



A Novel Approach to Assessing the Prevalence and Drivers of Illegal Bushmeat Hunting in the Serengeti

ANA NUNO,* NILS BUNNEFELD,† LOIRUCK C. NAIMAN,‡ AND E. J. MILNER-GULLAND*

*Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot SL5 7PY, United Kingdom, email ana.nuno08@imperial.ac.uk

†School of Natural Sciences, University of Stirling, Scotland FK9 4LA, United Kingdom

‡Frankfurt Zoological Society, P.O. Box 14935, Arusha, Tanzania

Abstract: *Assessing anthropogenic effects on biological diversity, identifying drivers of human behavior, and motivating behavioral change are at the core of effective conservation. Yet knowledge of people's behaviors is often limited because the true extent of natural resource exploitation is difficult to ascertain, particularly if it is illegal. To obtain estimates of rule-breaking behavior, a technique has been developed with which to ask sensitive questions. We used this technique, unmatched-count technique (UCT), to provide estimates of bushmeat poaching, to determine motivation and seasonal and spatial distribution of poaching, and to characterize poaching households in the Serengeti. We also assessed the potential for survey biases on the basis of respondent perceptions of understanding, anonymity, and discomfort. Eighteen percent of households admitted to being involved in hunting. Illegal bushmeat hunting was more likely in households with seasonal or full-time employment, lower household size, and longer household residence in the village. The majority of respondents found the UCT questions easy to understand and were comfortable answering them. Our results suggest poaching remains widespread in the Serengeti and current alternative sources of income may not be sufficiently attractive to compete with the opportunities provided by hunting. We demonstrate that the UCT is well suited to investigating noncompliance in conservation because it reduces evasive responses, resulting in more accurate estimates, and is technically simple to apply. We suggest that the UCT could be more widely used, with the trade-off being the increased complexity of data analyses and requirement for large sample sizes.*

Keywords: compliance, indirect questioning, poaching, sensitive questions, UCT, uncertainty, unmatched-count technique

Una Aproximación Novedosa para Evaluar la Prevalencia y Factores de la Cacería Ilegal en el Serengeti

Resumen: *Evaluar los efectos antropogénicos sobre la biodiversidad, identificar los conductores del comportamiento humano y motivar el cambio conductual son el núcleo de la conservación efectiva. Sin embargo el conocimiento sobre el comportamiento de la gente está comúnmente limitado porque el verdadero alcance de la explotación de los recursos naturales es difícil de comprobar, sobre todo si es ilegal. Para obtener estimados de comportamiento rompe-reglas se ha desarrollado una técnica con la cual realizar preguntas delicadas. Usamos esta técnica, técnica de conteos sin equivalentes (TCSE), para obtener estimados de caza furtiva, para determinar la motivación y la distribución estacional y espacial de la caza furtiva, y para caracterizar los hogares dedicados a la caza furtiva en el Serengeti. También evaluamos el potencial de sesgos de encuestas con base en las percepciones de entendimiento, anonimato y malestar de los encuestados. El 18% de de los hogares admitieron estar involucrados en la caza. La caza ilegal era más probable en hogares con trabajos estacionales o de tiempo completo, menor tamaño y mayor residencia en la aldea. La mayoría de los encuestados encontró las preguntas de la TCSE fáciles de entender y no tuvieron problemas en contestarlas. Nuestros resultados sugieren que la caza furtiva permanece con una amplia extensión en el Serengeti y las*

Paper submitted September 10, 2012; revised manuscript accepted April 10, 2013.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

actuales fuentes alternativas de ingreso pueden no ser lo suficientemente atractivas para competir con las oportunidades proporcionadas por la caza. Demostramos que la TCSE es muy adecuada para investigar la inconformidad en la conservación porque reduce las respuestas evasivas, resultando en estimados más acertados y técnicamente es fácil de aplicar. Sugerimos que la TCSE puede ser usada más ampliamente, aunque el incremento en la complejidad del análisis de los datos y el requerimiento de tamaños de muestra grandes pueden ser un inconveniente.

Palabras Clave: caza furtiva, conformidad, cuestionamientos indirectos, incertidumbre, preguntas delicadas, técnica de conteos sin equivalente (TCSE)

Introduction

Illegal behavior, such as poaching and poisoning of wild animals, is common worldwide and threatens biological diversity in many terrestrial and aquatic ecosystems (Keane et al. 2008; Mateo-Tomás et al. 2012). The first steps in devising effective strategies to reduce illegal behavior are to assess its extent and nature and to identify those who are not in compliance. However, the true extent of illegal activities is hard to quantify due to people's fear of prosecution and the cryptic nature of the behavior (Gavin et al. 2010). Illegal behavior is thus a frequent source of uncertainty that affects management decisions and compromises evaluations of conservation interventions (Mateo-Tomás et al. 2012). Effective conservation planning therefore requires use of methods that detect and quantify illegal activities accurately.

A number of methods have been used to measure and monitor illegal resource use, such as law-enforcement records, market surveys, and self-reporting (Gavin et al. 2010). The choice of method depends on the type of information being sought, budget, capacity, and the nature of the illegal behavior (Gavin et al. 2010). Direct questioning is generally considered a cost-effective method to assess the harvest of natural resources. However, interviewees may not be willing to discuss participation in illegal or sensitive activities (e.g., taboo activities) and may refuse to answer survey questions, which leads to a nonrandom group of respondents, or lie to project a favorable image of themselves (social desirability bias) (St. John et al. 2010).

Indirect questioning techniques have been developed that minimize these sources of error in surveys. These techniques aim to increase respondent willingness to answer and reduce bias by making it impossible to directly link incriminating data to an individual (Warner 1965). They have been applied, for example, in surveys on racial prejudice (Blair & Imai 2012) and illegal immigration (GAO 2007). St. John et al. (2010) used randomized response technique (RRT) to estimate rule-breaking among fly fishers and has called for its wider application. Apart from RRT, applications of indirect questioning techniques are limited in conservation (but see St. John et al. 2010), and there is little understanding of their effectiveness at minimizing question sensitivity and increas-

ing perceived anonymity. Trade-offs between question complexity and respondents' understanding deserve further consideration, particularly given that in developing countries conservation interventions often take place in predominately illiterate communities.

