A COMPARISON OF CAMERA TRAPPING AND LIVE TRAPPING TECHNIQUES FOR THE SURVEYING OF SMALL MAMMALS IN SABAH, MALAYSIAN BORNEO

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By

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Abstract

- 1. Camera traps are quickly becoming a staple in the surveying of medium and large terrestrial mammals, but their application in the surveying of small mammals has yet to be established. This study aims to test the effectiveness of camera trapping in comparison to traditional live trapping techniques, and verify whether the relative abundance index 'camera trapping rate' can be used as a valid inference of species abundance.
- 2. Data was taken from 21 sites across the Kalabakan Forest Reserve and the Maliau Basin Conservation Area in Sabah, Malaysian Borneo. The small mammal community was sampled using two methods: baited steel mesh traps and camera traps. Density estimates of small mammal species were derived from the live trapping using the R package **secr**, and regressed against the camera trapping rate. The two methods were also compared for their ability to detect species and estimate species richness.
- 3. Live trapping methods detected more species, more often and at less cost than the camera trapping methods in the Bornean rainforest. There was no significant relationship between density estimates derived from the live traps and camera trapping rates across any species except the slender treeshrew.
- **4.** Camera trapping rates cannot be used as a substitute for abundance estimates, until further development in technology and study design significantly improve their detection rate of small, terrestrial mammals. They may be useful in studies requiring only simple presence data, but may underestimate the community present. We do not recommend that any wildlife management decision be based off small mammal camera trap data.

Key words: small mammal; camera trapping; live trapping; relative abundance index; density; species richness.

Introduction

The main objective of conservation management is to maintain an ecosystem's current state, or to achieve predetermined goals relating to its structure or function by manipulating biological processes (Legg & Nagy 2006). In order for this to be achieved, a deep understanding of an areas biodiversity is needed, as well as the monitoring of populations and changes to their population dynamics. To obtain this critical data there is an ever increasing need for more robust assessments (Boddicker, Rodriguez & Amanza. 2002) and proven methodological approaches (Rodriguez 2003). Through the surveying of wildlife populations this data can be generated to identify priority species and conservation action areas (Danielson et al. 2007).

A wide variety of techniques have been developed for the surveying of terrestrial mammal species (Thompson & Thompson 2007). Many of these techniques have provided reliable data on the target species and their response to management efforts (Mckelvey & Pearson 2001), over both spatial and temporal scales (Hamm, Diller & Kitchen 2002). Each of these surveying techniques has specific advantages and disadvantages, mainly regarding detectability, usability by researchers, and field and labour costs. It is often, ultimately, resource availability that determines method

selection, especially in conservation work where the effective use of resources is paramount (Guil et al. 2010). A sound understanding of each method's efficacy is therefore required in order to select the appropriate technique for studies (Barea-Aznón et al. 2007). Therefor, there is an increasing need for comparative studies that assess the performance of different sampling techniques across different mammal species and sizes. However, such research remains somewhat rare (Garden et al. 2007).

Many studies rely on the physical capture of individuals in direct sampling. Live trapping has been used successfully in a wide variety of taxa to detect species richness, abundance, and population densities across environmental gradients (Kelt 1996), whilst allowing the collection of additional data such as gender and morphological measures (Wiewel, Clark & Sovada 2007). Cage traps are often used for the sampling of medium-sized mammals (McCarthy et al. 2013), and small aluminium traps (e.g. DeBondi et al. 2010) or pitfalls traps (e.g. Garden et al. 2007) are widely used for smaller mammals. Despite the wide utility of these methods, they present some significant drawbacks. As well as being time and labour intensive (Wiewel, Clark & Sovada 2007), live trapping can provide little data on species that require specialised capture techniques or demonstrate especially low detection probabilities (Sollmann et al. 2013). The method also requires that the individual be detained for several hours and handled, potentially stressing the animal and interfering with its normal activities (DeBondi et al. 2010).

Remote camera traps that are triggered by passing animals have been used widely to sample a variety of medium and large terrestrial mammals (Trolle et al. 2008). The

use of cameras to record images of wildlife without human presence is not a new technology, with the first cameras being used for scientific study in the 1920s (Hance 2012). However, major improvements in technology have resulted in a massive increase in camera trap studies over recent years (Hance 2012). Camera traps are advantageous in their practicality; data on multiple species can be collected over increasing spatial and temporal scales (Kelly & Holub 2008), they can be left running continuously for long periods in adverse conditions, and are particularly effective for detecting wide-ranging and elusive species (Foster & Harmsen 2012). Animals need not be detained and can continue with their normal activity without disturbance (DeBondi et al. 2010).

