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REVIEW AND SYNTHESIS

Searching for sustainability: are assessments of wildlife harvests behind the times?

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Abstract

The unsustainable harvest of wildlife is a major threat to global biodiversity and to the millions of people who depend on wildlife for food and income. Past research has called attention to the fact that commonly used methods to evaluate the sustainability of wildlife hunting perform poorly, yet these methods remain in popular use today. Here, we conduct a systematic review of empirical sustainability assessments to quantify the use of sustainability indicators in the scientific literature and highlight associations between analytical methods and their outcomes. We find that indicator type, continent of study, species body mass, taxonomic group and socio-economic status of study site are important predictors of the probability of reported sustainability. The most common measures of sustainability include population growth models, the Robinson & Redford (1991) model and population trends through time. Indicators relying on population-specific biological data are most often used in North America and Europe, while cruder estimates are more often used in Africa, Latin America and Oceania. Our results highlight both the uncertainty and lack of uniformity in sustainability science. Given our urgent need to conserve both wildlife and the food security of rural peoples around the world, improvements in sustainability indicators are of utmost importance.

Keywords

Bushmeat, harvest, hunt, indicators, indices, sustainability, wildlife.

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INTRODUCTION

The harvest of wildlife for human consumption and use is a major threat to global biodiversity and paradoxically, to the very people who depend on it. Millions of people around the world rely on wildlife as a major source of protein, calories, micronutrients and in many cases, livelihoods (Fa *et al.* 2002; Corlett 2007; Brashares *et al.* 2011; Golden *et al.* 2011). Although humans have been hunting wildlife for millennia, increasing human populations, improved hunting technologies, expanded market access and logging roads that bring people deeper into tropical forests all contribute to increased pressure on wildlife populations.

Overexploitation is now one of the major threats to mammals, reptiles and birds, second only to habitat destruction (Vié *et al.* 2009). The hunting of wildlife is considered the 'single most geographically widespread form of resource extraction' in the tropics (Fa *et al.* 2002); published accounts of the scale and magnitude of wildlife hunting in the tropics conclude that wildlife hunting for human consumption is largely unsustainable (Milner-Gulland *et al.* 2003; Fa *et al.* 2005). This situation has come to be known as the 'bushmeat crisis'; bushmeat, a colloquial African term meaning 'meat from the bush', and 'crisis', the unsustainable levels at which wildlife is being harvested.

Similar to fisheries and forests, wildlife can be viewed as a renewable resource whose regenerative capacity allows some level of harvest, while sustaining stock populations at ecologically viable levels. A given level of harvest is considered sustainable if it is at or below the level that permits the resource to regenerate itself in perpetuity. Sustainable use of biological resources has been promoted as a workable solution to averting species extinctions and maintaining acceptable levels of ecosystem health and structure, while at the same time taking into account human needs (Ginsberg & Milner-Gulland 1994; Bodmer & Lozano 2001).

How, then, do we determine if a given hunting level is sustainable or not (and by extension, heading towards a crisis)? Upon closer examination, there is much ambiguity in the scientific literature about how best to measure whether wildlife harvest in a given system is sustainable. In a landmark review, Milner-Gulland & Akçakaya (2001) called attention to the fact that indicators used most commonly to evaluate the sustainability of wildlife hunting 'do not perform well under realistic conditions'. However, these authors only evaluated a small subset of the most commonly used indicators. Although a substantial amount of research has aimed to assess the sustainability of wildlife hunting regimes, particularly across the tropics (e.g. Cowlishaw *et al.* 2005; Fa *et al.* 2005), the methods and results of these efforts remain fragmented. Here, we review and synthesise empirical work to date on wildlife harvest sustainability, and construct a data set from the results of these studies to examine the following questions:

(1) What methods are used most frequently in the scientific literature to assess the sustainability of wildlife harvesting?
(2) Does the choice of the sustainability indicator used in a study predict the likelihood that the study will conclude harvests are unsustainable?

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(3) Are species' traits, local habitat type and the socio-economic context of the countries in which the wildlife harvesting takes place significant predictors of reported sustainability?
(4) Are there geographical biases in where different sustainability assessments are used?

In addressing these questions, we provide a quantitative assessment of the wildlife harvesting literature, discuss theoretical support for the most commonly used sustainability indicators and provide recommendations for future directions in the field.

When is wildlife hunting sustainable?

In the Convention on Biological Diversity (1993), *sustainable use* is defined as 'the use of the components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations' (Article 2, CBD 1993). Theory behind sustainable use of renewable resources emerged in the fisheries literature in the 1950s to counter the view that such resources were inexhaustible (Rosenberg *et al.* 1993). Still today, the literature and theory on sustainability are more fully developed for aquatic systems than for terrestrial harvests (Milner-Gulland & Akçakaya 2001).

One of the basic sustainability models applied to harvested biological populations is the surplus production model and maximum sustainable yield (MSY). In the logistic model, the simplest of all continuous-time, density-dependent growth models, a population's maximum production (recruitment) occurs at a population size of around one-half carrying capacity, which is the point at which total population growth rate is maximised (although in some fisheries cases this occurs at 30% of carrying capacity, see: Clark 1991; Mace 1994; Worm *et al.* 2009). Though *maximum* yield for many populations may be attained at around one-half carrying capacity, harvest can equal production at any point along the recruitment curve (Clark 2010), although Allee effects might become important at very low population levels (Rowcliffe *et al.* 2003). Therefore, in its simplest sense, hunting is sustainable when the use or harvest of the resource does not exceed production, but the size of this harvest will also depend on other management goals that may include maximising production, maximising economic revenue, minimising the probability of extinction or the conservation of a full suite of species in an ecosystem as suggested by the CBD definition (1993).

As many authors have noted, however, sustainability, while conceptually sound, is notoriously difficult to operationalise (Ludwig *et al.* 1993; Quinn & Collie 2005). A large number of sustainability indicators have appeared in the wildlife literature in response to the recognition of declining renewable resources, and the plethora of different indicators is partly a response to the frequent absence of adequate biological data. In this paper, we systematically review commonly used methods for assessing biological sustainability in wildlife harvesting and consider their major advantages and shortcomings (Table 1). These methods are generally much less sophisticated than those encountered in the current fisheries and forestry harvesting literature. The availability in fisheries and forestry of much richer data sets, often with detailed age and size specific information on population structure, support methods that either employ hierarchical Bayesian methods of analysis (Kuparinen *et al.* 2012) or state-of-the-art methods for optimal decision analyses under uncertainty (Yousefpour *et al.* 2012).

