Robust Estimation of Snare Prevalence Within a Tropical Forest Context Using N-Mixture Models.

Hannah J. O'KELLY[1*], Marcus J. ROWCLIFFE[2], Sarah M. DURRANT[2] and E.J. MILNER-GULLAND[3]

1 The Wildlife Conservation Society (WCS) Cambodia Program, # 21, Street 21, Phnom Penh, Cambodia

2 The Zoological Society of London (ZSL), Institute of Zoology, Regent's Park, London NW1 4RY, UK

3 Department of Zoology and Merton College, Tasso Leventis Professor of Biodiversity, University of Oxford, Oxford OX1 3PS, U.K.

* Corresponding author **okellyhj@gmail.com**

Abstract

Hunting with snares is indiscriminate and wasteful, and this practice is currently one of the gravest threats to terrestrial vertebrates in the tropics. However, as snares are difficult to detect and often dispersed widely across large, inaccessible areas it is problematic to reliably estimate their prevalence and no standard survey methods exist. Conservation managers need reliable, timely, information on the spatio-temporal patterns of hunting and on responses to interventions, and we present an innovative sampling and analysis framework that allows for the rigorous estimation of snare detectability and 'abundance', but which can be feasibly implemented in challenging field contexts. This new approach was used to undertake a large-scale systematic snare survey in Keo Seima Wildlife Sanctuary, in Eastern Cambodia, and the resulting data were analysed using a novel application of N-mixture models. A range of environmental and management factors were examined as potential determinants of snare abundance and detectability, and proximity to the Vietnamese border was shown to be overwhelmingly the most influential factor. Snares were more common in the wet season rather than the dry season, and the detection probability of snares was shown to be low (~ 0.33), as predicted. No clear relationships between snaring levels, anti-poaching patrol effort and ungulates densities were evident from these data. There was clear evidence that certain factors, such as the percentage of dense forest cover, will exert confounding effects on both detectability and abundance, highlighting the critical need to take account of the imperfect detection when designing threat monitoring systems.

Key Words

snare; hunting; n-mixture models; detection probability; tropical forests; threat monitoring

1. Introduction

Illegal hunting, be it for local subsistence or to supply ever-expanding markets with meat, pets, trophies and other body parts, arguably constitutes the greatest current threat facing wild vertebrates in tropical Asia and Africa (Corlett 2007; Fa & Brown 2009; Harrison et al. 2016). Unsustainable hunting can have dire consequences not just in terms of causing species extirpations and degrading the ecological integrity of forest systems, but also through its impact on the livelihoods of the rural, often marginalised, people who depend on these resources (Milner-Gulland & Bennett 2003; Fa et al. 2016).

Traditional approaches to the monitoring poaching and other forms of illegal resource use (i.e. interview-based techniques, self-reporting, direct observation) all have methodological challenges associated with them (Gavin et al. 2010). This is largely due to the fact that offenders typically have strong incentives to conceal the true nature of their activities from investigators, potentially leading to severe and unquantifiable bias in estimates of the prevalence of illegal resource-use (Keane et al. 2008; Gavin et al. 2010). With the global roll-out of standardised law enforcement monitoring systems such as SMART, there has been a growing interest in threat data collected during routine patrols (i.e. encounters of infractions; e.g. Jachmann 2008; Linkie et al. 2015), and the use of such cheap and readily available data will undoubtedly continue to increase. However, as essentially a by-product of efforts to deter illegal activities, these data typically also contain severe biases which can limit their utility for threat monitoring purposes (Gavin et al. 2010; Keane et al. 2011).

Any attempt to estimate the prevalence of a given threat can be affected by the same two sources of bias which affect all ecological surveys, imperfect detection and unrepresentative spatial sampling (Williams et al. 2002). The importance of considering these potential biases when designing ecological monitoring programs has been repeatedly highlighted (Yoccoz et al. 2001; Legg & Nagy 2006; Nichols & Williams 2006) but these issues are equally applicable to the monitoring of threats such as hunting. Employing a probabilistic sampling strategy and investing in sufficient survey effort can ensure representativeness (Brashares & Sam 2005), but accounting for detection error can be more challenging. The problem of imperfect detection is of particular relevance to illegal hunting, not only because it precludes reliable monitoring of this threat, but also because a key factor in successful poaching deterrence is a high rate of detection (Leader-Williams & Milner-Gulland 1993; Hilborn et al. 2006). And yet, to our knowledge, there are no published studies which attempt to estimate the extent or impact of illegal hunting using systematic surveys which account for imperfect detection.