One of the illegal behaviors of concern, for which indirect questioning may be useful, is poaching. Quantifying poaching helps in targeting conservation interventions, assessing effects, and determining the costs of conservation (Mduma et al. 1998; Nielsen 2006), but its illegal nature makes this a particularly difficult task. For example, the Serengeti ecosystem encompasses some of the largest herbivore and carnivore populations in the world, and poaching is considered a major driver of changes in wildlife abundance (Hilborn et al. 2006; Sinclair et al. 2008). Bushmeat is widely consumed by local communities surrounding protected areas in the Serengeti, where hunting is conducted for subsistence and to generate cash (Loibooki et al. 2002; Johannesen 2005). People are generally aware of law enforcement and that hunting is conducted illegally (Bitanyi et al. 2012). Because of the sensitive nature of hunting in this area, given the potential repercussions, there is enormous uncertainty surrounding the prevalence and distribution of poaching, incentives to poach, and socioeconomic characteristics of the people involved. It is estimated that 8–57% of households in the western Serengeti engage in bushmeat hunting, and this percentage differs greatly among studies (Table 1).

The general drivers of poaching range from economic incentives, to lack of knowledge of laws, to tradition, and fairness (see Keane et al. [2008] for a review). Previous studies in the Serengeti report the cultural, socioeconomic, seasonal, and spatial factors that are associated with illegal bushmeat hunting (Table 2). The information about poaching households presented in these studies derives from interviews with arrested hunters, is self-reported through direct questions, or relies on dietary recall. Some of the information on who engages in hunting is contradictory. The potential relations between hunting and alternative sources of income and protein, as well as demographic variables, are particularly important to understand because this information should be used to design interventions to control bushmeat hunting.

Table 1. Estimated prevalence of bushmeat hunting by communities surrounding the Serengeti National Park in previous studies.^a

<i>Prevalence (% of households hunting)</i>	<i>No. households surveyed</i>	<i>No. villages sampled</i>	<i>Comments by authors</i>	<i>Reference</i>
8	590	8	"Hunting may well exceed the levels reported [which can] probably be attributed to the contentious nature of the issue and the fear of repercussion."	Kaltenborn, Nyahongo & Tingstad 2005
9	421	8	"Thirty-seven households admitted to poaching . . . Poaching households reported killing 4.8 wildebeest in the last 12 months compared to 0.4 wildebeest per non-poaching household."	Knapp 2007
10	477	10	"The collected data needs to be treated cautiously, because we may have been lacking important information due to fear from respondents."	Mfunda & Røskaft 2010
27	297	6		Johannesen 2005
29	715	24	"Individuals in households were asked if they were involved in hunting . . . Many respondents chose not to answer (155 out of 715 responded)."	Campbell et al. 2001
32	300	10	"Respondents were not asked whether they participated in illegal hunting, but many voluntarily claimed to be involved." "More group respondents than individual respondents claimed to be hunters, demonstrating that results can be influenced by the methods."	Loibooki et al. 2002

^aData obtained through direct questioning.

We investigated the potential of an indirect questioning technique for studying noncompliant and sensitive harvest behavior. We used the unmatched-count technique (UCT) and identified sociodemographic characteristics of noncompliant households to assess prevalence of illegal hunting in the Serengeti. We based our hypotheses concerning the likely characteristics of hunting and the households engaged in it on the findings of previous studies (Table 2). We extracted the variation explained by respondents coming from different villages and related this to spatial characteristics, such as distance to protected areas and nearest urban area. Finally, we considered the effectiveness of the technique at minimizing question sensitivity by analyzing respondents' perceived anonymity and discomfort.

Methods

Study Area

The local communities surrounding the protected areas in the western Serengeti (Fig. 1) are traditionally composed of pastoralists, agropastoralists, and hunters, but current livelihood strategies consist of a combination of

occupations (Sinclair et al. 2008). The villages are multiethnic, owing largely to immigration. Households are generally polygamous, and education is up to the primary level (Loibooki et al. 2002; Kaltenborn et al. 2005). In 2002, there were approximately 0.43 million people living in the Bunda and Serengeti districts that surround the Serengeti National Park (SNP) (NBS Tanzania 2006).

Bushmeat is, in theory, a state-controlled natural resource in Tanzania. Hunters must obtain a license, and quotas for harvest in hunting concessions outside the national park are set annually. However, there is a high rate of noncompliance, potentially owing to the legal complexity and high fees associated with obtaining a license, lack of benefit sharing, poor governance, and centralized control of resources (Nelson et al. 2007). Bushmeat hunting in the Serengeti is mainly nonselective and conducted through wire snaring, although use of weapons and hunting dogs and night hunting with flashlights are also common (Holmern et al. 2002). The seasonally available migratory ungulates, such as wildebeest (*Connochaetes taurinus*), represent the bulk of harvested wildlife, but poaching affects a wide range of resident ungulates, such as impala (*Aepyceros melampus*) and topi (*Damaliscus lunatus*), and nontarget species, such as spotted hyena (*Crocuta crocuta*) (Hofer et al. 1996). In our study area,

Table 2. Summary of the explanatory variables and their reported effects in other studies of bushmeat hunting in the Serengeti.

<i>Explanatory variable</i>	<i>Reported effects</i>
Ethnic group	Arrested poachers are mainly of the Kurya and Ikoma tribes (Ndibalema & Songorwa 2008). No significant differences between ethnic groups (Mfunda & Røskaft 2010).
Household size	Larger households have less involvement in hunting (Johannesen 2005). Household size has no effect on hunting involvement (Mfunda & Røskaft 2010).
Household migration	Immigrants to the area are more frequently involved in hunting (Mfunda & Røskaft 2010).
Household employment	Poaching and nonpoaching households equally likely to report seasonal employment but poaching households less likely to have full-time employment (Knapp 2007).
Season	Poaching occurs all year round but mainly during the dry season when the wildebeest are in the study area (Kaltenborn et al. 2005; Holmern et al. 2007).
Hunting as source of cash	Most arrested hunters report hunting only for their own consumption (Holmern et al. 2002). The main reasons for hunting are economic rather than just subsistence (Loibooki et al. 2002; Johannesen 2005).
District	Higher proportion of hunters in the Serengeti district than in Bunda (Johannesen 2005).
Distance from village to protected areas	The number and proportion of hunters in a village is negatively correlated with distance (Campbell & Hofer 1995). Distance does not affect hunting involvement up to 17 km from the PA (Johannesen 2005).
Access to alternative sources of protein or income	Lower hunting prevalence in villages close to urban areas and Lake Victoria (Loibooki et al. 2002).

all forms of legal hunting effectively ceased in 2003, when all legal hunting rights were bought by a local nongovernmental organization (Knapp et al. 2010). Law enforcement is carried out by Tanzania National Park rangers and personnel of the Grumeti Fund.

Surveys

We used the UCT to determine household participation in bushmeat hunting. Survey respondents were randomly al-

located into a control group or a treatment group. Control group members received a list of nonsensitive items (behaviors such as herding and trading), whereas the treatment group received the same list but with the addition of the sensitive item (poaching). In UCT all respondents are asked to indicate how many, but not which, items apply to them (Droitcour et al. 1991). Differences in means between subsamples are used to estimate the prevalence of sensitive behaviors.