Camera trap images can be used to estimate density and changes in density of species whose markings allow for individual recognition (e.g. tigers – Karanth, Nichols & Kumar 2011). Most mammal species, however, are not individually recognisable from photographs, especially small mammals, and so indices of abundance are often used as an alternative (Dreiseen & Jarman 2014). The use of indices is controversial (Sollmann et al. 2013), but density estimates are cost and labour intensive, especially with rare and elusive species. Indices are often assumed to vary with population size. However, for an index to be reliable it must be calibrated with an independent estimation of abundance (O'Brain 2011).

A number of studies have looked at the relationship between abundance indices from camera traps and other independent estimates or indices. Rovero and Marshall (2009) found a strong linear relationship between density derived from line-transects and camera trapping rate, in Harvey's duiker *Cephalophus harveyi*.

Conversely, another study found that densities of both clouded leopard *Neofelis diardi* and leopard cat *Prionailurus bengalensis* were not reflected in their camera trap derived abundance indices (Sollmann et al. 2013). Although an increase is becoming evident, little work has been done using camera traps to survey small mammal species. DeBondi et al. (2010) found that occupancy estimates from both live and camera trapping methods were similar in most of the study species, but no study that we found has compared independently derived density estimates with relative abundance indices obtained from camera traps in small mammals.

The principle objective of this study was to compare the efficiency of camera trapping to live trapping as a sampling technique for recording small mammal species richness, and to provide a reliable relative abundance index that reflects differences in density across space.

Methods

This study used unpublished data collected by Oliver Wearn during his PhD at the Institute of Zoology, and Imperial College, London. The data was collected in collaboration with the Stability of Altered Forest Ecosystem (SAFE) Project in Sabah, Malaysian Borneo (Ewers et al. 2011).

Study sites and sampling design

Small mammals were sampled across three land-uses; primary old growth forest within the Maliau Basin Conservation Area, repeatedly logged forest in the Kalabakan Forest Reserve, and in oil palm plantations on the Kalabakan Forest Reserve

boundary. Sampling plots were chosen randomly to overlap with the experimental designs of the SAFE Project, which is designed to minimise confounding factors including latitude, slope and elevation across the land-uses (Ewers et al. 2011). Nine plots were selected in old growth, 16 in logged, and nine in oil palm, and divided into grids made up of $(4 \times 12 =) 48$ points, which were separated by 23m.

Field methods

Live trapping: Small mammal trapping was conducted at plot level. Each session was made up of seven consecutive trapping days. Two locally made steel-mesh traps (28cm x 18cm x 12cm) were placed at or near ground level (0-1m) within 10m of each grid point (96 traps total) and baited with palm oil fruit. Traps were checked each morning and captured individuals anaesthetised (following Wells et al. 2007), using diethyl ether. They were measured, identified to species level using Payne, Francis & Phillips (2007), and marked using a subcutaneous transponder tag (Francis Scientific Instruments, Cambridge, UK), before being released at the capture location. Live trapping was carried out between May 2011 and March 2014, and many plots were sampled multiple times. During this period there were no major mast-fruiting events.

Camera trapping: Random subsets of grid points within the plots were chosen for camera trap deployment (mean points per plot = 15). The camera traps (Reconyx HC500, Holmen, Wisconsin, USA) were set to operate continuously day and night.

Cameras were set up as close as possible to the points and strictly within 5m. This random deployment of cameras is rarely used, but is essential for avoiding the underdetection of species and revealing species-specific patterns of space-use (Wearn et al.

2013). Cameras were fixed to trees, wooden poles, or within locally made security cases, when in areas of high human traffic. The camera sensors were positioned at 30cm from the ground to maximise detection for a range of species size (though this was slightly flexible depending on the terrain encountered at each location).

Disturbance to vegetation around the camera was kept to a minimum and no bait or lure was used. Camera trapping was carried out between May 2011 and April 2014, and most plots were sampled multiple times (mean effort per plot = 625 trap nights).

Site selection for analysis

To avoid interfering with the success of either trap method, the two trap types were not set on the plots at the same time. Plots that had both trapping methods carried out on them within the same year were selected. The lack of major mast-fruiting events during the survey period, and the consistency of weather in Sabah (average rain: 220mm per month (Dambul & Jones 2007)), meant that changes in species population dynamics within this time were unlikely. Camera trap studies that have previously targeted small mammals have used longer sampling periods than those used for live trapping studies (e.g. Larrucea & Bussard 2008), and so our surveying lengths are appropriate for comparison between the two methods. This selection process resulted in 27 suitable sessions within the plots for comparison – seven from old growth, 14 from logged and six from oil palm.

Statistical analysis

Field data: To evaluate the rigour of camera trapping in surveying small mammals in comparison to live trapping, a subset of the photographs obtained were used. Camera

traps also obtained photos of non-target species, and so photographs of medium and large sized mammals, domestic animals and birds were excluded. Exposures where the species was unidentifiable were also excluded from analysis. Individuals were identified to species level where possible using Payne, Francis & Phillips (2007). As camera traps are continuous-time detectors (unlike live traps) photographic events were considered to be independent if they a) contained different individuals or b) were separated by more than half an hour. As we were interested in small mammal detection at the plot rather than trap level, data was pooled for the live traps and cameras at each site.