The development of flexible hierarchical models has greatly improved researchers' ability to simultaneously account for variation which is related to spatial or temporal variation in an underlying ecological process of interest (i.e. occurrence or abundance) and variation which is due to the imperfect observation of this process (i.e. detectability Royle & Dorazio 2008; Kéry & Royle 2016). One class of hierarchical models are the multinomial and binomial mixture models of Royle (2004 a,b), which to date have been most frequently used in the analysis of avian point count data, although they have also been employed in the study of mammal and amphibian populations (Mazerolle et al. 2007; Zellweger-Fischer et al. 2011). A natural extension of these methods is to adapt them for modelling observations of hunting rather than of wildlife.

We present a case study in which binomial mixture models, or 'N' mixture models, are used to generate a robust estimate of snaring prevalence in a protected area in Eastern Cambodia. As elsewhere in the tropics, wire snares are a common method of hunting in this region, as the equipment involved is affordable and easily accessible, and the technique is effective for a wide range of vertebrate species (Noss 1998; Becker et al. 2013). This form of hunting is particularly detrimental because in practice it is often indiscriminate and wasteful (Lindsey et al. 2011; Gray et al. 2017), and the use of snares is therefore illegal in Cambodia. However, the covert nature of this activity means that it is extremely difficult to detect perpetrators or snares, and consequently the enforcement of snaring prohibitions is challenging (Noss, 1998). Although some surveys have been undertaken in Africa (i.e. Wato et al. 2006; Lindsey et al. 2011; Becker et al. 2013) none of them address the detection issue, and almost no studies have been carried out in Southeast Asia (but see Linkie et al. 2015). This is despite the fact that hunting with snares represents one of the gravest threats to terrestrial biodiversity in the region (Gray et al. 2017). Without accurate measurement of such threats, managers cannot easily evaluate the success of conservation actions designed to reduce snaring levels, or design more effective interventions as a result (Hockings et al. 2000).

The aim of this study was to develop an approach which could reliably estimate the abundance and detectability of snares, but that could be implemented within a typically challenging tropical forest context. Our objectives were both methodological and relevant to management, and related both to the field component and the subsequent modelling process:

Objective 1. Develop an appropriate sampling design for a snare survey to produce data suitable for analysis within a hierarchical modelling framework. *Objective 2*. Analyse the resultant snare survey data using N-mixture models to generate a detectability-corrected spatially explicit index of snare abundance. *Objective 3*. Within this modelling framework, investigate *a priori* hypothesised relationships between a range of potential covariates and both snare detectability and snare abundance.

2. Methods

2.1 Methodological Framework

Any application of N-mixture models requires both spatial and temporal replication within the data (Royle 2004a, 2004b; Kéry et al. 2005), hence a sampling design was required which incorporated both multiple sites and repeated surveys of each site. In practical terms, although relatively numerous, snares are extremely difficult to detect (O'Kelly et al. 2017). They also tend to be aggregated in space at one scale (i.e. where one hunter operates) whilst also dispersed across a large survey area (i.e. the entirety of the protected area). Therefore, the sampling design necessarily involved a balance between maximising the efficiency of data collection and adhering to best practice in terms of scientific rigour.

N-mixture models are extensions of the Poisson generalized linear model (GLM) or generalized linear mixed model (GLMM), but they include an additional stochastic component that explicitly models the observation process (Kéry & Royle 2010, 2016). These models can produce estimates of abundance without the need for the identification of individuals, and they are particularly appropriate for scenarios where data are relatively sparse (Royle 2004a, 2004b). These models are also useful for investigating how both the abundance and detection processes vary as a function of both ecological and management factors (i.e. Chandler et al. 2009; Chandler & King 2011).

Our modelling approach incorporated two stages, the first of which examined covariates for which we had some clear *a priori* hypothesis regarding their relationship to abundance and/or detectability. The second phase involved including additional covariates in order to explore the relationship between threats (i.e. snaring rates), interventions (i.e. patrol effort) and impacts (i.e. wildlife densities). Whilst the relationships and potential causal linkages of the second stage are of fundamental interest to conservation managers, they are difficult to predict *a priori* or to interpret with any certainty.

2.2 Study Site

The Keo Seima Wildlife Sanctuary (KSWS) covers a 292,690ha mosaic of evergreen, semi-evergreen forest and deciduous forest in eastern Cambodia. Biodiversity values within KSWS are high, as it holds globally or regionally significant populations of elephants and wild cattle, and multiple species of primates, carnivores and large birds (Evans et al. 2012; O'Kelly et al. 2012).

The 20,000 people living near or within KSWS comprise both indigenous ethnic minorities and ethnic Khmer, the latter having arrived during a more recent wave of in-migration. Agriculture is the dominant livelihood activity but residents are also heavily forest dependent and a critical source of income for many families is tapping of liquid resin from *Dipterocarpus* trees, which takes place widely throughout the reserve (Evans et al. 2012). The most significant threat to key wildlife species in KSWS is over-hunting and several large mammal species have been extirpated from the area (O'Kelly et al. 2012). Populations of many other taxa have been drastically reduced by hunting with guns and, more commonly, snares, both of which are prohibited.

