $A$ ) in the same study areas ( $n_A = 138$ ,  $n_B = 111$ , leopard cat:  $W = 3525$ ,  $p < 0.001$ ; common palm civet:  $W = 3249$ ,  $p < 0.001$ ).

Within-study comparisons of RAls between species had contradicting results. For study  $A$ , we observed higher RAls for common palm civets than for leopard cats in both areas, but the difference was only significant in DFR (DFR:  $n_{DFR} = 101$ ,  $W = 3907$ ,  $p < 0.001$ ; TFR:  $n_{TFR} = 38$ ,  $W = 4777.5$ ,  $p = 0.167$ ). Contrary, in study  $B$ , leopard cats had higher RAls than common palm civets in both areas, but the difference was significant only in TFR (DFR:  $n_{DFR} = 47$ ,  $W = 1221$ ,  $p = 0.352$ ; TFR:  $n_{TFR} = 64$ ,  $W = 2814.5$ ,  $p < 0.001$ ).

When comparing RAls for each species between sites, both studies yielded more similar results. In study  $A$  leopard cat RAls were higher in TFR than in DFR, but not significantly so ( $n_{TFR} = 38$ ,  $n_{DFR} = 101$ ,  $W = 4904.5$ ,  $p = 0.285$ ). In study  $B$  leopard cat RAls were constant between the two sites ( $n_{TFR} = 64$ ,  $n_{DFR} = 47$ ,  $W = 1379$ ,  $p = 0.445$ ). While common palm civet RAls were significantly higher in DFR ( $n_{TFR} = 38$ ,  $n_{DFR} = 101$ ,  $W = 5755$ ,  $p = 0.029$ ) for study  $A$ , they were higher in DFR but not significantly different from TFR in study  $B$  ( $n_{TFR} = 64$ ,  $n_{DFR} = 47$ ,  $W = 1779.5$ ,  $p = 0.068$ ). All results are listed in [Table 3](#).

RAls for Sunda clouded leopards and leopard cats did not reflect the same spatial patterns as density estimates from SCR models:



**Fig. 1.** Average RAI ratios over 1000 simulations for two species A and B. Unless stated otherwise, there are 100 individuals of B and 50 of A and individuals move over home ranges of 10 units<sup>2</sup>. In boxplots, thick lines represent the median, boxes the lower and upper quartile, and whiskers the lowest and highest observation. (A: scenario 1) RAI ratio B:A for differences in baseline trap encounter rate  $\lambda_0$  between species. (B: scenario 2) RAI ratio B:A for difference in home range areas. Species A moves over 20 units<sup>2</sup>. (C: scenario 3) RAI ratio B:A when there are two types of trap setup. Species A has a constant  $\lambda_0$  (0.3) but species B has different  $\lambda_0$  at setup type 2. (D: scenario 4) Changes in RAI when abundance decreases linearly over the course of five repeated surveys, with a rate of 8% of the initial population (time = 0) each survey; simultaneously, (a)  $\lambda_0$  remained constant, (b)  $\lambda_0$  increases 4%, (c) 8%, and (d) 16% of the initial  $\lambda_0$  per survey. End-line numbers are RAIs at time = 4 in % of RAI at time = 0.

The average RAIs for Sunda clouded leopards were twice as high in TFR as in SLFR (Table 4), while density estimates were similar in both sites (Wilting et al., 2012). For the leopard cat RAIs were nearly identical across the three study sites, whereas density estimates differed considerably among the three study areas (Table 4).

#### 4. Discussion

Camera traps opened up an invaluable opportunity to monitor wildlife populations non-invasively, even in logistically challenging environmental settings. Since camera-traps operate (largely) independent of observers and collect data on many different species simultaneously, they have been promoted as a survey method that is easy to standardize and can be used in multi-species studies. This has led many to believe that camera-trap surveys represent a one-fits-all approach to population monitoring. Although the issue of imperfect and variable detection probability has been discussed extensively (e.g., Link and Sauer, 1998; Pollock et al., 2002), studies still fall back on using relative abundance indices, either because sound statistical methods for population estimation cannot be applied for the species of concern, or because project leaders are not aware of these statistical methods, or simply prefer the “easy to apply” RAIs. Whereas there seems to be increasing

awareness of the problems related to comparing RAIs between different species, comparing RAIs of a single species across time and/or space is still common practice. The desire to extract as much information as possible from a data set is understandable, but we showed that resorting to non-calibrated relative abundance indices bears strong risks of making wrong inference, both for within and among species comparisons.