Species detection and richness: The number of species caught by each trapping method was totalled for each plot, and a Wilcoxon sign-rank test used to compare the total number of species caught. A Chi-square test of independence was used to calculate detection differences by the sampling techniques across the plots, for a species-specific analysis.

Data was then pooled for all sites within each land-use to look at cumulative species richness. To obtain comparable estimates of species richness between the two surveying methods, the interpolation and extrapolation with Hill number methodology was applied (Chao et al. 2014) to the raw estimates of species richness (Sobs), using the R package iNEXT (Hsieh, Ma & Chao 2014). Rarefaction curves allow us to see the size of the entire small mammal fauna susceptible to the trapping methods, represented by the notional asymptote. The individual-based rarefaction curves show rarefied species richness plotted against a given number of individuals, selected randomly from the observed sample (Colwell et al. 2012). Sinext was defined

as the number of species expected when extrapolating to 5000 individuals. To estimate 95% confidence intervals, 100 replicate bootstrapping runs were used.

Initial cost, field costs per survey, and cost per day were calculated independently for each sampling method, and compared. The species richness accumulation curves were also rarefied in relation to the cost of each sampling method – initial cost plus cost per day up to £25000, following the same extrapolation procedure.

Density estimates vs camera trapping rate: Spatially explicit capture-recapture (SECR) methods were used to estimate the small mammal population densities from the live trapping at the species level for each plot. These were calculated using the R package **secr**, developed by Efford (2015). This estimates density using an array of detectors, by fitting a spatial detection model using the maximum likelihood. **secr** requires two input files: the locations of the traps at each site (i.e. coordinates) and the detection histories of the individually marked animals (i.e. sampling session, animal ID, occasion and trap ID). The raw data was transformed into these required files. For the detection history this involved going through each plot selecting trapped individuals of each species. The package is also able to include varying effort within the traps during a session. For each live trap (96 per plot), a numeric object was created within the trap layout file for effort over the duration of the session, with 1 indicating that a trap was open all night or had captured an individual, 0.5 indicating that a trap had been sprung during the night but had not caught anything, and 0 indicating that the trap was not in operation on that occasion. These input files were then assembled as an object of class 'caphist' (capture history) to fit the model.

In the analysis, Poisson distribution was assumed, a buffer of 100m was applied, and single trap option was chosen which allows for only one capture per trap occasion. A null model ($D\sim1$, $g0\sim1$, sigma ~1) and specified model ($D\sim$ Session, $g0\sim1$, sigma ~1), each with half normal detection frequency, were run on all species and the suitability of models compared using a likelihood ratio test.

For comparison with the camera traps we used a relative abundance index for each species photographed: λ (detections per camera trap night (CTN)). To remain consistent with camera trapping literature the detection function d was used, which has units per 100 CTNs, i.e. $\lambda = (d/\text{CTN})*100$. The camera trap rate was regressed against the density estimates for each species at each of the sites to test the relationship between camera trapping rate and live trapping density estimates.

This study was approved by the University of Bristol ethical review group (UIN number: UB/15/028), and all analyses were done in R version 2.12.2 (R Development Core Team, 2014). Figures were plotted using the R package ggplot2 (Wickham 2009).

Results

Species detection and richness: A total of 23 small mammal species were recorded across the three land uses during the survey period (Table 1). However, neither sampling method recorded all species. Live trapping detected 20 target species and camera trapping detected 15 target species, plus 39 non-target species that were too

large to fit into the live traps and were excluded from the analysis. Eight species were recorded by live traps only, and three species recorded by camera traps only. Of the 12 species detected by both methods, 10 were recorded at more plots by live trapping than by camera trapping (Table 1). Very few individuals were caught across the oil palm plantation plots (total: camera traps = 3; live traps = 48) and these plots were excluded from further analysis.

Detection of small mammal species by live trapping ranged from 3 to 17 species at each plot, with an average of 10.24 species per plot (s.e. = 0.816). Camera traps detected between three and eight species at each plot - the average number of species detected per plot was around half of that detected by live trapping (mean = 5.86, s.e. = 0.295). The species richness of small mammals detected by camera traps across the 21 plots was significantly different to the live trapping results (Wilcoxon test: Z = -3.640, P < 0.001), indicating that detection by both methods is not the same (Fig. 1). Detection across the sample plots differed between the two sampling techniques in 10 out of the 23 species recorded (X^2 values, Table 1.). Out of these species, only the tufted ground squirrel was detected more by the camera traps.