This technique has not been used within conservation or natural resource management, and first we conducted an exploratory pilot study to confirm that it was not inappropriate or too complicated to be used in the study area (A.N., unpublished data). The control and treatment of UCT response cards are provided in Supporting Information.

Data were collected from February to June 2011 in the western Serengeti, Tanzania. We randomly selected 15 villages in the Serengeti and Bunda districts that were up to 15 km from a protected area (Fig. 1).

The interviews were conducted by local interviewers from the study village or neighboring areas. Interviewers selected 1 household in each village and then skipped 2 households before approaching the next household to interview, making sure not to sample adjacent households so as to minimize spatial autocorrelation between neighboring households. Approximately 1.7–5.6% of the households in each village were sampled. Interviews were conducted with the head of household or any other household member provided they were 18 years old or older. If a suitable respondent was not present, an adjacent household was surveyed instead.

Surveys (Supporting Information) were administered to, on average, 79 households per village. The questionnaire started with questions on individual and household sociodemographic characteristics. Next, the UCT was used to ask about the participation of any household member in bushmeat hunting and other livelihood activities over the last 12 months. A die was used to randomly assign households to control or treatment UCT groups. In the treatment group, bushmeat hunting was listed alongside 4 other livelihood activities, and respondents were asked how many of these activities their household had engaged in. In the control group, bushmeat hunting was absent from the list. Respondents were asked separately 4 UCT questions about participation in these activities in the dry and wet seasons and in which season they had obtained cash income. Finally, the respondents' opinion was sought about the questioning technique (UCT) itself, specifically their levels of understanding and feelings of anonymity and discomfort when answering the UCT questions.

The hunting UCT questions were preceded by a nonsensitive training question in which respondents were asked to say how many animals on a list cause them problems (e.g., elephants, leopards). This was to put them at

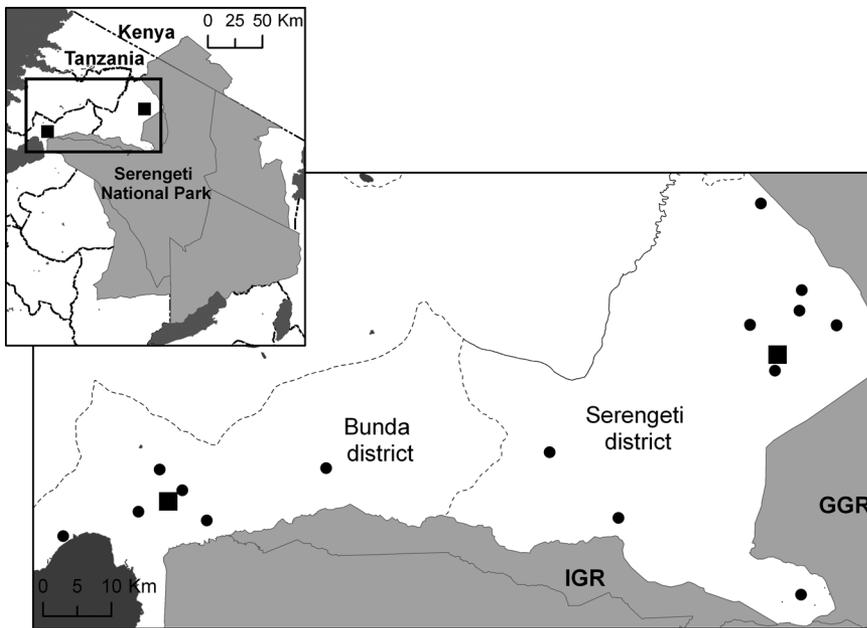


Figure 1. Protected areas (light gray), lake (dark gray), districts (boundaries represented by dashed lines), and study villages (circles) in the western Serengeti (squares, urban areas [i.e., district administrative towns]; GGR, Grumeti Game Reserve; IGR, Ikorongo Game Reserve).

ease and engender a positive attitude toward the survey, check for the validity of the control, and ensure they understood the method. To minimize ceiling and floor effects, in which answer anonymity was not possible because the respondent engaged in all or none of the listed activities, nonsensitive items included at least one item whose prevalence was extremely low and one item with very high prevalence (Tsuchiya et al. 2007). Nonsensitive items that are completely different from the target item may cause suspicion (Hubbard et al. 1989); therefore, all items referred to livelihood strategies (or wild animals in the case of the training question).

Before administering the questionnaires, the interviewers provided a brief description of the general aims of the project and emphasized the voluntary and anonymous nature of the questionnaire. Because we aimed to protect respondents' anonymity and minimize survey sensitivity, no personal or geographical data were collected that could be used to identify specific households.

Data Analyses

Linear mixed models were fitted with village and card type (control or treatment) within village as random effects to account for spatial dependence of observations. A random effect for individuals was also included to account for the grouping structure of the data because every respondent answered multiple UCT questions. To estimate behavior prevalence, models were fitted only with the random effects and question topic and card type as fixed effects. Then, UCT answers to bushmeat questions were fitted with question topic, card type, demographic variables, and interactions of the card type variable with each demographic variable (Holbrook & Krosnick 2010). The interactions between sociodemographic variables

and treatment status indicated differences between the reported numbers of behaviors in the 2 conditions for each predictor variable.

To analyze spatial effects on hunting prevalence, best linear unbiased predictors (BLUPs) (Pinheiro & Bates 2000) of the random effect of village were extracted from the top model, in which the random effect of treatment card within village measured the unexplained deviance of each village from mean hunting prevalence. A graphical inspection of the data showed a potential nonlinear effect of distance to the national park. Generalized linear models were fitted with a Gaussian error structure and identity link function, with district and logarithmic transformations of villages' population size, distance to urban area, and squared and linear distance to the national park and Lake Victoria as explanatory variables.