##### 4.1. Species ecology, study design and RAIs

Comparison of indices over time, in space or among species can reveal changes/differences in relative abundance *only* if detection is constant (O'Brien, 2011). But variation in detection can arise from simple ecological differences across any of these scales. One of the most tangible of these ecological factors is home range size. In scenario 2, we showed that the RAI of a species will decline proportionally to its home range size, since species or individuals with larger ranges tend to encounter more camera-traps. In reality, changes in RAI with home range size may of course not be strictly proportional. In our simulations we implicitly assumed that individual movement rate increased with increasing home range by holding the baseline detection rate constant across range sizes. If baseline detection were to go down with increasing range size,



**Table 1**

Results from scenarios 1 (Encounter Rates), 2 (Home Ranges) and 3 (Trap Setup): mean RAI with standard deviation (SD) and results from Poisson regression to test for difference of the means.

Scenario	RAI (SD) A	RAI (SD) B	A < B <sup>a</sup>	A > B <sup>a</sup>
<b>1 – Encounter rate</b>				
$\lambda_0$ (A)/ $\lambda_0$ (B) <sup>b</sup>				
0.2/0.1	0.74 (0.05)	0.75 (0.05)	4.4	3.7
0.3/0.1	1.11 (0.07)	0.75 (0.05)	0	99.7
0.4/0.1	1.49 (0.08)	0.75 (0.05)	0	100
0.5/0.4	1.86 (0.10)	2.98 (0.12)	100	0
0.6/0.4	2.23 (0.11)	2.98 (0.11)	100	0
0.7/0.4	2.60 (0.12)	2.98 (0.11)	81.4	0
<b>2 – Home range</b>				
Area (B) <sup>c</sup>				
5	2.19 (0.11)	1.13 (0.06)	0	100
10	2.18 (0.11)	2.23 (0.09)	12.7	2.8
15	2.18 (0.10)	3.30 (0.12)	100	0
<b>3 – Trap setup</b>				
$\lambda_0$ (B)/type 2 traps <sup>d</sup>				
0.15/20%	1.11 (0.07)	2.01 (0.08)	100	0
0.1/20%	1.11 (0.07)	1.94 (0.09)	100	0
0.05/20%	1.11 (0.07)	1.86 (0.09)	100	0
0.15/50%	1.12 (0.06)	1.67 (0.08)	100	0
0.1/50%	1.12 (0.07)	1.49 (0.08)	99	0
0.05/50%	1.11 (0.07)	1.30 (0.08)	64.1	0

<sup>a</sup> Percentage of iterations in which a Poisson regression indicated significantly ( $p < 0.05$ ) lower/higher RAIs for species A than species B.

<sup>b</sup> Levels of baseline trap encounter rate ( $\lambda_0$ ) for species A ( $N = 50$ ) and B ( $N = 100$ ).

<sup>c</sup> Area sizes (units<sup>2</sup>) over which individuals of species B move (individuals of species A move over 20 units<sup>2</sup>).

<sup>d</sup> Baseline trap encounter rates  $\lambda_0$  of species B with traps of setup type 2 and percentage of type 2 traps.

**Table 2**

Results of scenario 4 (Repeated Surveys): Mean relative abundance indices for the surveys 1–5 (standard deviation), the average estimated rate of change of the RAIs ( $R$ -hat, true rate of change =  $-0.08$ ) and whether there was a significant change in RAIs over time.

$I(\lambda_0)^a$	1	2	3	4	5	$R$ -hat	↓ <sup>b</sup>	↑ <sup>b</sup>
0	2.98 (0.11)	2.74 (0.11)	2.50 (0.10)	2.26 (0.10)	2.02 (0.09)	$-0.08$ (0.01)	100	0
0.04	2.98 (0.11)	2.84 (0.11)	2.70 (0.11)	2.53 (0.10)	2.35 (0.10)	$-0.05$ (0.01)	100	0
0.08	2.98 (0.11)	2.95 (0.11)	2.90 (0.12)	2.80 (0.11)	2.67 (0.11)	$-0.02$ (0.01)	76.5	0
0.16	2.97 (0.11)	3.18 (0.12)	3.30 (0.13)	3.34 (0.13)	3.32 (0.13)	$+0.03$ (0.01)	0	78.2

<sup>a</sup> Relative annual increase in  $\lambda_0$ .