Individual-based rarefaction curves showed the characteristic asymptote. This was reached by live trapping in logged forest and camera trapping in old growth, indicating that in these land-uses the methods were respectively sampling all species susceptible to them (Fig. 2). Live trapping produced a higher total species richness estimate for lower sampling effort irrespective of land-use, albeit giving an imprecise estimate in old growth. However, in logged forest a minimum of 500 sample

individuals was required to obtain communities that did not significantly differ in richness, and in old growth only 90 sample individuals.

Financial costs were significantly greater for camera trapping than live trapping (P < 0.001; Table 2). With the camera traps, amounts of £23000 and £20000 were required to reach an asymptote of accumulative species in the logged and old growth forests respectively (Fig. 2). In comparison, live trapping required £2500 in the logged, and £15000 in old growth.

Density estimates vs camera trapping rate: In several of the species, data was too sparse (too few captures and/or recaptures) to generate density estimates. Out of the 20 species recorded by live trapping, we were able to generate density estimates for 13 species. The likelihood ratio test of the two fitted models produced significantly different density estimates in two species (dark-tailed tree rat: $X^2(26) = 60.807$, P < 0.001; Whitehead's rat: $X^2(30) = 147.830$, P < 0.001), and so the more specific D~session model was selected. Density estimates for these species across the plots are shown in Fig. 3. SECR estimates of realised population sizes have been shown to be less biased than estimates from non-spatial methods, showing sufficient precision and confidence interval reporting (Efford & Fewster 2013). We therefore take these estimates as the "true" values of species density for comparison, to see if the camera traps are picking up the same trends through space.

From the camera traps, the overall trap rate success for small mammals captured was 6.38 per 100 CTN. Trap rate success varied significantly among species (Kruskal-Wallis H: $X^2(13) = 161.230$, P < 0.001). Spiny rat had the highest trap success

(3.33/100 CTN) and was photographed at all plots. There was high variability in trap rate success between individual plots, varying from 2.67/100 CTN to 22.19/100 CTN.

Density estimates of species and camera trapping rates were compared for species caught by both methods at five or more plots. Only six of the 13 species density estimates that were calculated had enough camera trap data for statistical comparison. Four of the species with density estimates were not detected at all by camera traps. Camera trap rate did not reflect the same spatial patterns as density estimates from the SECR model (Fig. 4). Five of the species showed no significant relationship between the two variables (linear regression: common treeshrew: R^2 (11) = 0.431, P = 0.0.27; large treeshrew: R^2 (7) = -0.079, P = 0.540; long-tailed rat: R^2 (12) = -0.055, P = 0.581; Low's squirrel: R^2 (16) = -0.037, P = 0.538; spiny rat: R^2 (17) = -0.040, P = 0.582), however the slender treeshrew returned a significant linear regression between camera trap rate and density estimates across the plots (R^2 (5) = 0.559, P = 0.032).

Discussion

This study was amongst the first to look at the efficacy of camera trapping for the surveying of small mammals, in relation to the tried and tested live trapping method.

Species detection and richness: Our results highlight that the failure of a sampling method to detect a species may not be indicative of species absence, but rather a result of unsuitable surveying method selection or inadequate sampling effort. The results suggest that camera trapping is less suitable for the surveying of small

mammals communities, since they missed many more species than the live traps. Across logged and old growth forest, camera traps detected fewer small mammal species, less often and at a higher cost than live trapping. These results are in contrast to previous studies that found the opposite to be true (DeBondi et al. 2010; Driessen & Jarmann 2014). Both these studies were conducted in Australian woodlands and included much larger mammals in their "small mammal" definition, which may account for the different conclusions. The conservation status of most of the species detected is undetermined, but live traps were able to pick up the endangered darktailed tree rat where the camera traps failed. However, unlike the live traps, cameras were able to record information on larger, non-target mammals. The detection of these non-target species during a survey can still provide valuable information (Kelly & Holub 2008). A combination of the two techniques would be most appropriate to gain a complete record of an areas biodiversity.

More species were detected in the logged forest than in the old growth. This is surprising, as resource availability would be expected to be higher in the old growth forest. However, studies have shown that some logged forest characteristics converge on old growth patterns within a few years of regrowth and can provide more resources due to their more open nature (DeWalt, Maliakal & Amanza 2003). Live trapping methods predicted a much higher species richness than camera trapping in the old growth forest, though the estimates did not differ significantly. This could be due to the placement of the live traps (up to one meter from ground level). This may have allowed them to sample some arboreal species, increasing the number of species susceptible to the trapping method.

Density estimates vs camera trapping rate: It is intuitive that camera trapping rate should be comparable to abundance, as density increases, so should the chance of an individual encountering a camera (Rovero & Marshall 2009). However, the present study found no significant relationship between density estimates and camera trapping rate of small mammals, except for the slender treeshrew. In fact, most species were not captured enough by cameras for a comparison to be made. This emphasises the need to calibrate relative abundance indices, to avoid making wrong inferences about populations and communities.