We used cumulative logit models to analyze respondents' self-reported levels of understanding, anonymity, and discomfort when answering the UCT questions. Specifically, we evaluated the effect of age, sex, education level, and status within household on respondents' perceptions as a multinomial response (very much, moderately, a little, or not at all) without making assumptions about the distance between ordered categories or their distribution. We were also interested in evaluating the effect of potential question sensitivity on perceived anonymity and discomfort. We assumed that being shown a treatment card (which includes hunting) could be more sensitive, particularly if more activities were reported (respondents may feel less able to mask involvement in the sensitive item). A 2-way interaction between UCT card (treatment or control) and number of reported activities (UCT answers) was included in the models fitted to anonymity and discomfort. Village was included as a random effect. These models were

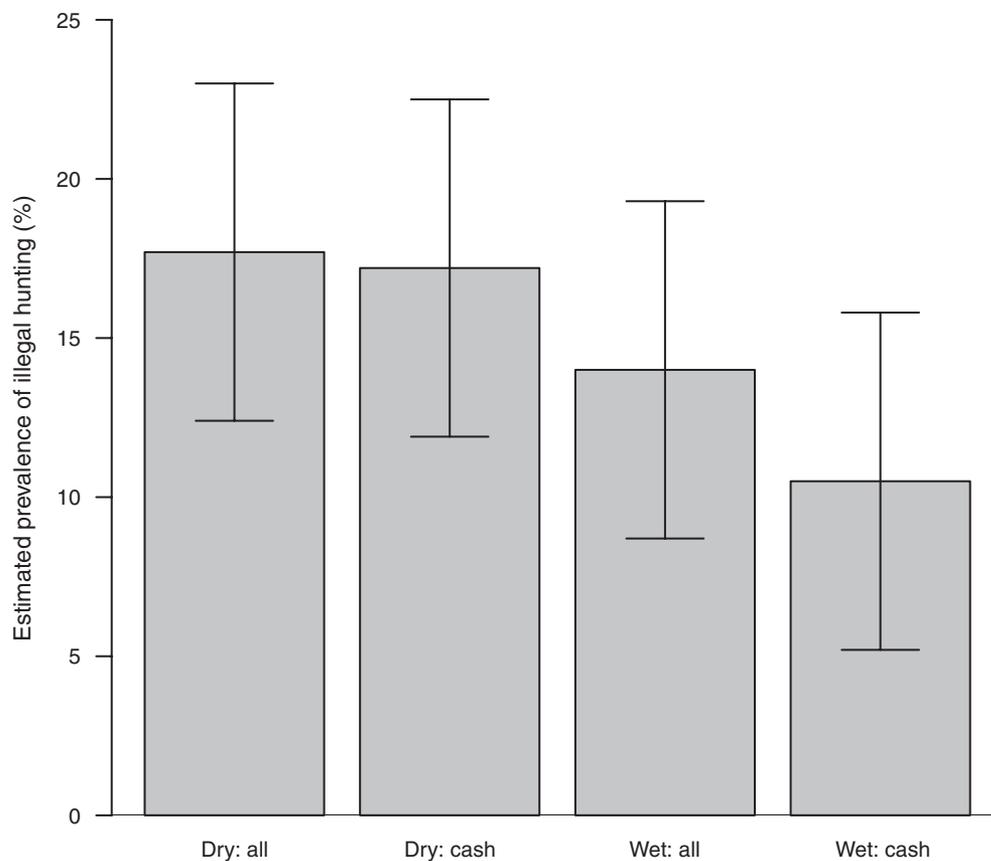


Figure 2. Estimated prevalence (SE) of illegal bushmeat hunting in the western Serengeti during the 12 months prior to the study. Estimates obtained from model fitted only with the random effects and question topic and card type (treatment or control) as fixed effects (dry, dry season; all, cash and other reasons; cash, cash income; wet, wet season).

implemented in the `clmm` function in the ordinal package (version 2012.01–19) (Christensen 2012) in R (version 2.15.1) (R Foundation for Statistical Computing 2012).

We used the corrected Akaike information criterion (AIC_c) to select and rank the most parsimonious models. When analyzing the number of reported activities to identify characteristics of noncompliant households, we considered for comparison only models with interactions. We averaged estimates across models with $\Delta AIC < 4$; $\Delta AIC \geq 4$ indicating considerably less support for the model (Burnham & Anderson 2002).

Results

We approached 1191 individuals, of which 28 refused to participate (nonresponse rate < 2.5%). In all cases, this occurred at the start of the survey before any questions were asked. Survey respondents and nonrespondents did not differ by sex ($\chi^2 = 0.92$, $df = 1$, $p = 0.34$), but older respondents (over 66 years) were approximately 7% less likely to respond than the other age groups (18–25, 26–

45, 46–65, and over 66 years old) ($\chi^2 = 13.05$, $df = 3$, $p = 0.01$). Before analysis we discarded questionnaires with missing data. Our total sample was 1093 individuals (Supporting Information). Respondents in the control group ($n = 551$) and treatment ($n = 542$) group did not differ on the basis of sociodemographic characteristics (Supporting Information). Correlation between predictor variables was low (all < 0.4).

Bushmeat hunting was conducted by approximately 18% (SE 5) of the households in the western Serengeti during the 12 months prior to survey administration. More households were involved in illegal hunting during the dry season than in the wet season, and hunting households predominately generated cash income from bushmeat, particularly in the dry season (Fig. 2). However, the differences between season and the season \times cash interaction were not significant.

Illegal bushmeat hunting was more likely in households with seasonal or full-time employment, lower household size, and longer household residence in the village and where the respondent had more education (Fig. 3). The estimated effects, presented in Fig. 3 as differences between levels, exhibited wide standard errors, but they