2.3 Sampling Design and Field Protocols

Sampling took place across the 187,983 ha core area of KSWS in 37 clusters of 12 x 1km^2 “sites”. Clustered sites formed a circuit around a set of permanent line transects used for long-term wildlife monitoring and positioned using a systematic design with a random starting point (O'Kelly et al. 2012). The cluster design maximised sampling efficiency but at the cost of inducing potential non-independence of sites within a cluster.

However, each cluster of sites was assumed to be spatially independent with respect to both hunter and prey movement during the study period. The distance between clusters was c.7km which is greater than the ranging distances of any of the target species and likely to be much further than the distances typically covered by hunters in this terrain (patches of <1 km2, HJOK pers obs).

Between February 2011 and February 2012, all 37 clusters were sampled over a two to four-day period, which ensured that sites were closed to changes in snare abundance over the course of the study. The majority of clusters (28) were surveyed by two field teams, over the same time period but working independently of one another. Nine clusters were surveyed by only one team due to logistical constraints. Teams walked a minimum of 2km per 1km^2 site, choosing routes likely to maximise the detection of snares, whilst also attempting to achieve maximum spatial coverage of each site.

Two main types of snare are common within KSWS; single snares (usually medium or large-sized and constructed using thick wire rope), and snare lines consisting of multiple smaller snares (typically constructed from much thinner wire, as is typically used for brake cables) set along a low drift fence constructed from bamboo and brushwood. The actual number of snares, and whether they are set, is clearly relevant with respect to mortality risk but during this study an observation corresponded to a snare “incident” regardless of the type or number of snares concerned. In terms of detectability, only the first snare in a drift line is important, as all others in the line will have a detection probability of close to 1.

The locations of all snare incidents encountered was recorded using GPS units, together with the number of snare(s), estimated age of snare(s), habitat type and evidence of any captures (i.e. live animals, carcasses, bones etc.). Cables and wires were removed from all snares, and anchor poles were cut, thus preventing future use of the structure.

3. Data Analysis

3.1 Binomial Mixture Models

The simplest of N-mixture models assumes that there are no changes in abundance over the survey period, in which case repeated counts (corresponding to visits by multiple survey teams in this case) within sample location *i* are treated as independent realizations of a binomial random variable with parameters N_i (local abundance) and p_i (detection probability). It is further assumed that N_i comes from some common distribution specified by parameters to be estimated from the data. The structure of these models is described in detail in Royle (2004a, b) and Kéry et al. (2005).

N-mixture models, like other classes of hierarchical model, can accommodate a range of covariates hypothesised to influence both abundance and detection probability. Site-level covariates are related to conditions which remain constant across surveys (e.g. forest type). Observation or survey-level covariates are related to individual surveys and thus may differ or remain the same across surveys (e.g. precipitation). The effects of covariates on abundance and detectability are modeled linearly in a GLM fashion via a log-link function. All models in this analysis were fitted using the package “unmarked” (Fiske & Chandler 2011) in R version 2.14.0 (R Core Team 2012). The fitting function “pcount” within the unmarked package fits the N-mixture model of Royle (2004).

3.2 Modelling Process

A wide range of factors are likely to influence the abundance, distribution, and detectability of snares. A full list of the potential covariates considered is given in Table 1A (supporting material). Correlations between covariates were examined to eliminate redundancy and all covariates were standardized. Route length was log-transformed and all other covariates were transformed into standard normal deviates. For this analysis, we specified a Poisson mixture distribution to model latent snare abundance. We used parametric bootstrapping to evaluate the goodness-of-fit of the final set of selected models using chi-square and Freeman Tukey fit statistics.

Given the complexity of the study system, we focused on a limited set of candidate models with the intension of avoiding over-parameterisation (Johnson & Omland 2004). We used a multi-step process to investigate *a priori* hypotheses on factors affecting abundance and detectability of snares, and to investigate additional relationships. For model selection, we used a ranking system based on Akaike's Information Criterion (AIC) and ΔAIC (assuming models with ΔAIC <2 are broadly equivalent in terms of fit).

In step one, we modelled snare abundance as a function of site-level covariates (% dense forest cover, terrain ruggedness, season, distance to village, distance to patrol station, distance to reserve boundary, distance to international border). Quadratic effects were included where non-linearity was expected (i.e. as a function of distance to village and terrain ruggedness) as was an offset using log-transformed effort (km walked) per site. The best fitting models were selected to take forward to the next step.

In step two, we modelled covariates hypothesised to affect detection probability. These included the site-level covariate of proportion of dense forest cover, which remained constant across visits, and the survey-level covariates of relative climb and survey effort which were specific to a visit. Top-ranked models selected from step one were extended to include all combinations of these covariates.