MATERIAL AND METHODS

Literature search

We conducted a comprehensive literature search using ISI Web of Science updated through 2010, using the following search criterion: (sustain* OR unsustain*) AND (hunt* OR harvest* OR exploit* OR offtake OR yield). This search was refined by the following subject areas: ecology, environmental sciences, environmental studies, zoology, biodiversity conservation, geography and anthropology. We searched for studies whose stated objectives included assessing the sustainability of wildlife hunting, that is, studies that used sustainability indicators to determine whether a harvest level was sustainable. We restricted papers to empirical, rather than theoretical work, (comparing indices to actual harvest rates, not purely simulation exercises), and excluded prescriptive papers that estimate future sustainable harvests rather than current harvest sustainability. We eliminated papers in which the objective of the authors was to assess the efficacy of culling or eradication programmes rather than the sustainable maintenance of wildlife populations. We restricted reviewed papers to terrestrial species (including birds), as assessment of fisheries sustainability is a separate and currently more developed body of literature. When more than one paper was published from the same study site by the same researcher or research group, the most recent paper was included, unless an earlier paper was more comprehensive (rare). After excluding unrelated papers based on title alone, a subset (20%) was examined for inclusion by two reviewers (K.W. and C.G.) to check for agreement on selection criteria (Pullin & Stewart 2006).

Data extraction

We extracted the following information from each paper: country and continent of study, species and taxon, year of publication, sustainability indicator used, and reported outcome for each sustainability evaluation (dichotomous variable, sustainable/unsustainable). The ecoregion for each study area was determined from information reported in the paper or, if unreported, from WWF's Terrestrial Ecoregions GIS Database (Olson *et al.* 2001) using ArcGIS 10 [Environmental Systems Resource Institute (ESRI), Redlands, CA, USA]. Species body masses were estimated from the following sources: mammals (PanTHERIA Database Jones *et al.* 2009), birds (Hoyo *et al.* 1992; Snow & Perrins 1998; Poole 2005; Dunning 2008) and reptiles (O'Shea & Halliday 2001). When sustainability assessments were based on multi-species groups instead of individual species, average body weight for all relevant species was used. Finally, we included the Human Development Index (HDI) rank for the country of each study site as an indicator of economic and technical capacity (UNDP 2010). Often, multiple species and/or multiple sustainability indicators were used in a single paper. In such cases, we counted each species, indicator and outcome as a separate observation, but accounted for non-independence in the analysis using 'study' as a random effect in a generalised linear mixed model (GLMM).

Data analysis

We developed a GLMM to evaluate whether the choice of the sustainability indicator, species' taxon and body mass, geographic

Table 1 Comprehensive list of indicators used for assessing the sustainability of wildlife hunting in the scientific literature

Indicator	Model/Parameters	Comparator/Outcome	Advantages	Disadvantages/Critiques	Key reference(s)
Population trends over time					
Population abundance/density	Multiple years of data on population abundance, density or abundance index	Increase, decrease or stable	Most direct form of assessing sustainability	Difficult to have adequate power to detect change. Declines may indicate trend towards new equilibrium, not sustainability	Hill *et al.* (2003) Baker *et al.* (2004) Lariviere *et al.* (2000)
Catch-per-unit-effort (CPUE)	Catch and effort data	Increase, decrease or stable	Obtained from hunters; generally easier than monitoring populations	Must be monitored over time. Relation between CPUE and abundance not necessarily straightforward (can have hyperdepletion, hyperstability, etc.)	Hill *et al.* (2003) Vickers (1994) Kumpel *et al.* (2010)
Demographic models					
Population growth rate (λ)	Demographic model/matrix projection model	If $\lambda \geq 1$, the mortality caused by harvesting is sustainable; if $\lambda < 1$, mortality due to harvesting is considered unsustainable	Mechanistic explanations for population trajectory, given harvesting.	Data intensive. Assumes harvesting is the main driver, and assumes all harvesting is accounted for	Lofroth and Ott (2007) Combreau *et al.* (2001)
Population viability analysis	Demographic model/matrix projection model	Determine how much human-added mortality is compatible with population persistence, compared with actual harvest	Mechanistic explanations for population trajectory, given hunting. Can take uncertainty into account to provide probabilities of persistence.	Data intensive	Combreau *et al.* (2001)
Surplus production models					
Robinson & Redford (1991)	$P = 0.6K(R_{max} - 1)$ K = carrying capacity R_{max} = Intrinsic rate of population increase F = mortality factor (F = 0.2, 0.4 or 0.6 depending on species longevity). Total annual harvests	If observed harvest is greater than estimated P, the harvest is considered unsustainable	Widely used in tropical 'bushmeat' hunting studies. Relatively few parameters needed; easier to implement than full models in data-deficient conditions	Often K, R_{max} not measured, but taken from other sites/conditions, potentially giving misleading production estimates. May not be precautionary enough. F addresses survival rates, but in a highly simplified way. Implicitly assumes one specific form of density dependence	Robinson & Redford (1991) Slade *et al.* (1998) Milner-Gulland & Akçakaya (2001)
Bodmer Model (1994) (Unified harvest model)	$P = (0.5D)(Y * g)$ D = population density Y = young/female g = average # gestations per year	If observed harvest is greater than estimated P, the harvest is considered unsustainable	Used in several 'bushmeat' hunting studies. Relatively few parameters needed; easier to implement than full models in data-deficient conditions	Similar to Robinson & Redford (1991) model, may not be precautionary enough; does not include species survival rates. Similar rudimentary natural mortality factor	Bodmer (1994) Bodmer *et al.* (1994) Robinson & Bodmer (1999)
Maximum sustainable yield (MSY)	$\frac{dN}{dt} = rN(1 - \frac{N}{K}) - H$ $MSY = \frac{rK}{4}$ N = population abundance K = carrying capacity r = intrinsic rate of population growth	If observed harvest is larger than MSY, it is considered unsustainable	Clear reference target, commonly used in fisheries	May have ambiguous results; a harvest less than MSY may indicate overexploitation from a small, overexploited population Milner-Gulland, E.J. & Rowcliffe, M.J. (2007)	Milner-Gulland (2007) Brook and Whitehead (2005) Jensen (2002)