<sup>b</sup> Percentage of iterations in which the Poisson regression model considered the decrease (↓) or increase (↑) in RAIs over time significant.

**Table 3**

Average RAIs, calculated as number of pictures per 100 trap nights (standard deviation), for leopard cats and common palm civets in the Deramakot (DFR) and Tangkulap-Pinangah (TFR) Forest Reserves, Malaysia, sampled with a random camera-trap set-up off of roads (study A) and a systematic camera trap setup with large parts of the cameras along roads (study B).

Area	Study A		Study B	
	No. pictures	Mean RAI (SD)	No. pictures	Mean RAI (SD)
DFR	101 Cameras, 8273 trap days		47 Cameras <sup>a</sup> , 1936 trap days	
Leopard cat	5	0.08 (0.37)	154	7.96 (12.87)
Common palm civet	42	0.56 (1.34)	94	4.85 (11.05)
TFR	38 Cameras, 3298 trap days		64 Cameras <sup>b</sup> , 2703 trap days	
Leopard cat	4	0.11 (0.34)	218	8.04 (13.10)
Common palm civet	6	0.31 (0.97)	66	2.41 (4.62)

<sup>a</sup> 24 Off-road cameras.

<sup>b</sup> 23 Off-road cameras.

we would not observe the proportional increase in RAIs. On the other hand, an increase in both home range and baseline detection rate would further inflate the positive bias in RAIs. Differences in home range size do not only apply on the inter-specific level. For many species home range size varies widely among regions of their distribution (McLoughlin et al., 2000). Even within a single population, home ranges can change over time, for example if resource availability and distribution changes over time and/or space (e.g.,

Macdonald and Carr, 1989), or they can vary between sexes. Apart from differences in space use, species-specific traits that can lead to differences in photographic rates include, for example, gregariousness (Treves et al., 2010).

Furthermore, we showed how strongly different study designs can affect RAIs, and thus how much results from the same study site can differ. RAIs of leopard cats and common palm civets were orders of magnitude larger when cameras were predominantly set

**Table 4**  
Average RAIs and density estimates from spatial capture–recapture models for leopard cats<sup>a</sup> and Sunda clouded leopards<sup>b</sup> in three forest reserves in Sabah, Malaysia (Borneo).

Area	Leopard cat				Sunda clouded leopard			
	Pictures	Individuals	RAI (SD)	D (SE)	Pictures	Individuals	RAI (SD)	D (SE)
DFR	154	23	7.96 (12.87)	9.56 (1.66)	9	1	NA	NA
TFR	218	41	8.00 (13.12)	12.40 (1.62)	26	5	0.97 (1.70)	0.84 (0.42)
SLFR <sup>c</sup>	231	60	7.98 (13.94)	16.50 (1.99)	17	5	0.56 (1.16)	1.04 (0.58)

<sup>a</sup> Results from Mohamed et al. (in press).

<sup>b</sup> Results from Wilting et al. (2012).

<sup>c</sup> 57 Camera traps (35 on roads, 22 off-road); 2874 trap days.

up along roads. The problem is further aggravated by the fact the species are affected differently by these changes in study design. Clearly, the placing of cameras along roads in study B benefitted the collection of leopard cat data much more than it did for common palm civets. Mohamed et al. (in press) showed that for leopard cats, the trap encounter rate at on-road camera traps was much higher than off-road. A similar pattern has been shown for jaguars (Sollmann et al., 2011). If we were ignorant of such issues, our conclusion of which species is more abundant based on RAIs, the leopard cat or the common palm civet, would be opposite depending on our study setup. Standardizing the study design can help reduce variation in detection across surveys and should include standardizing equipment, since different camera trap brands and models can differ in their ability to detect species (Kelly and Holub, 2008). While researchers can control the study design changes in landscape features over time (e.g., use of logging roads, which depends greatly on the harvesting plan, prescribed burns, etc.), which in turn can affect animal movement, are usually beyond our control.

Even when looking at trends of RAIs for a single species and under constant study design we cannot guarantee that detection remains constant across time or space. For example Matthews et al. (2011) show that camera trap visitation rates of fishers *Martes pennanti* differed between two samples at the same study site and were negatively related to population density. Sargeant et al. (2003) observed the same for swift foxes *Vulpes velox* and kit foxes *Vulpes macrotis*. As demonstrated in scenario 4, even a slight change in detection over time can blur population trends. If the concurrent increase in detectability is higher than the decrease in population size, the apparent trend can even be inverted.