In step three, we examined models containing covariates that theoretically may affect abundance but for which the functional relationship between variables is likely to be of a more complex nature. The covariates considered during this phase included ungulate densities (distance sampling-derived density estimates from line transects within each cluster) and various of measures of anti-poaching patrol effort (km patrolled on foot and motorbike). Finally, we used the top-ranking models to create spatially explicit predictions of detectability-corrected snare abundance across the entire core area, based on known covariate values.

4. Results

4.1 Snare Encounters and model selection

During the 2,200km of search effort across the 440km^2 survey area, 140 snaring incidents were encountered (64 single snares and 76 snare lines) (Figure 1). The sites with one or more encounters (ranging between 1-6 per site) were dispersed across 18 of the 37 clusters. Over 1,300 wire/cables were removed by survey teams and all snare lines encountered were destroyed.

For the abundance component of the modelling process, the top four models (ΔAIC <2) included dense forest, distance to reserve boundary, distance to international border, distance to village, and season (Table 2A supporting material). These models were taken forward to step two of the process.

When all combinations of these detection-related covariates were added to the models selected above, AIC ranking resulted in a further four top models (Table 2A supporting material). All of these models were taken forward to the more exploratory stage of the analysis described below. Goodness-of-fit statistics are provided in Table 3A (supporting material).

In the final phase of the modelling process the inclusion of covariates related to patrol effort generally had a negative effect on snare abundance but only minimally improved model fit (Table 4A supporting material) The inclusion of covariates relating to animal density generally did not improve model fit as measured by AIC (Table 4A supporting material). Therefore, the top-ranking model from step two was used to create spatial prediction of snare abundance based upon the known range of influential covariates (see section 4.3).

4.2 Estimates of Detectability and Abundance

When applied to avian point count data, for which they were originally developed, N-mixture models produce estimates of the average abundance of birds per sample location. In this study, given the use of survey effort in km as an abundance offset, abundance can be interpreted as the expected number of snare incidents per 1km surveyed. Since the width of the survey routes was not fixed, the effective area sampled is unknown and expected density of snares per site cannot be calculated. In addition, because counts corresponded to snare incidents rather than actual numbers of snares, the resultant measure can be most appropriately viewed as an index of snare abundance.

None of the covariates tested at step three of the modelling process improved model fit significantly and hence we proceeded with the top-ranked models from step two (Table 1). For each of these highest-ranking models, back-transformed estimates of expected probability of detection and indices of abundance when all the relevant covariates are fixed at their mean are given in Table 5A. Abundance estimates for models containing covariates differ substantially from the null model, which treats abundance and detectability as constant. Estimates of detectability remain relatively consistent across models, at either around 0.28 or 0.36, indicating that on average only one snare incident is detected for every three that could potentially be detected.

4.3 Predicted Snare Distribution

Spatially explicit predictions of detectability-corrected snare abundance across the entire core area are mapped in Figure 2, based on the best model from step 2 (Table 1). Snaring is heavily concentrated in the Southern sector of the site, close to the Vietnamese border and around villages and patrol stations. North of the main road, levels of snaring drop off rapidly and a large proportion of the Northern sector of the reserve appears to be virtually devoid of snares. It is worth noting that the Southern sector of the reserve is also the area with the highest proportion of dense evergreen forest whereas the Northern sector is dominated by open dry forest (Figure 1).

4.4 Covariate Effects on Abundance and Detectability

The inclusion of covariates within models allows us to quantify relationships between abundance and key environmental gradients. We can examine predictions of abundance for any of the covariates individually, by specifying a range for each of the covariates of interest whilst fixing all other covariates at their mean value.

Using this approach, predicted estimates of snare abundance in the dry season are approximately one third lower than equivalent estimates for the wet season. In terms of forest type, a typical location has just under 50% dense forest cover, and snare abundance is extremely low in sites with below average cover. Above this average level, predicted abundance increases rapidly as the proportion of dense forest cover increases, and predictions for sites with full cover are over six times higher than for an average site. With respect to proximity to villages, predictions of snare abundance initially decrease as distance to village increases, up to approximately seven kilometres, after which they begin to increase with greater distances from villages. At 13 kilometres from a village, snare abundance is predicted to be three times higher than the average, but abundance is at its highest around the outskirts of villages, where it is predicted to be four times higher than average. Snare abundance decreases both with distance to the reserve boundary and with distance to the international border. However, whereas predicted snare abundance within one kilometre of the reserve boundary is over just 25% higher than the average, predicted abundance within one kilometre of the international boundary is greater than the average by two orders of magnitude, indicating the stark difference between the strength of these effects. When terrain ruggedness is included in models, predictions of snare abundance increase as terrain ruggedness increases, but differ from the average by less than 10%. Surprisingly, snare abundance appears to decrease with distance to patrol station. However, this effect is relatively weak, with predicted abundance at one kilometre from a station just 20% higher than the average, whilst predictions at the maximum distance of 26 kilometres from a station are 35% lower than the average.