Table 1. (continued)

Indicator	Model/Parameters	Comparator/Outcome	Advantages	Disadvantages/Critiques	Key reference(s)
US National Marine Fisheries Service algorithm (Potential biological removal)	PBR = N_{min}*0.5R_{max} *F_R N_{min} = minimum population estimate R_{max} = maximum per capita rate of population increase F_R = recovery factor between 0.1 and 1	Harvest level exceeding the 'potential biological removal level' is considered unsustainable	Clear reference target; Shown by Milner-Gulland & Akçakaya (2001) and others to perform well in simulation tests; Relatively few parameters needed. Accounts for uncertainty by using minimum abundance term, and accounts for bias with F_R term	The intent of the algorithm is to be sufficiently precautionary to allow depleted populations to recover; thus it may not maximise production	Milner-Gulland & Akçakaya (2001) Wade (1998) Cowlishaw *et al.* (2005)
Comparison between sites					
Population abundance/density	Comparison of population abundance/density in hunted and unhunted (or lightly hunted) sites	Significant differences (generally hunted sites have lower species abundances) are interpreted as unsustainable	Differences are testable Common index in bushmeat hunting studies	Populations can be harvested 'sustainably' at an infinite number of population sizes, as long as offtake does not exceed production rates. Differences in population sizes alone cannot be used to assess sustainability. Sites must be otherwise comparable.	Robinson & Redford (1994) Sutherland (2001) Fitzgibbon (1995)
Population age/sex structure	Comparison of population age/sex structure in hunted and unhunted (or lightly hunted) sites	Significant differences are interpreted as unsustainable	Differences are testable Common index in bushmeat hunting studies	Differences in age/sex structure alone cannot be used to assess sustainability	Hurtado-Gonzales & Bodmer (2004) Velasco *et al.* (2003)
Market indices					
Prices of game and alternatives	Market prices	Price trends over time; if prices of wildlife increase, considered an economic signal of diminished supply, and therefore considered unsustainable	Market data often easier to acquire than species demographic data in many tropical settings	Supply and demand can be influenced by multiple factors (e.g. taste preferences, law enforcement, environmental changes, technology changes), thereby confounding sustainability inference	Milner-Gulland and Clayton (2002) Albrechtsen*et al.* (2007) Cowlishaw *et al.* (2005)
Quantity of species sold	Quantity	Quantity of species available over time; declines signify unsustainability	As above	As above	Albrechtsen *et al.* (2007)
Changes in species composition	Species composition over time	Changes indicate unsustainability (or recovering populations)	As above	As above	Albrechtsen *et al.* (2007) Rowcliffe *et al.* 2003); Crookes *et al.* (2005)
Trends in distance of wildlife from source to market	Wildlife source distance information over time	Wildlife source distance; if distance is increasing, hunting is considered unsustainable	As above	Distance to market may be influenced by other factors (e.g. law enforcement, environmental changes)	Albrechtsen *et al.* (2007) Cowlishaw *et al.* (2005) Crookes *et al.* (2005)
Harvest					
Harvest rates	Harvest data, but no effort data	Temporal trend or comparison with other sites	Obtained from hunters; easier than monitoring populations through time	Ambiguous results, depending on area and effort used for each harvest	Hurtado-Gonzales & Bodmer (2004)
Change in distance required for hunting	Distance to hunts	Trends in distance over time or in comparison with other sites	Data relatively easy to obtain	Changes in distance to hunting can have multiple causes, (e.g. changes in supply, demand; local depletion)	Smith (2008) van Vliet & Nasi (2008)

Table 1. (continued)

Indicator	Model/Parameters	Comparator/Outcome	Advantages	Disadvantages/Critiques	Key reference(s)
Changes in species composition at village level	Species composition over time	Changes indicate unsustainability (or recovering populations)	Obtained from hunters; generally easier than monitoring populations; multiple prey species evaluated	Need to distinguish between effects of selective vs. non-selective hunting techniques	Albrechtsen *et al.* (2007) Rowcliffe *et al.* (2003)
Other indicators					
Robinson and Bennett's (2000) estimate of sustainable harvest rates at 152 kg km^{-2}	Total harvest rate	Global harvest rate of 152 kg km^{-2}; calculated for the neotropics only	Simple rule-of-thumb	Does not account for uncertainty or inter-site variation in productivity	Robinson & Bennett (2000) Gavin (2007)
Hill and Padwe's (2000) potential sustainable yield	Human population density	Potential sustainable yields when 5 km^2 available per consumer	Simple rule-of-thumb	Does not account for uncertainty or intersite variation in productivity	Hill and Padwe (2000) Gavin (2007)
Robinson and Bennett's (2000) human population density $\leq$ 1 person km^{-2}	Human population density	Sustainable yields with human population densities $\leq$ 1 person km^{-2}	Simple rule-of-thumb	Does not account for uncertainty or intersite variation in productivity	Robinson and Bennett (2000) Gavin (2007)
Compensatory mortality	Quantifying compensatory mortality based on river flooding	Sustainable if harvests less than mortality due to seasonal flooding	Simple counts	Very case-specific	Caputo *et al.* (2005)
10% Harvest rule	Population sizes	Arbitrary 10% rule applied to several species	Simple rule-of-thumb	Proportion may differ in different species	Caro *et al.* (1998)

region of study, ecoregion, HDI rank or publication year had significant associations with the reported outcome of sustainability assessment. GLMM allows for the testing of non-normally distributed data, and can account for non-independence in the data with random effects terms. Additionally, we tested for multicollinearity among variables using the variance inflation factor (VIF); all VIF values were <2, indicating no major collinearity issues (Zuur *et al.* 2007). We used a logistic link function to model a binary response variable (sustainable/unsustainable), and specified study site as a random effect to account for non-independence of multiple sustainability assessments conducted at the same study site (Crawley 2007; Bolker *et al.* 2009; Zuur *et al.* 2009). We compared 20 candidate models using Akaike Information Criterion corrected for small sample size (AICc), and constructed a 95% confidence set of models using Akaike weights (Burnham & Anderson 2002). The significance of differences among factors of categorical explanatory variables was investigated using Wald's Z statistic (Bolker *et al.* 2009). All analyses were done in R (version 2.12, R Development Core Team 2010), and included the lme4 package for the GLMM analysis (Bates & Maechler 2010).