To make a valid comparison across time and space with a relative abundance index, the assumption must be made that species detection rate is constant across these dimensions (Sollmann et al. 2013). This assumption is rarely tested in studies using relative abundance indices (Williams et al. 2002). The variability in detection rate between the two sampling methods is the biggest hindrance for the viability of camera trap derived relative abundance indices for small mammals in this study. In camera trapping there are many other variables other than abundance that will influence trap rate. Despite being set low to the ground, it is highly likely the cameras did not detect many individuals. Detection by camera traps has shown a strong dependence on animal body size, favouring large species. Rowcliffe et al. (2011) found that the effective detection distance for small mammals was less than two meters, drastically reducing the cameras effectiveness. By passing under the camera's field of view they can also be missed. This could be improved in future studies by angling the camera down. Low detection rates can also be influenced by camera model (Kelly & Holub 2008). A delay between the sensor detecting an individual and the triggering can give the animal chance to run away. However the cameras used in

the present study have no delay between detection and firing, and this should not have influenced our low detection rates. Infrared camera performance also reduces in hot climates when the environmental temperature becomes to close to the animals body temperature (Lyra-Jorge et al. 2008). The use of bait would increase visits, and duration of visits, of individuals to the cameras. The use of multiple bait types may be the most efficient way to survey species richness especially, as different bait types will attract different subsets of the community (O'Farrell et al. 1994). This is also notable for live trapping methods. However, bait stations may attract animals into the survey area, which could bias estimates. Once all these variables have been overcome, camera trapping could potentially become a viable tool in the surveying of small, terrestrial mammals.

In conclusion, this study disputes previous research indicating that camera traps can be successfully applied to the systematic surveying of small, terrestrial mammal populations. They can however still provide useful information on presence/abundance inferences, though these will be more reliable and complete if paired with another surveying method. To get a better picture of the community being sampled future studies should look at ways to increase detection rate of small mammals with the camera trap, and further test their viability used closed populations. There is an ever-increasing need for efficient surveying techniques, but this should not be put ahead of adequate data collection and robust analysis.

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References

Barea-Azcón, J. M., Virgos, E., Ballesteros-Duperon, E., Moleon, M. & Chirosa, M. (2007) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. *Biodiversity and Conservation*, 16, 1213-1230.

Boddicker, M., Rodriguez, J. J. & Amanza, J. (2002) Indices for assessment and monitoring of large mammals within an adaptive management framework. *Environmental Monitoring and Assessment*, 76 (1), 105-123.

Chao, A., Gotelli, N. J., Hsieh, T.C., Sander, E. L., Ma, K.H., Colwell, R. K. & Ellison, A. M. (2014) Rarefraction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45-67.

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S. Y., Mao, C. X., Chazdon, R. L. & Longino, J. T. (2012) Models and estimators linking individual-based and sample-based rarefraction, extrapolation, and comparison of assemblages. *Journal of Plant Ecology*, 5, 3-21.

Danielsen, F., Mendoza, M. M., Tagtag, A., Alviola, P. A., Balete, D. S., Jensen, A. E., Enghoff, M. & Poulsen, M. K. (2007) Increasing conservation management by involving local people in natural resource monitoring. *Ambio*, 36, 566-570.

Dambul, R. & Jones, P. (2007) Regional and temporal climatic classification for Borneo. *Geografia*, 5 (1), 1-25.

DeBondi, N., White, J. G., Stevens, M. & Cooke, R. (2010) A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research*, 37, 456-465.

DeWalt, S. J., Maliakal, S. K. & Denslow, J. S. (2003) Changes in vegetation structure and composition along tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management*, 182, 139-151.

Driessen, M. M. & Jarman, P. J. (2014) Comparison of camera trapping and live trapping of mammals in Tasmanian coastal woodland and heathland. *Camera Trapping: Wildlife Management and Research* (eds D. Meek & P. Fleming), pp 253-262. CSIRO Publishing, Australia.

Efford, M. G., & Fewster, R. M. (2013) Estimating population size by spatially explicit capture-recapture. *Oikos*, 122, 918-928.

Efford, M. G. (2015) *Secr 2.9: spatially explicit capture recapture in R*. Department of Zoology, University of Otago, New Zealand.

Ewers, R. M., Didham, R. K., Fahrig, L., Ferra, G., Hector, A., Holt, R. D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J. L. & Turner, E. C. (2011) A large-scale forst fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366 (1582), 3292-3302.

Garden, J. G., McAlpine, C. A., Possingham, H. P. & Jones, D. N. (2007) Using multiple surbey methods to detects terrestrial reptiles and mammals: what are the most successful and cost-efficient combinations? *Wildlife Research*, 34, 218-227.

Gotelli, N. J. & Colwell, R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391.

Guil, F., Agudín, S., El-Khadir, N., Fernandez=Olalla, M., Figueredo, J., Domíngues, F. G., Garzon, P., Gonzalez, G., Muñoz-Igualada, J., Oria, J. & Silbestre, F. (2010) Factors conditioning the camera-trapping efficiency for the Iberian lynx (*Lynx pardinus*). *European Journal of Wildlife Research*, 56 (4), 633-640.