In the more exploratory models, predicted snare abundance for a site with no patrol visits is less than 5% higher than predicted abundance for a site with the average number of patrol visits (3.5). There was also a negative relationship between wild cattle and wild pig density and snare abundance, whereas the relationship between muntjac density and snare abundance was positive.

The same approach can be used to explore how both site level and survey level covariates affect detectability. Detectability decreased with increasingly dense forest cover, such that predicted detectability in sites with 10% forest cover is seven times higher than a site with 100% forest cover. A steeper relative slope on the route surveyed also reduced detectability such that predictions of detectability on the flattest routes are up to 10 times higher than for the steepest routes surveyed. Finally, route length had a positive relationship with detectability; for example, predictions of detectability for routes of three kilometres were 20% higher than for routes of two kilometres.

5. Discussion

5.1 Determinants of Snare Detectability and Abundance

The relationships between snare abundance and dense forest cover, terrain ruggedness, distance to boundary, and distance to international border corresponded to *a priori* predictions, as did the relationships between detectability and dense forest cover and relative climb of survey routes.

The importance of dense forest cover in influencing snare placement is unsurprising, given that hunters rely on this type of forest to construct and conceal snares, and that wildlife populations also depend heavily on the availability of this habitat type. However, the fact that dense forest negatively affects the detectability of snares, whilst simultaneously exerting a positive effect on snare abundance, demonstrates how crucial it is to account for imperfect detection in these types of surveys in order to avoid biased results.

Proximity to population centres and markets are a major determinant of hunting occurrence and in this case we see the overwhelming influence of the location of the Cambodian/Vietnamese border on snare abundance. This can be attributed to the extremely high demand on the Vietnamese side (Shairp et al. 2016; Sandalj et al. 2016), which is driving an influx of hunters into KSWS from across the border (WCS Cambodia Program, unpublished data).

The relationship between snare abundance and distance to village illustrates how multiple processes can influence snare distribution at different scales. Snaring levels are high in the southern part of the reserve, close to the Vietnamese border, and also close to the larger settlements located in the southeastern and southwestern corners of the reserve. However, several other snaring patterns are also evident. Reserve residents commonly set snares around the outskirts of their fields (to combat crop raiding), in the immediate vicinity of the village. When residents go into the forest specifically to hunt, the distance they travel is presumably limited by several factors including their mode of transport (i.e. on foot or by motorbike) and their food and/or fuel supplies. Nevertheless, some residents travel considerable distances from their villages in order to visit their resin trees, and in these instances, they may spend several days or even weeks at temporary “resin camps” and they will set snares during this time (WCS Cambodia Program, unpublished data). This gives rise to a complex, non-linear relationship between snare abundance and distance to village.

Prior to this study, conflicting hypotheses existed regarding the seasonality of snaring within this landscape. The predominant theory was that snaring levels increased in the dry season when access to the reserve is easier and wildlife populations tend to be aggregated around water and food sources. However, other local reports had suggested that hunters focused their efforts during the wet season, to take advantage of the greater cover afforded by dense foliage and damp ground, and possibly also a reduction in anti-poaching patrol effort, as a well as a gap in the local agricultural calendar. The results of this survey indicate that hunting levels are appreciably higher during the wet season.

The apparent negative relationship between snare abundance and distance to patrol stations may seem counter-intuitive but it is important to note that patrol stations within the KSWS have been placed strategically, in locations where threat levels are known to be particularly acute and/or in locations known to be particularly important for key wildlife species. Indeed, areas of perceived high animal density are precisely the areas likely to be targeted both by hunters *and* by management and enforcement agencies. Levels of hunting may remain proportionally higher in these areas despite the presence of a station (although presumably they would be lower than pre-station levels). Alternatively, the presence of a station may afford localised protection which allows prey populations to recover, only for them to be subsequently targeted by hunters who are aware of this recovery.

Various types (i.e. vehicle, motorbike and foot) and combinations of patrol effort were tested as potentially useful covariates, but these data provided little support for patrol effort as an important predictor of snare abundance. The complex relationship between enforcement effort and illegal activities has been highlighted within the literature (Keane et al. 2008, 2011) and may explain in part the apparent lack of any obvious deterrent effect. However, it seems likely that these results may also be related to the spatial and temporal scale of this study. Due to limited patrol coverage by law enforcement teams during the study period, a large proportion of survey sites had no patrol effort associated with them. This was particularly pronounced in the case of foot patrols, which were only recorded in less than 10% of survey sites, despite being the most efficient type of patrol to locate snares (WCS Cambodia Program, unpublished data). Furthermore, temporal lags of varying lengths may occur between patrols and any subsequent deterrent effect, and the duration of any such effect is unknown. The spatial scale at which any deterrent effect will operate at is also unknown and is likely to be dependent on a multitude of factors, such as patrol type and habitat characteristics (Keane et al. 2011). In this study the unit of analysis was a one km square site and patrol effort was calculated as the number of patrols deployed within that site over a one year period preceding the survey. This seemed a realistic scale at which a deterrent effect might be evident, but a wide range of alternatives spatial and temporal specifications could have been chosen.