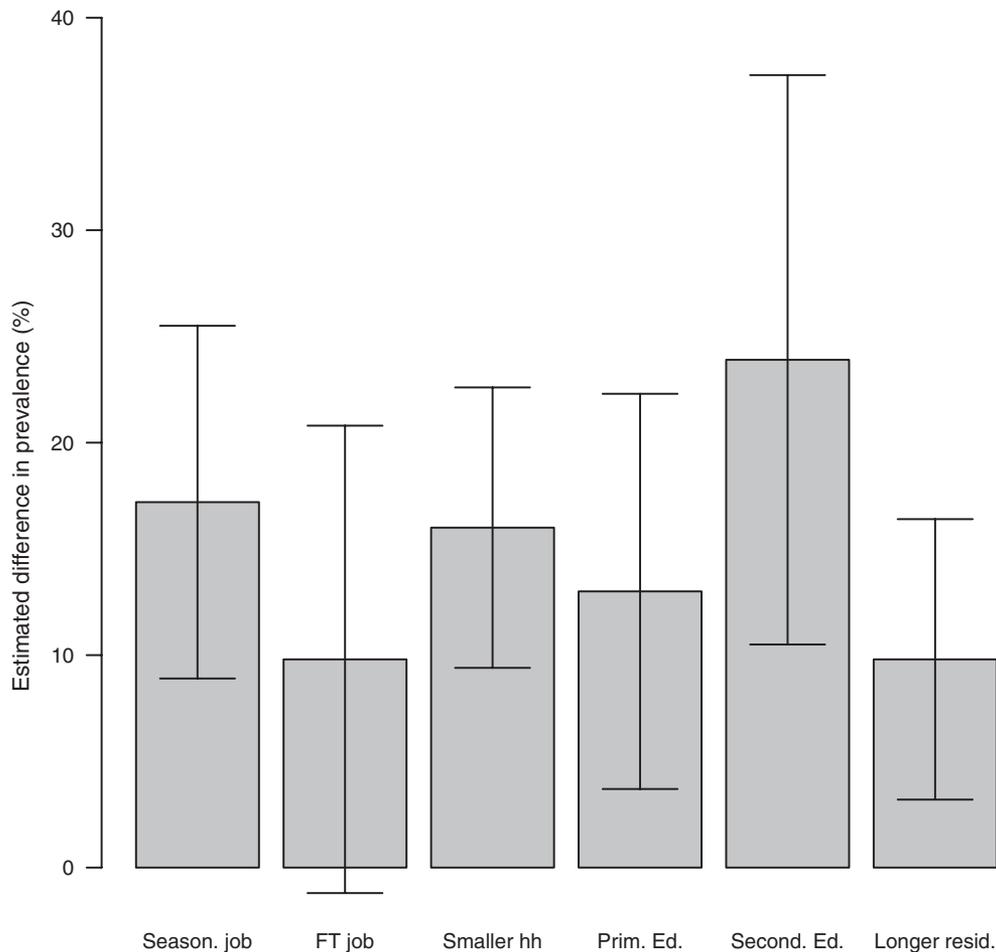


Figure 3. Effects of main sociodemographic categorical variables presented as the estimated difference (SE) in prevalence of illegal hunting, where each prevalence level is compared with a reference level. A baseline prevalence of 6.5% includes all reference levels: no seasonal (Season.) job, no full-time (FT) job, smaller households (hh), respondent with no formal education, and shorter residence in the village (Prim., primary; Ed., education; Second., secondary; resid., residency).

did not overlap zero, except for occurrence of full-time employment, which decreased our confidence in the direction of this effect. Hunting prevalence was also explained by the question topic (poaching during the wet season for cash income was less common).

Other variables also included in the top models but with much less support were the number of children in the household, respondent sex, and whether or not the respondent was the head of the household (Supporting Information). Ethnicity was not retained in the top models.

The nesting factor of village, which included potential interviewer effects (each village was surveyed by a different local interviewer), explained 21.9% of the variance that was not explained by any of the fixed effects. This village-level variance was best predicted by the village's distance to the national park and to urban areas. After accounting for the sociodemographic effects analyzed in the main model, distance to national park had a nega-

tive effect on hunting prevalence up to around 5 km away from the park, beyond which hunting prevalence increased as distance to the park increased (Fig. 4a). Villages farther away from urban areas had higher hunting prevalence (Fig. 4b). Villages with higher population sizes had lower unexplained hunting prevalence, but this variable received little support for inclusion in the top models. District and distance to Lake Victoria were not retained in the top models (Supporting Information).

The majority (65%) of survey respondents found the UCT questions very easy to understand (9% reported them as difficult). Similarly, <10% of respondents said they felt very uncomfortable answering the questions, and 77% said they were not uncomfortable at all. However, 70% of respondents said that they thought their answers were not anonymous (Supporting Information).

The model results suggest there were no major problems with respondent perceptions that may have affected the survey results. The null model was the most

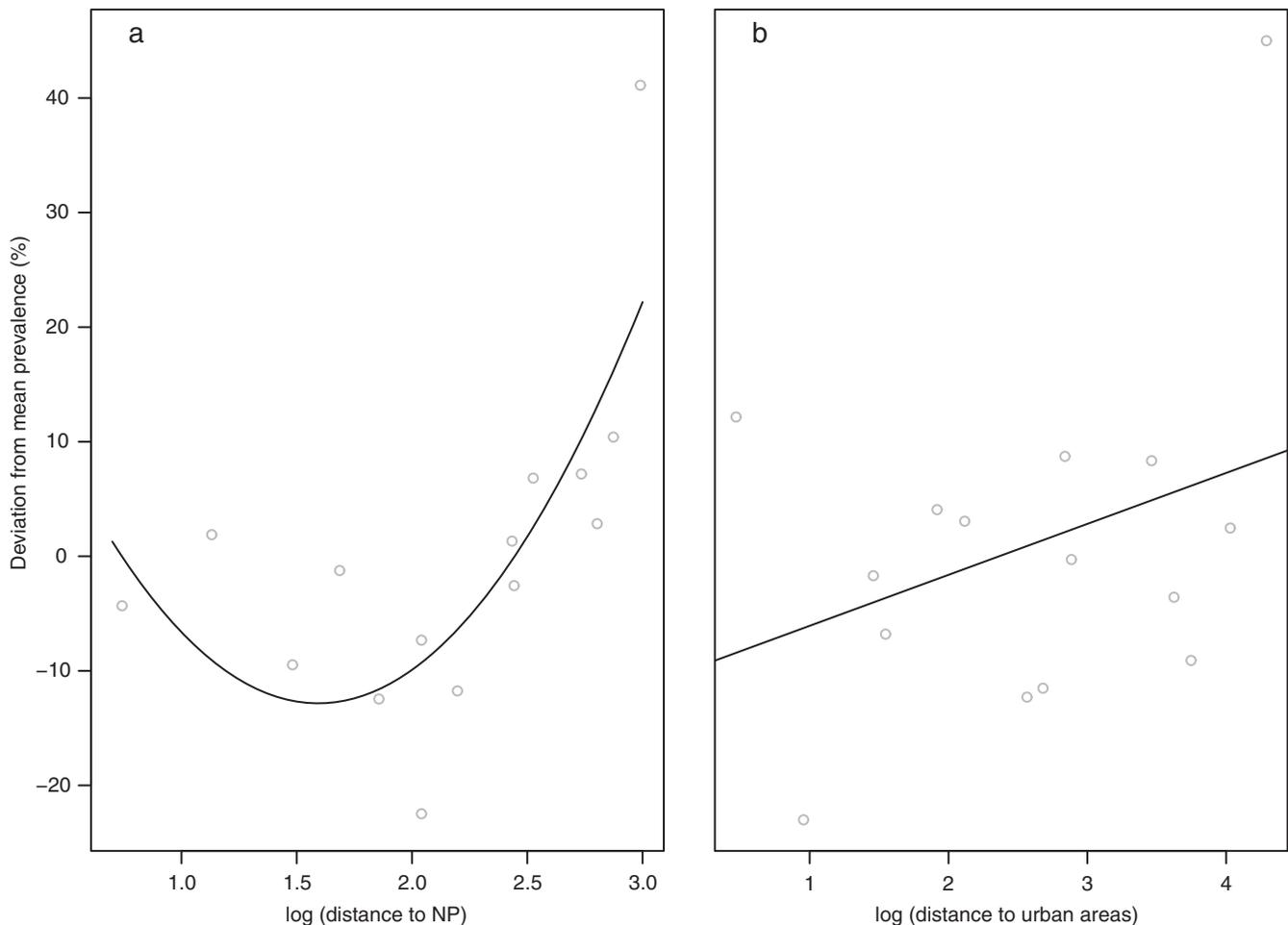


Figure 4. Effect of the distance to (a) Serengeti National Park and (b) urban areas on the hunting prevalence of each village ($n = 15$) (deviation from the estimated mean from a mixed-effects model). The circles show villages' data and the trend lines represent effects taken from model outputs.