Finally, for a subset of papers using the model described by Robinson & Redford (1991), which accounts for the single largest number of individual sustainability assessments (for details, see Table 1), we determined sensitivity and specificity of the model relative to other indicators used on the same set of data, relying on comparator indicators that are supported in the literature [population trends through time, and the potential biological removal model (PBR); Table 1]. Sensitivity and specificity are measures of the performance of tests with binary outcomes, where sensitivity is the probability that a test correctly classifies the outcome of interest (specified in this case as unsustainability), while specificity is the probability that a test correctly classifies the negative outcome of interest (in this case sustainability).

RESULTS

Our literature search yielded 3172 studies of harvest sustainability, of which 102 fulfilled all of our *a priori* criteria (see Appendix S1). In these studies, 750 separate evaluations of harvest sustainability were assessed (see Appendix S2), covering 231 unique species (153 mammal species, 60 bird species and 18 reptile species). Fifty-five of the studies were single-species assessments and 47 were multi-species assessments. A total of 487 of the 750 (65%) harvests were deemed 'sustainable' by the authors, while 263 (35%) were deemed 'unsustainable'. Overall, there has been a general increasing trend over time in papers evaluating the sustainability of wildlife hunting since 1993, with a possible levelling off in recent years (Fig. 1). Two models contributed to the 95% confidence set of the GLMM model (cumulative Akaike weights $\geq$ 0.95; Table 2). Cumulative Akaike weights can also be used to rank the relative importance of each explanatory variable in predicting the probability of reported sustainability (Burnham & Anderson 2002; Zuur *et al.* 2009). This provided strong inferential evidence that sustainability indicator, continent, species body mass, taxa and HDI rank are all important predictors of reported sustainability, whereas ecoregion and publication year were not (Table 3). Because the most explanatory model (lowest AICc) was weighted more than three times the second model (Table 2), we used parameter estimates from the lowest ranked model.

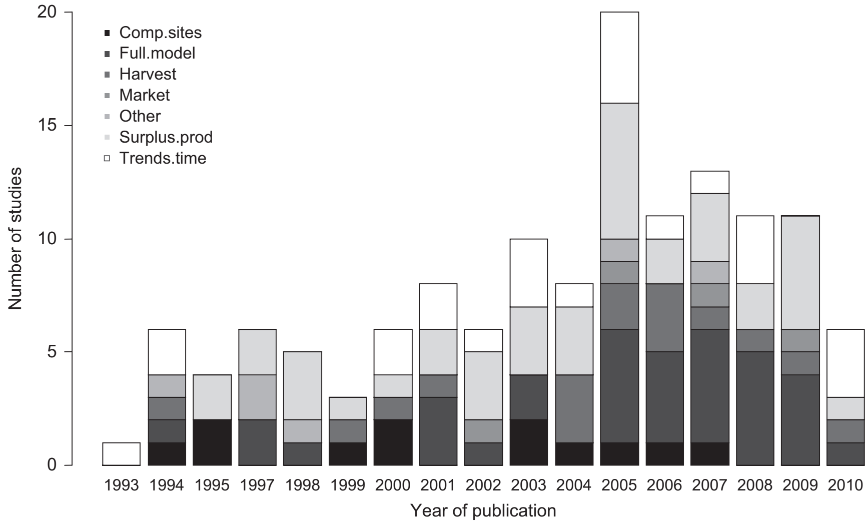

Figure 1 Trend through time of peer-reviewed papers addressing wildlife sustainability.

Sustainability indicators

The probability of reported sustainability was strongly associated with sustainability indictor type (cumulative Akaike weight = 1). The top five most commonly used sustainability measures included (1) demographic models of population growth ('Full model'), applied in 24% of the studies, but which made up only 9% of all individual sustainability assessments; (2) the Robinson & Redford (1991) model, used in 21% of the studies, but accounted for 34% of all assessments; (3) population trend methods, used in 17% of the studies, and 20% of all assessments; (4) harvest-based indicators (12% of studies and 15% of all assessments) and (5) comparisons of demographic parameters between sites ('Compare sites'), employed in 9% of studies and 6% of assessments (Fig. 2). Relative to the reference group (population trends through time), two assessment methods were significantly different: full models and the 'Other' category were negatively associated with the probability of reported sustainability (Wald $Z = -2.21$, $P = 0.027$; and Wald $Z = -2.05$, $P = 0.04$ respectively; Table 5, and see Fig. S1).

Species traits

The 102 studies yielded 231 unique species examined for harvest sustainability (153 mammal species, 60 bird species and 18 reptile species). Breaking down the total number of individual assessments, there were 269 assessments of ungulates, 110 assessments of birds, 109 assessments of primates, 91 assessments of rodents, 64 assessments of carnivores and 107 assessments of other taxonomic groups (Table 4). Species body mass (log) was negatively associated with sustainability (cumulative Akaike weight = 1, Table 3; Wald $Z = -2.86$, $P = 0.004$; Table 5). Relative to the reference group (rodents), harvests of birds, carnivores, primates and other mammals were significantly less likely to be deemed sustainable, (Wald $Z = -3.29$, $P = 0.001$; Wald $Z = -2.82$, $P = 0.005$; Wald $Z = -4.37$, $P < 0.0001$; and Wald $Z = -2.56$, $P = 0.01$ respectively; Table 5 and see Fig. S2).