The relationship between snaring levels and wildlife population densities is of fundamental interest to conservation managers but care must be taken when attempting to demonstrate causal linkages between the two. Relationships are likely to be spatially and temporally scale dependant, as above, and may be obscured by confounding variables. For example, an area with apparently low levels of snaring and low wildlife densities may have naturally fewer animals due to some unmeasured habitat characteristics, thus rendering it unappealing to prospective hunters. However, this same scenario could be as a result of overhunting in area which previously had higher wildlife densities, which were then depleted through hunting, eventually causing hunters to shift their activities to other more productive areas. Further complexity can arise when wildlife abundance and hunting levels are determined by the same factors. In the KSWS both wildlife densities and hunting levels are high in the southern section of the reserve, which is the area closest to the international border and also the area with the greatest proportion of dense forest. Proximity to the border may directly influence snaring levels but it does not directly influence wildlife abundance, whereas the presence of dense forest is likely to be a direct determinant of snare occurrence *and* wildlife occurrence.

Although the modelling results yield little support for individual species densities as significant predictors of snare abundance, the direction of effects within models is of interest and appears to corroborate other sources of information, including biological monitoring data and field observations. The positive relationship between snare abundance and red muntjac density does suggest that hunters purposefully set snares in areas of higher muntjac abundance. This species is known to be a preferred prey choice for hunters and likely experiences high hunting pressure (Drury 2005; O'Kelly et al. 2012). Despite this, muntjac remain moderately abundant in comparison to other ungulate species, there is no evidence of a decline apparent from biological monitoring data and they persist widely throughout the reserve (O'Kelly et al. 2012). When taken together, the temporal trend data for this species and the spatial relationships inferred from the snare survey results appear to indicate a relative resilience to hunting pressure, a supposition which has been suggested in other studies (Steinmetz et al. 2010).

Including wild pig and cattle densities as covariates within models did not improve model fit, but it did suggest a negative relationship between these species' densities and snare abundance. Wild pig is one of the commonest species to appear in hunting records (FA/WCS, unpublished data) and biological monitoring data suggest that, whilst still relatively healthy, this population is undergoing a decline (O'Kelly et al. 2012). The wild cattle population within KSWS is small, declining, and potentially particularly vulnerable to the threat of hunting (O'Kelly et al. 2012). Although it is likely that snaring is having a negative impact on wild pig and cattle populations, the evidence provided by this study is inconclusive and further work is needed to establish to what extent snaring is contributing to these declines.

5.2 Methodological Implications

Previous studies which utilise snare encounter data routinely collected by law enforcement teams (e.g. Becker et al. 2013; Linkie et al. 2013) are limited by the fact that law enforcement patrols are reactive and strongly non-random in nature, meaning that such data are inherently biased (Keane et al. 2008). Studies which focus on snares but ignore the critical issue of detectability (e.g. Wato et al. 2006; Lindsey et al. 2011; Becker et al. 2013) risk yielding unreliable results because they rely on biased estimators of occurrence or abundance (MacKenzie et al. 2002). Our approach addresses these issues and generates robust estimates whilst also remaining feasible to implement in difficult field conditions.

The modelling process described here allows us to disentangle potentially confounding effects on both detectability and abundance, such as forest cover in this study, that could otherwise lead to misleading results. It also helps us to better understand the spatial dynamics and causal mechanisms underlying snaring, by offering a flexible framework within which to model the often complex and non-linear relationships between detectability and occurrence and a range of natural and anthropogenic covariates. Within this study the effect of distance to village on snare abundance provides a good example of such a relationship.

Despite the potential of the approach described here, there are still some methodological issues which require further investigation. The level of temporal replication in this study was minimal, primarily due to logistical constraints. Increasing the number of site visits (or using more simultaneous observers) in future surveys might allow for improved modelling of detection probability. In addition, our sampling design was based on clusters of sites, again due to logistical constraints, and this may have resulted in some spatial non-independence. The use of covariates helps to address this issue and where models fit well as indicated by GoF tests, as in this study, the dependence structure may not be a major concern. Future studies should also consider explicitly modelling how the characteristics of an individual snare incident might affect detection probability (i.e. single snares, short snare lines, long snare lines; type of wire/cable used; age of snares; whether snares or set or not etc.).

5.3 Management Implications

This approach allows us to produce detectability-corrected predictive maps of snare abundance and also provides a means of evaluating how changes in key covariates might potentially affect hunting prevalence and detection probability. Both of these aspects offer considerable management utility as they can be used to guide current and future interventions in a more targeted way, in the expectation of improving management effectiveness.