It is even harder to imagine a situation where one can safely assume no variation in detection among different species. Several studies evaluating the performance of camera traps for mammal surveys have demonstrated that the cameras' ability to detect individuals correlates with species body size (Tobler et al., 2008; Rowcliffe et al., 2011). Even supposedly similar species can vary in their detection probability, for example, a camera trapping study showed that Andean cats *Leopardus jacobita* had a much higher baseline detection probability than the similar-sized Pampas cat *Leopardus colocolo* (Reppucci et al., 2011). We showed in the encounter rate scenario that at low trap encounter rates, absolute differences in trap encounter rate have greater repercussions in the data set than at high detection levels. This is intuitive, since the relative differences in RAIs will be proportional to the relative differences in detection. With cryptic and rare species, researchers are generally dealing with low detection rates, further aggravating the potential for bias in RAIs.

None of the above discussed factors are mutually exclusive. For leopard cats and Sunda clouded leopards, the different spatial patterns in RAIs versus densities were probably caused by slight differences in study design (e.g., different numbers of on-road and off-road cameras), as well as differences in detection and ranging behavior of the species among sites (Wilting et al., 2012; Mohamed et al., in press).

#### 4.2. RAIs in other contexts

The problems of detectability discussed here apply equally to other objectives of inference and other survey methods. For example, photographic rates or detection/non-detection data have also been used to investigate habitat and space use or for ecological niche modeling (e.g., Pettorelli et al., 2009; Foster et al., 2010; Gray and Phan, 2011). Even in these situations, the failure to account for imperfect and spatially varying detection can bias results, especially when detection co-varies with those habitat variables thought to influence presence/abundance (Pollock et al., 2002; Gu and Swihart, 2004; MacKenzie et al., 2006). The assumption of constant detection across species, sites or other scales is obviously also unrealistic for any other survey method. For example, birds or amphibians are frequently monitored using point count methods, where detectability can vary with habitat type, time of day or climatic factors (e.g., Pollock et al., 2002).

#### 4.3. RAIs and sample size

It is worthy to note that simulation results from the subset of 36 camera traps (online Supplementary Material S2) show slightly different patterns than for the full data set. Across all four simulation scenarios rates of significance (for differences in RAI between species A and B in scenarios 1–3, as well as for the population decline in scenario 4) are much lower and never attain 100%. For example, in scenario 4, even when there is no change in detection over time we fail to pick up a significant population decline in 41% of the iterations. In general, with small data sets random variation plays a larger role and thus can blur true trends and differences in data much more easily. We are aware that our larger simulation with 400 camera traps is an unrealistically high number for any field study, and that 36 are probably much closer to the reality of most camera trap projects. In addition, our simulation study ignores other sources of variation in RAIs that are inevitable in real studies, such as variation in space (we use the same expected number of photos for all cameras). We opted to simulate a large and standardized data set to focus on biases in RAIs introduced by deterministic processes and have less confounding effects from other sources of variation (e.g., random and spatial) in the data. As such our simulations show what can go wrong when comparing RAIs even under “ideal” sampling situations. In contrast to our simulated data, there are strong variations in RAIs between fewer individual camera traps from the empirical data set, which is reflected in large standard deviations (Table 3). Detecting trends from such data is much more difficult and ideally involves the modeling of covariates that explain (some of) this variation. Readers should be aware that in real data sets, small sample size and unaccounted for variation can introduce further bias or blur true underlying trends. In this situation, even when assumptions about constant detection probability are met, inference about differences or changes in populations is difficult.

#### 4.4. Alternatives

Unfortunately, when capture–recapture is not an option for population estimation, it is much easier to recommend what not to do with camera-trapping data than what to do instead. There are some analytical options that researchers can explore. Chandler and Royle (in press) developed a spatial capture–recapture model without individual identity that estimates density from spatially replicated point counts, making use of spatial correlation among counts. Though promising, the authors caution that the model relies heavily on the underlying parametric assumptions and is sensitive to spatial study design. When some tagged or otherwise marked individuals are available for sampling, mark–resight models, both non-spatial (e.g., White, 1996; McClintock et al., 2006, 2009a,b) and spatial (Chandler and Royle, in press), can be applied to estimate population parameters. While these models have been used successfully in camera-trapping studies (e.g., Mace et al., 1994), trapping and tagging an adequate number of individuals can be challenging and some researchers may feel that the need to capture animals defies the non-invasive character of camera-trapping.