Geographic variables

A majority of sustainability assessments occurred in Africa and South America (204 and 424 assessments respectively, or 84% of total assessments), and the remainder were spread across North America (8%), Europe (3%), Oceania (3%) and Asia (2%), (Table 4). By continent, only Oceania was significantly associated (negatively) with reported sustainability relative to the reference group, Africa (Wald $Z = -2.46$, $P = 0.014$; Table 5). 'Medium',

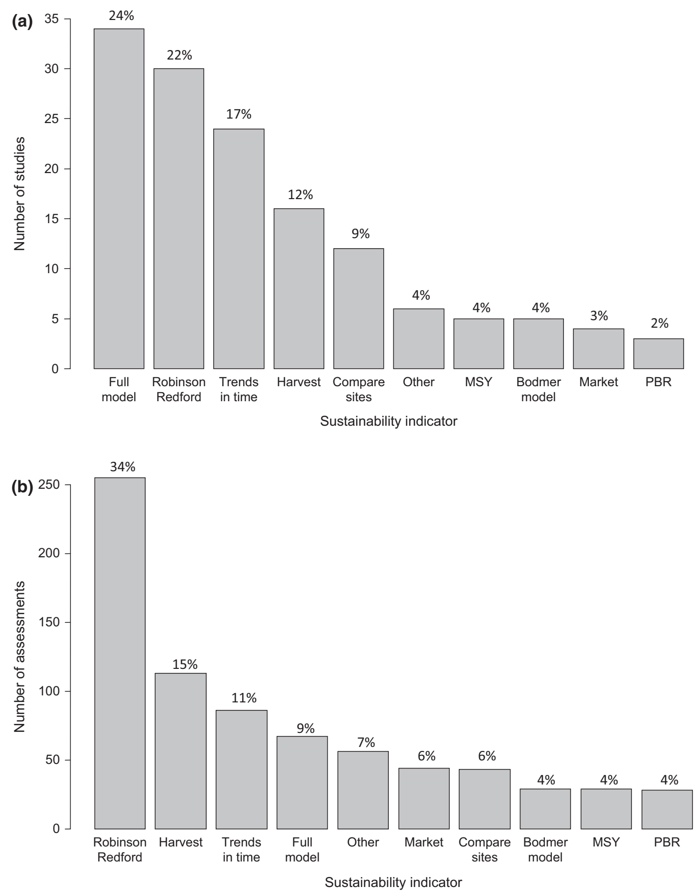

Figure 2 Total number of studies (a) and assessments (b) by sustainability indicator type.

Table 2 95% Confidence set (Models 1 and 2) and 99% confidence set (Models 1–3) of best-ranked generalised linear mixed models (cumulative Akaike weights $\geq$ 0.95) from a set of 20 candidate models

Rank	Model	K	AICc	ΔAICc	AICwt	Deviance
1	I + T + C + BM + H	27	761.82	0	0.77	705.9
2	I + T + C + BM + H + E	32	764.32	2.50	0.22	736.9
3	I + T + C + BM + Y	25	769.26	7.43	0.02	717.5

K, number of parameters; I, sustainability indicator; T, taxa; C, continent; BM, body mass; H, HDI rank; E, ecoregion; Y, pubyear; AICc, Akaike information criterion corrected.

Table 3 Cumulative Akaike weights of explanatory variables used to model the probability of sustainable harvests

Variable	Relative importance (based on cumulative Akaike weights)
Continent	1
Indicator	1
Species body mass (log)	1
Taxa	1
HDI rank	0.98
Ecoregion	0.22
Publication year	0.02

'High' and 'Very High' ranked countries on the HDI were positively associated with reported sustainability relative to 'Low' ranked countries (significant associations for 'Medium' HDI Rank, Wald $Z = 3.12$, $P = 0.002$, and 'Very High' HDI Rank, Wald $Z = 2.36$, $P = 0.018$; Table 5 and see Fig. S3). The 'gold standards' of sustainability indicators, which use direct data on population trends and/or demographic characteristics [e.g. monitoring populations through time, and using full population models to determine population growth rate (λ)], are mainly used in North America, Europe and Asia. Other indicators, which do not necessarily use direct data from the wildlife population being evaluated (e.g. Robinson & Redford (1991) model, Bodmer (1994) model, market indices, harvest-based indicators and others (Table 1), are used almost exclusively in Africa, South America and Oceania (see Fig. S4).

Comparison of Robinson & Redford (1991) model to other indicators

Generally, studies using the Robinson and Redford model did so in tropical developing regions, where biological and population-level data are difficult to acquire. However, we found five papers (Hill *et al.* 2003; Siren *et al.* 2004; Cowlishaw *et al.* 2005; Noss *et al.* 2005; Zapata-Rios *et al.* 2009) that used the Robinson and Redford model and that were also able to compare their results with at least one other indicator (trends through time, catch-per-unit-effort (CPUE) and the PBR model, Table 1). We pooled trends through time, CPUE and PBR indicators and compared these results with the Robinson and Redford model (Table 6). With 86 comparisons, specificity of the Robinson and Redford model (the probability of correctly classifying sustainability) was 92% (95% CI: 82–98%), while sensitivity (the probability of correctly classifying unsustainability) was 42% (95% CI: 25–61%).

Table 4 Characteristics of wildlife harvesting sustainability assessments, 1993–2010

	Studies No. (%)	Observations no. (%)
Continent		
Africa	20 (19.2)	204 (27.2)
Asia	5 (4.8)	12 (1.6)
Europe	9 (8.7)	25 (3.3)
North America	31 (29.8)	60 (8.0)
Oceania	11 (10.6)	25 (3.3)
South America	28 (26.9)	424 (56.5)
HDI rank		
Low	8 (7.5)	32 (4.3)
Medium	25 (23.6)	283 (37.7)
High	32 (30.2)	352 (46.9)
Very High	41 (38.7)	83 (11.1)
Indicator		
Bodmer model	5 (3.6)	29 (3.9)
Compare sites	12 (8.6)	43 (5.7)
Full model	34 (24.5)	67 (8.9)
Harvest	16 (11.5)	113 (15.1)
Market	4 (2.9)	44 (5.9)
Maximum sustainable yield	5 (3.6)	29 (3.9)
Other	6 (4.3)	56 (7.5)
Potential biological removal	3 (2.2)	28 (3.7)
Robinson & Redford (1991)	30 (21.6)	255 (34.0)
Trends time	24 (17.3)	86 (11.5)
Taxa		
Bird	34 (18.6)	110 (14.7)
Carnivore	35 (19.1)	64 (8.5)
Edentata	9 (4.9)	35 (4.7)
Mammal (other)	12 (6.6)	43 (5.7)
Primate	23 (12.6)	109 (14.5)
Reptile	11 (6.0)	29 (3.9)
Rodent	20 (10.9)	91 (12.1)
Ungulate	39 (21.3)	269 (35.9)
Ecoregion		
Desert	6 (5.7)	10 (1.3)
Savanna/grassland	15 (14.2)	108 (14.4)
Temperate forest	19 (17.9)	41 (5.5)
Tropical forest	46 (43.4)	552 (73.6)
Tundra/taiga	15 (14.2)	20 (2.7)
Various (generalist)	5 (4.7)	19 (2.5)
Species Body		
Range (g)	[16–3 825 000]	
Mass		
Mean (g) (± SD)	[49 762 ± 224 778]	