A survey of the type described here could be repeated periodically to estimate temporal change in snaring patterns and this would allow managers to monitor the actual impact of enforcement interventions, and to assess the relative success of different anti-snaring strategies. However, it is acknowledged that this type of survey entails a significant investment of resources, which may have to be diverted away from already severely overstretched law enforcement regimes.

These law enforcement regimes may already involve the collection of snare encounter data as part of routine patrols, particularly as standardised systems for law enforcement monitoring such as SMART are rapidly becoming the global standard (SMART Partnership 2015). The appeal of using increasingly ubiquitous SMART data to monitor threats such as hunting is obvious. However, the analysis and interpretation of such data is fraught with difficulties (Gavin et al. 2010; Keane et al. 2011), and there is an urgent need to complement it with a better understanding of the underlying biases. The type of independent threat assessment undertaken in this study is crucial to this enterprise, as it can provide a means of validating and calibrating SMART data-derived measures.

6. Conclusion

In KSWS, as elsewhere, managers require reliable, real-time information on spatio-temporal patterns of hunting in order to implement effective anti-poaching measures. Disentangling the multiple processes which underlie apparent patterns of snare abundance presents significant methodological challenges and implementing data collection activities on the ground entails a raft of practical considerations. In this study, we have presented an integrated sampling methodology and analysis framework which offers considerable potential for more reliable estimation of the extent and distribution of illegal resource use, despite the often cryptic and highly variable nature of these activities. Although resources for assessing the status and trends in threats such as hunting are typically limited, often a variety of sources of relevant data may exist (including high quality data from biological monitoring and basic law enforcement monitoring data). Multiple data sources can facilitate triangulation (Gavin et al. 2010) and having some more robust measures of threat can both contribute to, and validate, this process of triangulation. We would contend, therefore, that periodic independent threat assessments of this nature represent a necessary and worthwhile investment of scarce conservation resources, particularly if carried out relatively infrequently.

Acknowledgements

We would like to gratefully acknowledge the support of the Wildlife Conservation Society (WCS) Cambodia Program during this study. We would especially like to thank Nut Meng Hor and the KSWS biological monitoring team for their assistance with data collection.

This research was funded through a NERC-ESRC studentship, with additional support from Imperial College London and the WCS Cambodia Program.

References

Becker M, McRobb R, Watson F, Droge E, Kanyembo B, Murdoch J, Kakumbi C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biological Conservation **158**:26–36.

Brashares JS, Sam MK. 2005. How Much is Enough? Estimating the Minimum Sampling Required for Effective Monitoring of African Reserves. Biodiversity and Conservation **14**:2709–2722.

Chandler RB, King DI. 2011. Habitat quality and habitat selection of golden-winged warblers in Costa Rica: an application of hierarchical models for open populations. Journal of Applied Ecology **48**:1038–1047.

Chandler RB, King DI, Chandler CC. 2009. Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. Forest Ecology and Management **258**:1669–1676.

Corlett RT. 2007. The Impact of Hunting on the Mammalian Fauna of Tropical Asian Forests. Biotropica **39**:292–303.

Drury R. 2005. Wildlife use and trade in the Seima Biodiversity Conservation Area, Mondulkiri, Cambodia. MSc Thesis. University College London.

Evans TD, O'Kelly HJ, Men Soriyun, Nut Menghor, Pet Phaktra, Sorn Pheakdey. 2012. Seima Protection Forest, Cambodia. Pages 157–186 in T. C. H. Sunderland, J. Sayer, and Hoang Minh-ha, editors. Evidence-based conservation: lessons from the lower Mekong. Earthscan Publications.

Fa JE, Brown D. 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. Mammal Review **39**:231–264.

Fa JE, van Vliet N, Nasi R. 2016. Bushmeat, food security, and conservation in African rainforests. In Tropical Conservation: Perspectives on Local and Global Priorities.

Fiske I, Chandler R. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software **43**:1–23.

Gavin MC, Solomon JN, Blank SG. 2010. Measuring and Monitoring Illegal Use of Natural Resources. Conservation Biology **24**:89–100.

Gray TNE, Lynam AJ, Seng T, Laurance WF, Long B, Scotson L, Ripple WJ. 2017. Wildlife-snaring crisis in Asian forests. Science **355**:255.2-256.

Harrison RD, Sreekar R, Brodie JF, Brook S, Luskin M, O'Kelly H, Rao M, Scheffers B, Velho N. 2016. Impacts of hunting on tropical forests in Southeast Asia: Hunting in Tropical Forests. Conservation Biology **30**:972–981.

Hilborn R, Arcese P, Borner M, Hando J, Hopcraft G, Loibooki M, Mduma S, Sinclair ARE. 2006. Effective Enforcement in a Conservation Area. Science **314**:1266.