Hamm, K. A., Diller, L. V. & Kitchen, D. W. (2002) Comparison of indices to estimate abundance of dusky-footed woodrats. *Wildlife Society Bulletin*, 3, 64-70.

Hance, J. L. (2012) The camera trap revolution: how a simple device is shaping research and conservation worldwide. *Life is Good: Conservation in an Age of Mass Extinction*, Mongabay, USA.

Hsieh, T.C., Ma, K. H. & Chao, A. (2014) *iNEXT: an R package for interpolation and extrapolation in measuring species diversity (Hill numbers)*. Submitted manuscript. (http://chao.stat.nthu.edu.tw/blog/software-download)

Karanth, K. U., Nichols, J. D. & Kumar, N. S. (2011) Estimating tiger abundance from camera trap data: field surveys and analytical issues. *Camera Traps in Animal Ecology: Methods and Analysis* (eds A. F. O'Connell, J. D. Nichols & K. U. Karanth), pp 97-118. Springer Publishing, Tokyo.

Kelly, M. J. & Holub, E. L. (2008) Camera Trapping of Carnivores: Trap Success Among Camera Types and Across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles County, Virginia. *Northeastern Naturalist*, 15 (2), 249-262.

Kelt, D. A. (1996) Ecology of small mammals across a strong environmental gradient. *Journal of Mammalogy*, 77, 205-219.

Larrucea, E. S. & Brussard, P. F. (2008) Habitat selection and current distribution of the pygmy rabbit in Nevada and California, USA. *Journal of Mammalogy*, 89, 691-699.

Legg, C. J., & Nagy, L. (2006) Why most conservation is, but need not be, a waste of time. *Journal of Environmental Management*, 78, 194-199.

Lyra-Jorge, M. C., Ciocheti, G., Pivello, V. R. & Meirelles, T. (2008) Comparing methods for sampling large- and medium-sized mammals: camera traps and track plots. *European Journal of Wildlife Research*, 54 (4), 739-744.

McCarthy, J. L., Belant, J. L., Breitenmoser-Würsten, C., Hearn, A. J. & Ross, J. (2013) Live Trapping Carnivores in Tropical Forests: Tools and Techniques to Maximise Efficacy. *The Raffles Bulletin of Zoology 2013*, 28, 55-66.

McKelvey, K. S. & Pearson, D. E. (2001) Population estimation with sparse data: the role of estimators verses indices revisited. *Canadian Journal of Zoology*, 79, 1754-1765.

O'Brien, T. G. (2011) Abundance, density and relative abundance: a conceptual framework. *Camera Traps in Animal Ecology: Methods and Analysis* (eds A. F. O'Connell, J. D. Nichols & K. U. Karanth), pp 71-96. Springer Publishing, Tokyo.

O'Farrell, M. J., Clark, W. A., Emmerson, F. H., Juarez, S. M., Kay, F. R., O'Farrell, T. M. & Goodlet, T. Y. (1994) Use of a mesh live trap for small mammals: are results from Sherman live traps deceptive? *Journal of Mammalogy*, 75, 692-699.

Payne, J., Francis, C. M., & Phillipps, K. (2007) *A Field Guide to the Mammals of Borneo,* 4th edition. The Sabah Society, Kota Kinabalu.

R Development Core Team. (2015) *R: A language and environment for statictical computing*. R Foundation for Statictical Computing, Vienna, Austira. (https://www.R-project.org/)

Rodriguez, J. P. (2003) Challenges and opportunities for surveying and monitoring tropical biodiversity – are sponce to Danielson et al. *Oryx*, 37 (4), 411-411.

Rovero, F. & Marshall, A. R. (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, 46, 1011-1017.

Rowcliffe, J. W., Carbone, C., Jansen, P. A., Kays, R. & Kranstauber, B. (2011)

Quantifying the sensitivity of camera traps: an adapted distance sampling approach.

Methods in Ecology and Evolution, 2 (5), 464-476.

Sollmann, R., Mohamed, A., Samejima, H. & Whiting, A. (2013) Risky business or simple solution – Relative abundance indices from camera trapping. *Biological Conservaton*, 144, 351-355.

Thompson, G. G. & Thompson, S. A. (2007) Usefulness of funnel traps in catching small reptiles and mammals, with comments on the effectiveness of the alternatives. *Wildlife Research*, 34, 491-497.

Trolle, M., Noss, A. J., Cordeiro, J. L. P. & Oliveira, L. F. B. (2008) Brazilian Tapir Density in the Pantanal: A Comparison of Systematic Camera-Trapping and Line-Transect Surveys. *BIOTROPICA*, 40 (2), 211-217.

Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H. & Ewers, R. M. (2013) Assessing the Status of Wild Felids in a Highly-Disturbed Commercial Forest Reserve in Borneo and the Implications for Camera Trap Survey Design. *PLoS ONE*, 8 (11), e77598.

Weiwel, A. S., Clark, W. R. & Sovada, M. A. (2007) Assessing small mammal abundance with track-tube indices and mark-recapture population estimates. *Journal of Mammalogy*, 88, 250-260.

Wells, K., Kalko, E. K. V., Lakim, M. B. & Pfeiffer, M. (2007) Effects of rainforest logging on species richness and assemblage composition of small mammals in Southeast Asia. *Journal of Biogeography*, 34, 1087-1099.

Wickham, H. (2009) *ggplot2: elegant graphics for data analysis.* Springer Publishing, New York.

Williams, B. K., Nichols, J. D. & Conroy, M. J. (2002) *Analysis and Management of Animal Populations: Modelling , Estimation, and Decision Making.* Academic Press, San Diego, USA and London, UK.

Tables and figures

Species	Common name	Live trapping (no. of plots)	Camera trapping (no. of plots)	Total (no. of plots)	X ² (d.f.= 1)	P value	
Rattus rattus	Black Rat	12	0	12	16.800	0.000	
Sundasciurus brookei	Brooke's squirrel	1	0	1	1.024	0.312	
Maxomys ochraceiventer	Chestnut-bellied Spiny Rat	6	2	8	2.471	0.115	
Tupaia glis	Common Treeshrew	16	17	33	0.141	0.707	
Niviventer cremoriventer	Dark-tailed Tree Rat	14	0	14	21.000	0.000	
Callosciurus adamsi	Ear-spot Squirrel	5	0	5	5.676	0.017	
Lariscus hosei	Four-striped Ground Squirrel	5	11	16	3.635	0.057	
Sundasciurus hippurus	Horse-tailed Squirrel	6	8	14	0.429	0.051	
Tupaia minor	Lesser Treeshrew	2	0	2	2.100	0.140	
Tupaia tana	Large Treeshrew	12	15	27	0.933	0.334	
Sundasciurus Iowi	Low's Squirrel	17	16	33	0.141	0.707	
Leopoldamys sabanus	Long-tailed Giant Rat	19	11	30	6.567	0.010	
Sundamys muelleri	Muller's Rat	14	2	16	14.538	0.000	
Echinosorex gymnura	Moon Rat	0	1	1	1.024	0.312	
Rattus exulans	Polynesian Rat	11	0	11	14.903	0.000	
Callosciurus prevostii	Prevost's Squirrel	0	1	1	1.024	0.312	
Tupaia gracilis	Slender Treeshrew	9	11	20	0.382	0.537	
Sundasciurus tenuis	Slender Squirrel	1	0	1	1.024	0.312	
Maxomys baedon	Small Spiny Rat	14	0	14	20.247	0.000	
Maxomys surifer	Spiny Rat	21	21	42	21.000	0.000	
Tupaia dorsalis	Striped Treeshrew	1	0	1	1.024	0.312	
Rheithrosciurus macrotis	Tufted Ground Squirrel	0	4	4	4.421	0.035	
Maxomys whiteheadi	Whitehead's Rat	20	1	21	34.381	0.000	

Table 1. Species reported and the number of plots at which they were detected for live trapping, camera trapping, and the two methods combined. The Chi-square test of independence and associated P-value compare the overall similarity of survey methods across plots.

Live trapping				Camera trapping			
	Cost (GBR)	Quantity	Total (GBP)		Cost (GBR)	Quantity	Total (GBP)
Initial equipment				Initial equipment			
Trap	2.91	150	436.89	Camera	256.31	59	15122.33
Pit tags	1.00	80	80.00	Locks	3.88	10	38.83
Reader	150.00	2	300.00	Security Posts	23.30	10	233.01
Other assorted equipment	300.00	1	300.00	Memory cards	6.41	118	756.12
				Batteries	1.55	1416	2199.61
				Chargers	19.42	12	233.01
				Silica gel	1.94	59	114.56
				Postage	800.97	1	800.97
				Other assorted equipment	300.00	1	300.00
		Total	1116.89			Total	19798.45
Field costs per 8 day survey				Field costs per 21 day survey			
Vehicle	15.53	8 days*	124.27	Vehicle	15.53	10 days**	155.34
Field labourer x4	97.09	8 days*	776.70	Field labourer x2	48.54	10 days**	485.44
		Total	900.97			Total	640.78
		Cost per day	1.34			Cost per day	0.24

Table 2. Cost expenditures for live trapping and camera trapping over the survey period for initial equipment and field costs (calculated for the surveying of one plot). Cost per day for live trapping is calculated by field costs/trap nights (trap nights = 96 (traps) x 7). Cost per day for camera trapping is calculated by field costs/trap nights (trap nights = 50×0.9 (assuming 10% failure of cameras) x 59 (traps))