DISCUSSION

Sustainability indicators

The global extent of wildlife hunting, the role of wildlife underpinning human food security and current extinction threats to wildlife highlight the need for appropriate sustainability indicators to monitor conditions and trends of harvested wildlife species. Several authors (e.g. Robinson & Redford 1994; Milner-Gulland & Akçakaya 2001; Sutherland 2001) have called attention to the importance of reliable methods for evaluating the sustainability of wildlife offtake and assessing the status of hunted wildlife populations. They note that theory often does not inform data collection and management planning as it should, which has serious implications for the quality of conservation and livelihood recommendations made from

Table 5 Coefficient estimates and significance of parameters in the top candidate model for the probability of sustainable outcome. Parameter coefficient estimates, standard errors, Wald Z test statistics and P-values reported

Variable	Factor	Estimate	SE	Z value	Pr(>|z|)
	(Intercept)	2.557	1.318	1.940	0.052†
Indicator type	Bodmer model	0.242	0.777	0.312	0.755
	Compare sites	0.071	0.739	0.096	0.924
	Full model	−1.669	0.757	−2.205	0.027*
	Harvest	0.791	0.650	1.216	0.224
	Market	−2.381	1.388	−1.715	0.086†
	Maximum sustainable yield	−0.389	0.930	−0.418	0.676
	Potential biological removal	−1.032	1.242	−0.831	0.406
	Robinson & Redford (1991)	0.046	0.559	0.082	0.934
	Other	−1.806	0.879	−2.054	0.040*
Continent	Asia	−20.860	1068	−0.020	0.984
	Europe	−1.141	1.478	−0.772	0.440
	North America	1.044	1.426	0.732	0.464
	Oceania	−2.615	1.062	−2.463	0.014*
	South America	0.008	1.044	0.008	0.994
HDI rank	Medium	2.983	0.955	3.123	0.002**
	High	2.031	1.336	1.519	0.129
	Very high	3.797	1.610	2.358	0.018*
Body mass	log (body mass)	−0.305	0.107	−2.855	0.004**
Taxa	Bird	−1.699	0.517	−3.290	0.001**
	Carnivore	−1.639	0.581	−2.824	0.005**
	Edentata	−0.040	0.675	−0.060	0.953
	Mammal (other)	−1.703	0.664	−2.562	0.010**
	Primate	−1.991	0.456	−4.369	0.000***
	Reptile	1.504	1.509	0.997	0.319
	Ungulate	−0.388	0.466	−0.831	0.406

One level of each categorical variable serves as the reference group for the other levels (i.e. contrast; coefficient estimate = 0). These are as follows: Population trends through time (Indicator type), Africa (Continent), Low (HDI Rank) and Rodent (Taxa).
Significance of coefficients is denoted as: ***P < 0.001, **P < 0.01, *P < 0.05, $^{\dagger}P$ < 0.10.

such research. Nowhere is this more urgent than in the places where people rely directly on wildlife meat for protein, calories, micronutrients and livelihoods (Golden *et al.* 2011). In such regions, the precautionary principle alone will not be sufficient to balance the needs of wildlife species and the people who depend on them; therefore, efforts to maximise harvests and the persistence of harvested populations must be improved.

Our systematic review of the literature found that the most commonly used sustainability indicators were demographic models of population growth, the Robinson and Redford model, population trends through time, harvest-based indicators and comparisons of demographic parameters between sites. Although all indicators will have trade-offs in terms of effort required for data collection, scale of coverage, timeliness, accuracy and precision, some of the commonly used indicators have weaker theoretical support and thus may provide only very coarse-scale information whose reliability can be questioned. Static, one-off indicators cannot ultimately predict sustainability; it has been shown that in a sustainable system, half of a random sample of sustainability indicator evaluations would indicate unsustainability due to stochastic processes about an equilibrium (Ling & Milner-Gulland 2006). Although we propose the monitoring of harvested populations through time as one of the gold standards in sustainability monitoring, this approach is likely to be more difficult in remote, tropical locations that lack infrastructure for such research. Additionally, without a clear relationship with hunting patterns, wildlife population trends may increase or decrease due to exogenous factors other than hunting, such as habitat or climatic changes, or unmonitored harvests elsewhere in the population (Hill *et al.* 2003). Demonstrating a decline between two points in time is not enough to diagnose unsustainability. Ideally, population monitoring is an ongoing process and is accompanied by adaptive harvesting strategies (Johnson *et al.* 2002).

Demographic models in the form of matrix population models ('Full models') are also considered a gold standard (Milner-Gulland & Akçakaya 2001) due to the full use of species' demographic information and the ability to determine optimal offtake by age or stage class (Getz & Haight 1989). However, such models often do not account for density dependence (Marboutin *et al.* 2003; Dobey *et al.* 2005), whereas the ability of harvested animals to persist in the presence of sustained exploitation may be evidence for density dependence (Marboutin *et al.* 2003). Ignoring density dependence where it occurs could lead to a conservative bias in allowable sustainable offtake, underestimating MSY and possibly explaining the negative bias of full models found in this study relative to monitoring population trends through time (Table 5). This result could also be due to animal dispersal/immigration that is not being properly captured by demographic harvest models (Pople *et al.* 2007).

The Robinson & Redford (1991) model is relatively easy to implement because it uses Cole's formula (1954) to calculate maximum finite rate of population growth (λ) and thus requires little actual demographic information from local contexts, and involves relatively simple calculations (Robinson & Redford 1994; Slade *et al.* 1998). Although initially intended as a crude indicator able to detect only whether harvests exceeded an estimated maximum possible wildlife production (Robinson & Redford 1994), its simplicity has drawn many users. Robinson & Redford (1994) themselves state that the model 'does not allow the conclusion that an actual harvest is sustainable', and that 'low harvests might be a consequence of depleted game densities, less than maximum birth rates, higher than minimum mortality rates, etc.' (Robinson & Redford 1994). Slade *et al.* (1998) contend that because the Robinson and Redford method uses Cole's formula and ignores mortality of juveniles or adults prior to age at first reproduction; it thus has a tendency to overestimate maximum production and thereby underestimate overharvesting. Despite a mortality factor (F) added to address this (Table 1), it has still been criticised as addressing the issue in a highly simplified way (Milner-Gulland & Akçakaya 2001; van Vliet & Nasi 2008). Our results of sensitivity and specificity support the argument that the Robinson and Redford model poorly classifies unsustainability.