parsimonious model that explained self-reported understanding of the survey technique (Supporting Information). Age, sex, education level, and status within household had low relative importance (<0.35) (Supporting Information). Reduction in perceived survey anonymity was explained by age and being shown the treatment cards that included the sensitive items. However, the importance of these variables was still low (0.66 for age and 0.59 for the treatment cards), and their small effect size and large standard errors reduced our confidence in the direction of their effects. Respondents' perceptions of increased discomfort were mainly explained by being shown the treatment rather than control cards (variable importance 0.89), reporting fewer UCT activities, particularly when being shown the treatment cards (importance 0.8) and not being the head of their household (0.53). Except for head-of-household status, the large standard errors for these variables decreased our confidence in whether the potential effect on discomfort was positive or negative.

Discussion

Effective conservation requires a better understanding and assessment of human behavior and its drivers in order to motivate behavioral change (Milner-Gulland 2012). The true extent of natural resource exploitation is, however, difficult to ascertain, particularly if it is illegal in nature (Gavin et al. 2010). Understanding the mechanisms behind responses to sensitive questions and separating out the confounding effects of the survey technique from the actual drivers of behavior are thus of the utmost importance but rarely considered. We investigated how techniques developed in the social sciences may be applied to minimize survey bias and increase respondents' willingness to share sensitive information and considered their potential shortcomings.

Bushmeat hunting in the Serengeti has often been described as a conservation threat (Campbell & Hofer 1995; Sinclair et al. 2008), and several interventions, such as law enforcement and schemes of commercial use of wild

animals, have been used to reduce poaching. The difficulty of quantifying harvest offtake and poaching involvement in the study area impedes the evaluation of intervention effectiveness. For example, estimates of the number of wildebeest hunted annually range from 40,000 (Mduma et al. 1998) to 118,000 (Campbell & Hofer 1995), and the reliability of estimates of hunting prevalence obtained through direct questions has often been questioned (Table 1). Eighteen percent of households admitted to being involved in hunting. Results from studies conducted elsewhere show that failing to include the effects of illegal behavior in planning and evaluation undermines the success of conservation interventions, reduces their credibility in the eyes of policy makers, and limits the ability to target interventions (Mateo-Tomás et al. 2012; St. John et al. 2012).

Information about the characteristics of rule breakers can help managers focus resources on the least compliant groups (St. John et al. 2010, 2012). Previous studies in the Serengeti have provided sometimes contradictory evidence about who engages in bushmeat hunting and why, where, and when they engage in it (Table 2). For example, poverty is the most commonly cited reason why people in the Serengeti poach bushmeat (Loibooki et al. 2002; Kaltenborn et al. 2005), but Knapp (2007) suggests the decision to poach may be more an issue of time availability than household wealth. Our results suggest households with seasonal or full-time employment were more likely to be involved in bushmeat hunting than households without any employment, supporting neither of the previous explanations.

Poaching in the Serengeti is generally considered mainly a seasonal activity engaged in when ungulate migrations pass by the villages during the dry season (Loibooki et al. 2002; Holmern et al. 2007). Our results suggest households in the Serengeti hunt all year round. The migratory ungulates are partially protected from hunting by the protected areas (Thirgood et al. 2004) and during the wet season, when they are located in areas less accessible to hunters and less suited to the use of snares (Campbell et al. 2001). Year-round poaching may result in more drastic consequences for resident species, such as impala and topi, as suggested by low densities of resident wildlife in several areas in the Serengeti (Campbell & Hofer 1995).

Our results also suggest that, given that hunting is predominately for cash, current alternative sources of income may not be sufficiently attractive to compete with the opportunities provided by hunting and the availability of cash from employment may even facilitate hunting. Recent research in the area points to the strong role of women in encouraging hunting because they value access to meat and ready cash (Lowassa et al. 2012). Although wealthier households tend to attribute less utility to hunting than less well-off households, they also seem to be less concerned about the risk of being caught (Moro

et al. 2013). In the Serengeti, despite the general awareness of the illegality of hunting and its repercussions, its monetary and protein-based benefits greatly exceed the costs (Bitanyi et al. 2012; Knapp 2012). Moreover, evidence from other areas shows that natural resource use is not restricted to the poorest people and may actually increase as other sources of income increase in generally poor communities. This evidence may indicate the existence of transition states out of poverty (Nielsen et al. 2012) and that the effect of increased income on hunter behavior may be ambiguous. For example, increased income may facilitate a change to more effective or selective hunting techniques (Damania et al. 2005).

A number of potential drivers of and explanations for illegal bushmeat hunting have been proposed. Among these, we did not consider, for example, awareness of hunting regulations (Bitanyi et al. 2012), risk perceptions (Knapp 2012), and cultural reasons (Lowassa et al. 2012) for hunting. Further studies that focus on understanding the multivariate causation processes driving poaching behavior in the study area are essential. We also found that, as suggested by others (Campbell et al. 2001; Nielsen 2006), villages are less involved in hunting as the distance to protected areas increases. However, we found that hunting prevalence increased substantially as distance to the park increased for villages >5 km away from the park.

Although indirect questioning techniques have been applied in a number of sociodemographic and cultural contexts (e.g., Solomon et al. [2007] in villages in Uganda and St. John et al. [2010] with fishers in the United Kingdom), relatively little attention has been given to the trade-offs between technique complexity and respondent understanding, discomfort, and perceived anonymity. For example, Razafimanahaka et al. (2012) reported problems with understanding of the RRT in one of their study villages in Madagascar. By focusing on respondents' perceptions, we considered the interpretability of the questioning technique within our study's sociocultural context. Our aim was to increase the reliability of our results by using a technique that respondents felt comfortable with. Comparative studies are particularly limited, although differences in accuracy and interpretability according to questioning technique have been reported (Coutts & Jann 2011).