^{*}Seven days trapping plus one for set up

^{**}Six days setup and four days take down

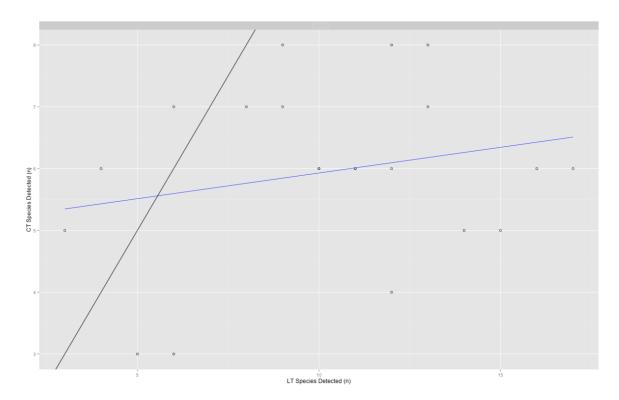


Fig.1. Scatterplot of species detected by live trapping and camera trapping at each plot. Blue line: linear regression. Black line: 1:1 line for comparison: plots above line – camera traps detected more species, plots below the line – live traps detected more species.

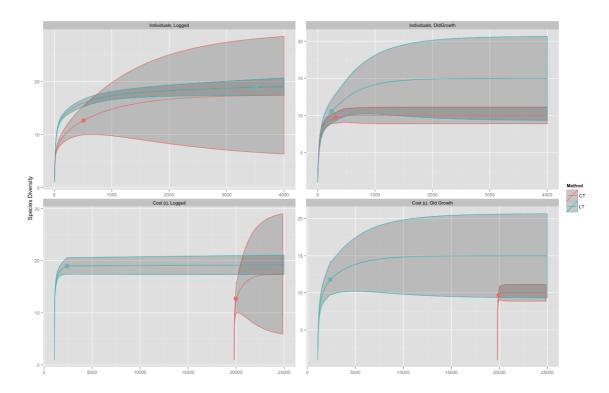


Fig 2. Individual-based and cost-based rarefied species accumulation curves describing the small mammal community richness in logged and old growth forest. The point on each curve is observed species richness, after which species richness is extrapolated. Shaded polygons denote 95% confidence intervals.

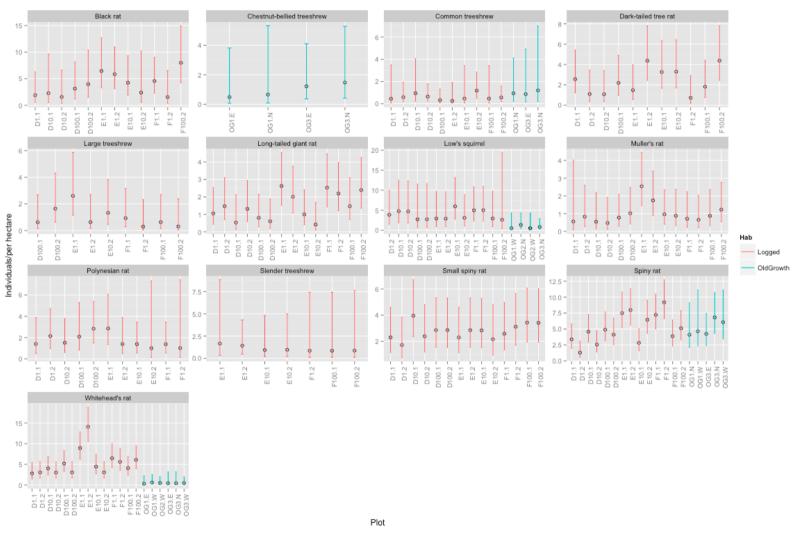


Fig.3. Density estimates (95% confidence intervals) per plot from live trapping of small mammal species in logged and old growth forest. 30

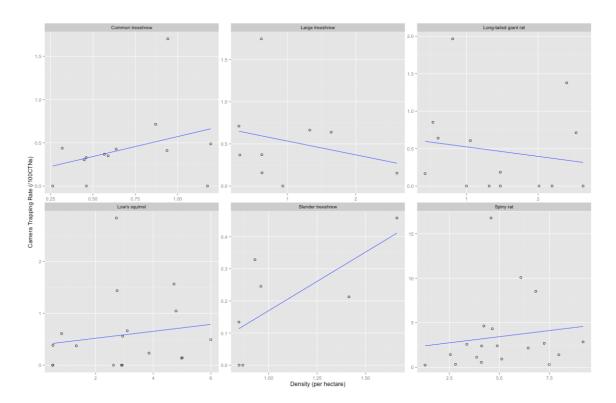


Fig.4. Density estimates correlated with camera trapping rates for each species.

Each point represents a plot in which the species was detected. Blue lines represent linear regression.