Alternatively, the Royle–Nichols model (Royle and Nichols, 2003) is based on species level detection/non-detection data and makes use of the relationship between the probability of detecting a species at a given site and its site-specific abundance. The model provides estimates of abundance at each sampling unit (i.e., camera-trap), but it is often unclear how to convert these point estimates into a meaningful estimate of overall abundance or density for a study site.

Another option is the trap encounter rate model by Rowcliffe et al. (2008), which estimates density as a function of encounter rates between animals and traps, animal movement speed and rate. As such, it accounts for differences in detection probability caused by different movement rates. The model assumes random movement of individuals and requires a completely random trap setup relative to animal movement, which, as shown in our empirical example, can result in prohibitively low numbers of photographs, and may logistically not be feasible at all. It further requires knowledge of, or the ability to estimate, movement speed and the amount of time individuals are active.

In addition, some authors have argued that calibrated (absolute) abundance indices can be used to monitor populations (Carbone et al., 2001). However, calibration to identify the functional relationship between the index and abundance should be performed with an independent data set and for each species and location (and potentially, point in time) in question (Jennelle et al., 2002). In reality this should be as feasible as conducting an actual abundance study.

Clearly, none of the above options is universally applicable. We believe that when interested in the abundance of a species that has no natural marks and that cannot easily be tagged, rather than defaulting to camera-traps researchers should consider alternative survey methods. Depending on your study area and species, non-invasive genetic sampling in combination with capture–recapture models (e.g., Gardner et al., 2009; Kéry et al., 2010), distance sampling (Royle et al., 2004; Thomas et al., 2010) or repeated point counts in combination with appropriate models accounting for detection (e.g., *N*-mixture models, Royle, 2004) can provide statistically sound population estimates. It goes without saying that all of these approaches come with their specific sets of assumptions and sampling design requirements.

Finally, in cases where alternative data collection is not an option, several studies have moved away from abundance and instead investigate occupancy using detection/non-detection data (e.g., Ahumada et al., 2011), arguing that abundance and occupancy should correlate. While there is empirical and mathematical

evidence that occupancy is related to abundance (Lawton, 1993; Gaston et al., 1997; MacKenzie and Nichols, 2004), changes in abundance are not necessarily reflected in occupancy, especially on a small scale (e.g., Matthews et al., 2011; Efford and Dawson, 2012; Mohamed et al., in press). For other study objectives, however, such as space or habitat use, species distribution and even interaction, occupancy models provide a statistically sound alternative to RAIs (e.g., Linkie et al., 2007; Tobler et al., 2009; Sollmann et al., 2012; Mohamed et al., in press).

#### 5. Conclusion

Estimating abundance and density for unmarked populations is an ongoing focus of research. Although a number of approaches are available, all of them have considerable limitations, causing researchers to fall back on RAIs, which are still part of the scientific literature. A cursory google scholar search through the existing camera-trapping literature from 2000 to 2012 revealed a minimum of 40 peer-reviewed scientific publications that used RAIs (excluding those that evaluated the performance of RAIs against other measures of abundance). The peer-review process likely limits the number of publications basing inference about populations on RAI. However, there is no such control mechanism when it comes to monitoring, assessment or management project reports. In these documents, which generally address an audience of wildlife managers that do not necessarily have a scientific background, RAIs are often presented as-is, without critical reflection of how to interpret them. We find that particularly worrying since it is usually these documents that decision makers will use to evaluate management schemes or conservation actions. Against this background, it is important to communicate that ‘detection bias’ is not some abstract concept biostatisticians should worry about, but that it arises from very basic ecological and sampling factors and has immediate implications for the data collected. We urge researchers and managers to take detection bias into account when designing studies, and discuss these issues explicitly when presenting results. The need to have efficient survey techniques is indisputable, but cannot be placed ahead of adequate data collection and sound analysis. Especially where the conservation of rare and endangered species is at stake, every possible effort should be made to obtain the data needed to adequately assess and monitor their populations.

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#### Appendix A. Supplementary material (S1–S3)

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.12.025>.

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