The UCT was developed to address some of the criticisms of RRT (i.e., that the technique may be constrained by belief in trickery or by respondents' feelings of confusion and education level [Hubbard et al. 1989; Landsheer et al. 1999]). The UCT has been more effective than direct questions for estimating prevalence of sensitive behaviors (Tsuchiya et al. 2007) and produces similar or higher estimates of illegal behaviors than RRT (Wimbush & Dalton 1997; Coutts & Jann 2011). Work on improving UCT's statistical efficiency is ongoing (e.g., Blair & Imai 2012). Our results demonstrate the UCT is well suited to

investigating noncompliance in conservation. The high levels of self-reported understanding, respondents' willingness to participate in the survey, and low reported levels of discomfort could be understood as signs of trust in the technique. Nevertheless, the respondents' education level affected their likelihood of reporting hunting and perceived anonymity was low, probably due to people being questioned face to face by interviewers from their own or neighboring villages.

The disadvantages in using indirect rather than direct questioning include the increased complexity of data analysis, requirement for higher sample sizes, potentially high standard errors, and the limited form that questions can take (questions that require a yes or no answer or questions that involve comparable, or mutually exclusive, options). Moreover, the results are still likely to underestimate actual noncompliance because there will still be participants who give evasive responses regardless of the survey instrument.

Most evaluations of conservation interventions are based on attitudes and behavioral intentions, but change in actual behavior is a much more pertinent measure of conservation success (Holmes 2003). Part of the reason actual and reported behaviors are so rarely quantified may be the difficulty in measuring sensitive behaviors. We describe an approach to obtaining information on involvement in poaching that can be applied in mainly illiterate communities and administered by local interviewers, factors that may promote local participation in monitoring. This suggests the technique may have wider application in developing countries, where resources for conservation are especially scarce (Danielsen et al. 2003). Furthermore, transparent and robust conservation decisions require full consideration of multiple types of uncertainty including observation uncertainty (Bunnfeld et al. 2011). Conceptual and methodological frameworks that explicitly consider uncertainty, such as adaptive management (Keith et al. 2011) and management strategy evaluation (Bunnfeld et al. 2011), would benefit from approaches such as we used here, which explore the different sources of bias in the observed data and disentangle the survey processes from the actual effects of interest.

Acknowledgments

We thank the Tanzania Wildlife Research Institute and Tanzania Commission for Science and Technology (COSTECH) for permission to carry out this study, and we are grateful to everyone in the villages who granted permission for data collection, collected data, or participated in the survey. We thank A. Fischer, A. Lowassa, and D. Rentsch for their advice and help during the study and A. Wallace for help in producing the maps. A.N. is supported by the Portuguese Foundation for Science and Technol-

ogy (FCT) (doctoral grant SFRH/BD/43186/2008). N.B., L.C.N., and E.J.M.G. were supported by the European Commission under the HUNT project of the 7th Framework Programme for Research and Technological Development, and E.J.M.G. was supported by a Royal Society Wolfson Research Merit award. We thank the editors, reviewers, and T. Holmern for their valuable comments on the manuscript.

Supporting Information

Response cards (Appendix S1), questionnaire (Appendix S2), and descriptive summaries and model selection tables (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Bitanyi, S., M. Nesje, L. J. M. Kusiluka, S. W. Chenyambuga, and B. P. Kaltenborn. 2012. Awareness and perceptions of local people about wildlife hunting in western Serengeti communities. *Tropical Conservation Science* 5:208–224.
- Blair, G., and K. Imai. 2012. Statistical analysis of list experiments. *Political Analysis* 20:47–77.
- Bunnfeld, N., E. Hoshino, and E. J. Milner-Gulland. 2011. Management strategy evaluation: A powerful tool for conservation? *Trends in Ecology & Evolution* 26:441–447.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Pages 488. 2nd edition. Springer, New York.
- Campbell, K., and H. Hofer. 1995. People and wildlife: spatial dynamics and zones of interaction. Pages 534–570 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. Chicago University Press, Chicago.
- Campbell, K., V. Nelson, and M. Loibooki. 2001. Sustainable use of wildland resources: ecological, economic and social interactions. An analysis of illegal hunting of wildlife in Serengeti National Park. U.K. Natural Resources, Kent.
- Christensen, R. H. B. 2012. ordinal—Regression models for ordinal data. R Foundation for Statistical Computing, Vienna. Available from <http://www.cran.r-project.org/package=ordinal/> (accessed May 2012).
- Coutts, E., and B. Jann. 2011. Sensitive questions in online surveys: experimental results for the randomized response technique (RRT) and the unmatched count technique (UCT). *Sociological Methods & Research* 40:169–193.
- Damania, R., E. J. Milner-Gulland, and D. J. Crookes. 2005. A bioeconomic analysis of bushmeat hunting. *Proceedings of the Biological Sciences/The Royal Society* 272:259–266.
- Danielsen, F., M. M. Mendoza, P. A. Alviola, D. S. Balete, M. Enghoff, M. K. Poulsen, and A. E. Jensen. 2003. Biodiversity monitoring in developing countries: What are we trying to achieve? *Oryx* 37:407–409.
- Droitcour, J., R. A. Caspar, M. L. Hubbard, T. L. Parsley, W. Visscher, and T. M. Ezzati. 1991. The item count technique as a method of indirect questioning: a review of its development and a case study application. Pages 185–210 in P. P. Biemer, R. M. Groves, L. E. Lyberg, N. A. Mathiowetz, and S. Sudman, editors. *Measurement errors in surveys*. John Wiley, New York.