Hockings M, Stolton S, Dudley N. 2000. Evaluating Effectiveness: A Framework for Assessing the Management of Protected Areas. IUCN - World Conservation Union, Gland, Switzerland.

Jachmann H. 2008. Illegal wildlife use and protected area management in Ghana. Biological Conservation **141**:1906–1918.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. Trends in ecology & evolution **19**:101–108.

Keane A, Jones JPG, Edwards-Jones G, Milner-Gulland EJ. 2008. The sleeping policeman: understanding issues of enforcement and compliance in conservation. Animal Conservation **11**:75–82.

Keane A, Jones JPG, Milner-Gulland EJ. 2011. Encounter data in resource management and ecology: pitfalls and possibilities. Journal of Applied Ecology **48**:1164–1173.

Kéry M, Royle JA. 2010. Hierarchical modelling and estimation of abundance and population trends in metapopulation designs. Journal of Animal Ecology **79**:453–461.

Kéry M, Royle JA. 2016. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1:Prelude and Static Models. Elsevier Science.

Kéry M, Royle JA, Schmid H. 2005. Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models. Ecological Applications **15**:1450–1461.

Leader-Williams N, Milner-Gulland EJ. 1993. Policies for the Enforcement of Wildlife Laws: The Balance between Detection and Penalties in Luangwa Valley, Zambia. Conservation Biology **7**:611–617.

Legg CJ, Nagy L. 2006. Why most conservation monitoring is, but need not be, a waste of time. Journal of Environmental Management **78**:194–199.

Lindsey P a., Romañach S s., Tambling C j., Chartier K, Groom R. 2011. Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. Oryx **45**:96–111.

Linkie M et al. 2013. Cryptic mammals caught on camera: Assessing the utility of range wide camera trap data for conserving the endangered Asian tapir. Biological Conservation **162**:107–115.

Linkie M, Martyr DJ, Harihar A, Risdianto D, Nugraha RT, Maryati, Leader-Williams N, Wong W-M. 2015. Safeguarding Sumatran tigers: evaluating effectiveness of law enforcement patrols and local informant networks. Journal of Applied Ecology 52:851–860.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248–2255.

Mazerolle MJ, Bailey LL, Kendall WL, Royle JA, Converse SJ, Nichols JD. 2007. Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies. Journal of Herpetology **41**:672–689.

Milner-Gulland EJ, Bennett EL. 2003. Wild meat: the bigger picture. Trends in Ecology & Evolution **18**:351–357.

Nichols JD, Williams BK. 2006. Monitoring for conservation. Trends in Ecology & Evolution **21**:668–673.

Noss AJ. 1998. The Impacts of Cable Snare Hunting on Wildlife Populations in the Forests of the Central African Republic. Conservation Biology **12**:390–398.

O'Kelly HJ, Evans TD, Stokes EJ, Clements TJ, Dara A, Gately M, Menghor N, Pollard EHB, Soriyun M, Walston J. 2012. Identifying Conservation Successes, Failures and Future Opportunities; Assessing Recovery Potential of Wild Ungulates and Tigers in Eastern Cambodia. PLoS ONE **7**:e40482.

O'Kelly HJ, Rowcliffe JM, Durant SM, Milner-Gulland EJ. 2017. Experimental Estimation of Snare Detectability Using Mixture Models. In review.

R Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org (accessed October 10, 2011).

Royle JA. 2004a. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. Biometrics **60**:108–115.

Royle JA. 2004b. Generalized estimators of avian abundance from count survey data. Animal Biodiversity and Conservation **27**:375–386.

Royle JA, Dorazio RM. 2008. Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities. Academic Press.

Sandalj M, Treydte AC, Ziegler S. 2016. Is wild meat luxury? Quantifying wild meat demand and availability in Hue, Vietnam. Biological Conservation **194**:105–112.

Shairp R, Veríssimo D, Fraser I, Challender D, MacMillan D. 2016. Understanding Urban Demand for Wild Meat in Vietnam: Implications for Conservation Actions. PLOS ONE **11**:e0134787.

SMART Partnership. 2015. Annual Report. Available from smartconservationtools.org.

Steinmetz R, Chutipong W, Seuaturien N, Chirngsaard E, Khaengkhetkarn M. 2010. Population recovery patterns of Southeast Asian ungulates after poaching. Biological Conservation **143**:42–51.

Wato YA, Wahungu GM, Okello MM. 2006. Correlates of wildlife snaring patterns in Tsavo West National Park, Kenya. Biological Conservation **132**:500–509.

Williams BK, Nichols JD, Conroy MJ. 2002. Analysis and Management of Animal Populations, 1st edition. Academic Press, San Diego, California, USA.

Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution **16**:446–453.

Zellweger-Fischer J, Kéry M, Pasinelli G. 2011. Population trends of brown hares in Switzerland: The role of land-use and ecological compensation areas. Biological Conservation **144**:1364–1373.