On the other hand, there are some situations where the Robinson and Redford model may be too conservative. In Slade *et al.*'s (1998) analysis, the Robinson and Redford model may have also *underestimated* maximum rates of increase for some species compared with production estimates from complete life tables (in five of 19 species examined). A number of authors echo the observation that although deemed unsustainable according to the Robinson and Redford model, some harvested populations showed no signs of depletion (Alvard *et al.* 1997; Ohl-Schacherer *et al.* 2007; Koster 2008), or harvest levels in their study sites have been maintained or even increased over time (Alvard *et al.* 1997; Novaro *et al.* 2000; Hill *et al.* 2003; Peres & Nascimento 2006; van Vliet & Nasi 2008). Salas & Kim (2002) and others voice concern over the model's assumption of a closed population, and that in fact localised hunting may be sustainable at larger spatial scales when unhunted populations contribute immigrants to hunted populations, effectively increasing the potential harvestable surplus. They and others (e.g. van Vliet & Nasi 2008) also note that, as density is the most sensitive variable in the Robinson and Redford model, measuring it accurately is perhaps more important than accurately measuring the other parameters in the model, although this is often not done due to difficult monitoring conditions. van Vliet & Nasi (2008) emphasise the number of assumptions required by this model and the uncertainty that is accumulated in these calculations, that is, in estimates of density, mortality factor F and rate of maximum population increase. In short, it is not possible to predict the net direction of biases in this commonly used model.

Another commonly used sustainability indicator, the comparison of wildlife abundance or other demographic parameters across two or more sites at one point in time (Table 1), cannot actually determine sustainability according to theory relying on logistic, density-dependent population growth (Robinson & Redford 1994), and is sensitive to underlying differences among compared sites. Under this theory, MSY occurs when a population is at one-half of its carrying capacity (although this will vary somewhat by taxa). Methods that demonstrate significant differences between hunted and unhunted sites can effectively demonstrate only local depletion (Hill *et al.* 2003). Local depletion may reflect sustainable harvest when greater spatial scales are taken into account, where animal dispersal and recolonisation can be accounted for (Siren *et al.* 2004). In some cases, hunting impact studies may not be able to distinguish between evasive prey behaviour and actual changes in animal density (Hill *et al.* 1997; Siren *et al.* 2004). Additionally, simple comparisons of biomass extraction in different areas can be misleading. Fa *et al.* (2002) and others show that mammal biomass is generally higher in Africa than in the Neotropics, and therefore, it is to be expected that more biomass per unit area can be extracted from African forests.

Table 6 Sensitivity and specificity measuring the performance of Robinson & Redford (1991) model vs. other sustainability indicators, when both were provided within a study. Results are based on 87 comparisons in five studies. Pooled indicators include population trends through time, catch-per-unit-effort and potential biological removal indicators (see Table 1 for indicator descriptions)

		Predicted by other (pooled) indicators		
		Unsustainable	Sustainable	Total
Predicted by Robinson & Redford (1991)	Unsustainable	14	4	18
	Sustainable	19	49	68
	Total	33	53	86

Species traits

Species traits are hypothesised to influence the potential productivity and resilience of a population in the face of harvest (Cardillo *et al.* 2005). Relative to the reference group (rodents), harvests of birds, carnivores, primates and other mammals (Marsupialia, Chiroptera, Lagomorpha) were significantly more likely to be characterised as unsustainable (Table 5). These trends match theoretical predictions and empirical observations that taxa with lower intrinsic rates of increase are more susceptible to overharvest (Bodmer *et al.* 1997; Price & Gittleman 2007). Ungulates (including duikers, brocket deer and pigs) play an important role in terms of both numbers and biomass consumed; it is notable that they may be relatively tolerant to hunting (Bodmer 1995; Alvard *et al.* 1997; Hurtado-Gonzales & Bodmer 2004; Reyna-Hurtado & Tanner 2007). In some cases, species may actually show an increase in abundance in more heavily hunted areas, such as the dwarf brocket deer in Argentina, purportedly due to decreased competition with another brocket deer species (Di Bitetti *et al.* 2008).

Additionally, sustainability will also depend on which age classes of a species are targeted. For example, bird nestlings will be harvested at a maximal rate, when all nesting sites are occupied at near carry capacity (Beissinger & Bucher 1992). If there is a proportion of the population that is non-breeding, hunting is expected to be more compensatory rather than additive (Beissinger & Bucher 1992; Kenward *et al.* 2007). Although relatively well studied in developed countries, there is still a need for field studies that address hypotheses on forms of density-dependent mortality and reproduction, and compensatory vs. additive mortality effects in tropical harvested species.

Geography of wildlife hunting assessments

We found strong geographical trends influencing the probability of reported sustainability, and geographical differences in where sustainability indicators are used. The HDI rank of the country of study plays an important role in predicting reported sustainability, where higher HDI ranked countries are associated with sustainability relative to lower ranked HDI countries (Table 5). The HDI rank is a comparative index of health, education and economic well-being, and therefore may predict technical and socio-political capacity to manage renewable resources. Oceania was the only region to have significantly lower probability of reported sustainability than Africa (Table 5), which may be explained at least in part by island isolation and lower probability of recolonisation of extinct meta-populations. Asia was poorly represented in the number of sustainability studies, which may reflect an endgame of many people and fewer protected areas, and researchers' perceptions that there is no sustainable hunting left in Asia (Bennett 2007). The stark geographical differences in where particular indicators are used may introduce unintended biases into the results of sustainability assessments, particularly as some cruder estimates (characterised by very little local biological and population-level data) are used largely in developing countries, which are the very places where humans have the most direct reliance.