- GAO (Government Accountability Office). 2007. Estimating irregular migration in a survey: the "two-card follow-up" method. U.N. Sixth coordination meeting on international migration. United Nations, New York.
- Gavin, M. C., J. N. Solomon, and S. G. Blank. 2010. Measuring and monitoring illegal use of natural resources. *Conservation Biology* **24**:89–100.
- Hilborn, R., P. Arcese, M. Borner, J. Hando, J. G. C. Hopcraft, M. Loibooki, S. Mduma, and A. R. E. Sinclair. 2006. Effective enforcement in a conservation area. *Science* **314**:1266.
- Hofer, H., K. Campbell, M. L. East, and S. A. Huish. 1996. The impact of game meat hunting on target and non-target species in the Serengeti. Pages 117–146 in V. J. Taylor and N. Dunstone, editors. *The exploitation of mammal populations*. Springer, London.
- Holbrook, A. L., and J. A. Krosnick. 2010. Social desirability bias in voter turnout reports: tests using the item count technique. *Public Opinion Quarterly* **74**:37–67.
- Holmern, T., J. Muya, and E. Røskft. 2007. Local law enforcement and illegal bushmeat hunting outside the Serengeti National Park, Tanzania. *Environmental Conservation* **34**:55–63.
- Holmern, T., E. Røskft, J. Mbaruka, S. Y. Mkama, and J. Muya. 2002. Uneconomical game cropping in a community-based conservation project outside the Serengeti National Park, Tanzania. *Oryx* **36**:364–372.
- Holmes, C. M. 2003. The influence of protected area outreach on conservation attitudes and resource use patterns: a case study from western Tanzania. *Oryx* **37**:305–315.
- Hubbard, M. L., R. A. Caspar, and J. T. Lessler. 1989. Respondent reactions to item count lists and randomized response. Pages 544–548 in *Proceedings of the American Statistical Association, Section for Survey Research Methods*. American Statistical Association, Washington, D.C.
- Johannessen, A. B. 2005. Wildlife conservation policies and incentives to hunt: an empirical analysis of illegal hunting in western Serengeti, Tanzania. *Environment and Development Economics* **10**:271–292.
- St. John, F. A. V., G. Edwards-Jones, J. M. Gibbons, and J. P. G. Jones. 2010. Testing novel methods for assessing rule breaking in conservation. *Biological Conservation* **143**:1025–1030.
- St. John, F. A. V., A. Keane, G. Edwards-Jones, L. Jones, R. W. Yarnell, and J. P. G. Jones. 2012. Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. *Proceedings of the Royal Society B* **279**:804–812.
- Kaltenborn, B. P., J. W. Nyahongo, and K. M. Tingstad. 2005. The nature of hunting around the western corridor of Serengeti National Park, Tanzania. *European Journal of Wildlife Research* **51**:213–222.
- Keane, A., J. P. G. Jones, G. Edwards-Jones, and E. J. Milner-Gulland. 2008. The sleeping policeman: understanding issues of enforcement and compliance in conservation. *Animal Conservation* **11**:75–82.
- Keith, D. A., T. G. Martin, E. McDonald-Madden, and C. Walters. 2011. Uncertainty and adaptive management for biodiversity conservation. *Biological Conservation* **144**:1175–1178.
- Knapp, E. J. 2007. Who poaches? Household economies of illegal hunters in Western Serengeti, Tanzania. *Human Dimensions of Wildlife* **12**:195–196.
- Knapp, E. J. 2012. Why poaching pays: a summary of risks and benefits illegal hunters face in Western Serengeti, Tanzania. *Tropical Conservation Science* **5**:434–445.
- Knapp, E. J., D. Rentsch, J. Schmitt, C. Lewis, and S. Polasky. 2010. A tale of three villages: choosing an effective method for assessing poaching levels in western Serengeti, Tanzania. *Oryx* **44**:178–184.
- Landsheer, J. A., P. Van Der Heijden, and G. Van Gils. 1999. Trust and understanding, two psychological aspects of randomized response. *Quality & Quantity* **33**:1–12.
- Loibooki, M., H. Hofer, K. Campbell, and M. L. East. 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation* **29**:391–398.
- Lowassa, A., D. Tadie, and A. Fischer. 2012. On the role of women in bushmeat hunting – Insights from Tanzania and Ethiopia. *Journal of Rural Studies* **28**:622–630.
- Mateo-Tomás, P., P. P. Olea, I. S. Sánchez-Barbudo, and R. Mateo. 2012. Alleviating human-wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna. *Journal of Applied Ecology* **49**:376–385.
- Mduma, S., R. Hilborn, and A. R. E. Sinclair. 1998. Limits to exploitation of Serengeti wildebeest and implications for its management. Pages 243–265 in D. M. Newberry, H.H.T. Prins, and N. D. Brown, editors. *Dynamics of Tropical Communities*. Blackwell Science, Oxford, United Kingdom.
- Mfunda, I. M., and E. Røskft. 2010. Bushmeat hunting in Serengeti, Tanzania: an important economic activity to local people. *International Journal of Biodiversity and Conservation* **2**:263–272.
- Milner-Gulland, E. J. 2012. Interactions between human behaviour and ecological systems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **367**:270–278.
- Moro, M., A. Fischer, M. Czajkowski, D. Brennan, A. Lowassa, L. C. Naiman, and N. Hanley. 2013. An investigation using the choice experiment method into options for reducing illegal bushmeat hunting in western Serengeti. *Conservation Letters* **6**:37–45.
- NBS Tanzania (National Bureau of Statistics – Tanzania). 2006. Tanzania census 2002 – analytical report. Volume X. Ministry of Planning, Economy and Empowerment, Dares Salaam.
- Ndibalema, V. G., and A. N. Songorwa. 2008. Illegal meat hunting in Serengeti: dynamics in consumption and preferences. *African Journal of Ecology* **46**:311–319.
- Nelson, F., R. Nshala, and W. A. Rodgers. 2007. The Evolution and Reform of Tanzanian Wildlife Management. *Conservation and Society* **5**:232–261.
- Nielsen, M. R. 2006. Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: implications for community based wildlife management. *Biological Conservation* **128**:509–516.
- Nielsen, M. R., M. Pouliot, and R. Kim Bakkegaard. 2012. Combining income and assets measures to include the transitory nature of poverty in assessments of forest dependence: evidence from the Democratic Republic of Congo. *Ecological Economics* **78**:37–46.
- Pinheiro, J., and D. Bates. 2000. *Mixed-effects models in S and S-Plus*. Page 528. Springer-Verlag, New York.
- Razafimanahaka, J. H., R. K. B. Jenkins, D. Andriafidison, F. Randriandrianina, V. Rakotomboavonjy, A. Keane, and J. P. G. Jones. 2012. Novel approach for quantifying illegal bushmeat consumption reveals high consumption of protected species in Madagascar. *Oryx* **46**:584–592.
- Sinclair, A. R. E., J. G. C. Hopcraft, H. Olf, S. Mduma, K.a. Galvin, and G. J. Sharam. 2008. Historical and future changes to the Serengeti ecosystem. Pages 7–46 in A. R. E. Sinclair and C. Packer, editors. *Serengeti III: human impacts on ecosystem dynamics*. University of Chicago Press, Chicago.
- Solomon, J. N., S. Jacobson, K. D. Wald, and M. C. Gavin. 2007. Estimating illegal resource use at a Ugandan park with the randomized response technique. *Human Dimensions of Wildlife* **12**:75–88.
- Thirgood, S. J., A. Mosser, S. Tham, J. G. C. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. M. Fryxell, A. R. E. Sinclair, and M. Borner. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* **7**:113–120.
- Tsuchiya, T., Y. Hirai, and S. Ono. 2007. A study of the properties of the item count technique. *Public Opinion Quarterly* **71**:253–272.
- Warner, S. L. 1965. Randomized Response: a survey technique for eliminating evasive answer bias. *Journal of the American Statistical Association* **60**:63–69.
- Wimbush, J., and D. Dalton. 1997. Base rate for employee theft: convergence of multiple methods. *Journal of Applied Psychology* **82**:756–763.