Scale, source-sink theory and refugia

Many authors note that there is a missing element to most commonly used sustainability analyses: spatial scale. From the meta-population approach, unhunted and hunted populations can be seen as source and sink populations, respectively, linked to each other to varying degrees by emigration and immigration. Peres (2001) referred to this as the 'rescue effect' of overharvested species, where immigrants from surrounding areas can rebuild depleted populations and replenish local game stocks. Siren *et al.* (2004) found different results from the Robinson and Redford model, depending on the extent of the spatial scale they examined. At smaller scales, they found several zones that were overharvested, but when looking at the larger catch basin scale, the harvest appeared sustainable. Novaro *et al.* (2000) compiled results from five separate studies on the sustainability of tapir hunting in South America. Four of five study results contradicted predictions of extirpation (based on the Robinson and Redford model and Bodmer model), and hunters continued harvesting tapirs over the length of the studies, in some cases up to 20–30 years later.

Studies that assess sustainability at very localised scales may be detecting 'depleted' populations, but this hunting may actually be in equilibrium with dispersing animals from unhunted populations outside of the hunted zone. Joshi & Gadgil (1991), McCullough (1996), Ling & Milner-Gulland (2008) and others explore the utility of spatial controls on areas under harvest, as a way to maximise harvest and minimise the risk of overharvest, even in the absence of detailed biological data. This notion of 'refugia' in space and time has been shown empirically by Novaro *et al.* (2005), but is still a vastly under-appreciated area of research. Although some authors emphasise issues of spatial scale, we also stress that temporal scale is a crucial element to assessing longer term sustainability. Although many sustainability studies are often of limited time frames – whether as part of rapid conservation NGO research or doctoral dissertation research – we advocate a more concerted effort at national and international scales to monitor harvested wildlife populations through time, as part of management efforts (Nichols & Williams 2006). Examples include waterfowl monitoring in the United States (Nichols *et al.* 1995), kangaroo monitoring in Australia (Pople *et al.* 2007) and global fisheries and aquaculture monitoring by the Food and Agriculture Organization of the United Nations (FAO 2010).

There are inherent methodological biases both in the field and in the scientific literature that preclude taking interpretations of our analysis too far. Aside from geographical biases of where different sustainability indicators are used, there may also be a selection bias of which populations and study sites are chosen. Conservation biologists may tend to focus on areas or species of particular concern that would be more likely to result in unsustainable harvests. Publication bias might imply that it is more likely that an 'unsustainable' harvest be reported, as the 'effect' of interest (Gates 2002). The recent levelling off in harvest sustainability papers (Fig. 1), however, might be evidence of a more nuanced understanding of sustainability, and although researchers continue to use the same indicators, they appear to be more conservative now in the statements they make about sustainability.

FUTURE RESEARCH DIRECTIONS

As argued elsewhere (Milner-Gulland & Rowcliffe 2007), long-term population monitoring programmes will be the most informative approach to provide baseline information against which any hunting effects and/or conservation interventions can be monitored; barring this, indicators of sustainability will continue to be used. Milner-Gulland & Akçakaya (2001) simulated harvests using six algorithms to assess the trade-offs between maximising total harvests and minimising risk of the population going below a population threshold of 2% of carrying capacity. Compared with the Robinson and Redford model, and two related versions of the Bodmer model (Bodmer 1994; Robinson & Bodmer 1999), the full demographic model performed best, with the PBR model (Wade 1998) model performing reasonably well. At present, only two empirical terrestrial studies employ the PBR model (Cowlishaw *et al.* 2005; Dillingham & Fletcher 2008). We suggest that these methods should be the focus of future studies, in favour over the Robinson and Redford model and Bodmer models (Robinson & Bodmer 1999). In addition to prioritising long-term population monitoring, research should be directed at acquiring basic life-history data for exploited species whose biology is not yet well known, and derived from the population of interest whenever possible. If direct assessments of population abundance or demography remain difficult (e.g. in tropical forest conditions), another avenue for further research is in the utility of CPUE indicators (Rist *et al.* 2008, 2010), as these are often easier to acquire and can be informed by much of the fisheries modelling, for example, integrated stock assessments (Maunder & Punt 2004). However, employment of methods of the sophistication of those employed in fisheries and forestry harvesting analyses (Kuparinen *et al.* 2012; Yousefpour *et al.* 2012) requires both reliable and detailed information on the abundance and demographic structure of species and their potential biological responses to processes impacted by global climate change and habitat transformations.

More recent emphasis in renewable resource management involves multi-species modelling, and modelling that incorporates uncertainty and takes into account harvester behaviour in addition to harvested population dynamics. Wildlife harvesting across much of the tropics involves a multi-species prey base, which may be important to consider simultaneously because of species interactions and the potential for hunting effort to affect different species disproportionately (Rowcliffe *et al.* 2003). Adaptive harvest management (AHM) is an iterative process of monitoring, assessment and decision making incorporating uncertainties in all of these areas (Johnson *et al.* 2002), and rests on the premise that harvest sustainability is enhanced with on-the-ground experimentation (Hilborn *et al.* 1995; Nichols *et al.* 1995; Walters 2001). The management of harvested waterfowl in North America since 1995 is an example of a successful adaptive management strategy (Nichols *et al.* 2007). Management strategy evaluation (MSE) is a modelling framework that has wide use in fisheries, with great potential for application to terrestrial wildlife management (Bunnefeld *et al.* 2011; Milner-Gulland 2011). MSEs extend AHM to incorporate the underlying social processes that influence harvester behaviour. Through probabilistic simulation models, stakeholders can evaluate trade-offs in different management scenarios (e.g. harvest levels), including varying areas and magnitudes of uncertainty.

CONCLUSION

Hundreds of millions of people around the world depend on wildlife for their nutrition and livelihoods. The sustainability of the harvesting of many of these species upon which people depend is at stake. We have shown that some of the most commonly used sustainability indicators rely on very little biological and population-level data from the population of interest, and although they have already received heavy criticism in the scientific literature, they continue to be used. It would be imprudent to continue using 'rule-of-thumb' indicators in the very regions of the world where people depend most on wildlife as food sources. Resource managers and conservationists should focus on research that seeks to maximise productive use of wildlife, while minimising the probability of species extinction. This will require better knowledge of tropical species' biology and ecology, more long-term monitoring of wildlife populations, spatial scale and source-sink considerations, and modelling methods that take into account uncertainty.

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AUTHORSHIP

KW and CG gathered data, JB and WG advised on overall framework, KW performed the analysis and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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