Sustainability indices for exploited populations

E.J. Milner-Gulland and H. Resit Akçakaya

Evaluating the sustainability of hunting is key to the conservation of species exploited for bushmeat. Researchers are often hampered by a lack of basic biological data, the usual response to which is to develop sustainability indices based on highly simplified population models. However, the standard indices in the bushmeat literature do not perform well under realistic conditions of uncertainty, bias in parameter estimation, and habitat loss. Another possible approach to estimating the sustainability of hunting under uncertainty is to use Bayesian statistics, but this is mathematically demanding. Red listing of threatened species has to be carried out in extremely data-poor situations: uncertainty has been incorporated into this process in a relatively simple and intuitive way using fuzzy numbers. The current methods for estimating sustainability of bushmeat hunting also do not incorporate spatial heterogeneity. No-take areas are one management tool that can address uncertainty in a spatially explicit way.

E.J. Milner-Gulland*
Dept of Environmental Science and Technology, Imperial College London, Prince Consort Road, London, UK SW7 2BP.
*e-mail: e.j.milner-gulland@ic.ac.uk

H. Resit Akçakaya
Applied Biomathematics, 100 North Country Road, Setauket, NY 11733, USA.

The hunting of wildlife for human consumption [BUSHMEAT (see Glossary) hunting] is a current topic of concern among conservationists. A resolution was passed at the World Conservation Congress (October 2000) calling for action to tackle the unsustainable commercial trade in bushmeat and the issue was also discussed at the Conference of the Parties to the Convention on International Trade in Endangered Species (CITES; April 2000). Research initiatives for tackling the problem have been announced by Conservation International, the Wildlife Conservation Society and the UK Dept of the Environment, Transport and the Regions; the World Bank has also recently commissioned a report about the bushmeat trade[1]. Unsustainable bushmeat hunting is a serious problem; sustainability assessments were recently published for 66 hunted species, 29 of which were found to be exploited unsustainably[2]. Local extinctions of hunted species are widespread, with west and central Africa being particularly hard hit. The recent extinction of Miss Waldron's red colobus *Procolobus badius waldroni*, a primate subspecies endemic to West Africa, was attributed to bushmeat hunting[3]. In spite of being the focus of attention, the problem is not confined to Africa or even to tropical forests. For example, large-scale poaching of the saiga antelope *Saiga tatarica* on the steppes of former Soviet-controlled central Asia has led to an 80% decline in population size since independence in 1991 (Ref. 4). Overhunting of bushmeat species is carried out for both subsistence and commercial purposes, its underlying causes are complex and varied, and many methods for tackling it have been suggested[2,5].

The need for sustainability indices

The first step in making the EXPLOITATION of wildlife more sustainable is to determine the sustainability of current levels of harvest. This has two aspects: (1) determining the OFFTAKE from an area; and (2) determining the effect that this offtake has on the species concerned. If the offtake is causing wildlife populations to decline to extremely low numbers or local extinction, it is clearly unsustainable and intervention is required.

Many researchers have carried out assessments of the SUSTAINABILITY of bushmeat hunting, with a particular focus on mammals in tropical forests. Major problems are the paucity of available biological data and the difficulty of collecting the data required for a full sustainability assessment. Consequently, assessments are plagued with uncertainty.

There are three kinds of uncertainty: process uncertainty caused by the inherent variability of natural systems; model uncertainty that reflects our ignorance about the system; and observational uncertainty arising from our attempts to obtain information about the system[6]. A precautionary approach to uncertainty requires that the benefit of the doubt should be given to the hunted species. Offtake levels should therefore be assumed to be on the high side of the range of possible values, and population size should be assumed to be on the low side.

Bushmeat researchers have approached the problem of uncertainty by developing quick and simple algorithms that provide crude estimates of sustainability. One such method, developed by Robinson and Redford[7] (Box 1), has become the standard in the field[2,8–11]. In spite of similar problems being tackled in the fisheries and resource management literature[12–14], the two literatures are not well integrated. In particular, the fisheries literature tends to rely on more sophisticated modelling. Recognition of the importance of uncertainty and of complexities such as spatial structure to the dynamics of ecological systems is growing in all fields of theoretical ecology, including conservation. However, theory often does not inform data collection and management planning as much as it could. This is an important problem because researchers could be making seriously misleading recommendations for conservation action by not using the most recently developed tools for estimating the sustainability of exploitation under uncertainty.

Here, we review the standard methods used in the bushmeat literature and discuss whether these simple algorithms are generating adequate results and in what circumstances they are most likely to fail. Are there methods in use in other fields of resource management that can take better account of uncertainty, but which remain simple enough for broad use by conservation practitioners?

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Box 1. An example of an algorithm for assessing the sustainability of bushmeat hunting

Robinson and Redford's method[a] is the most widely used algorithm for assessing bushmeat hunting sustainability. It is appealing because it is simple, uses parameter values that are relatively easy to obtain, and gives a threshold value against which sustainability can be judged. It uses data on population densities and rates of increase to estimate the maximum sustainable level of production, which can be compared with actual data on offtakes. There are four parameters.

(1) Density at carrying capacity (*K*). This can be obtained from data collected in unexploited and lightly hunted areas, or from empirical relationships between density, diet and body size.
(2) Intrinsic rate of population increase (R_{max}). This parameter is extremely difficult to estimate (Box 2).
(3) Density at which maximum production occurs (maximum sustainable yield level).
(4) Maximum production (*P*). The point at which maximum production occurs depends on the life-history strategy of the species[b]: Robinson and Redford's assumption of 60% of carrying capacity is probably suitable for forest ungulates.

They calculate maximum sustainable production as (Eqn I):

$$P = 0.6\,K\,(R_{max} - 1)\,F \qquad \text{[I]}$$

where *F* is a factor accounting for natural mortality. *F* varies with longevity, on the assumption that a high natural mortality rate implies that a high proportion of the harvest would have died anyway. Hunters can thus afford to take a higher proportion of the population than if natural mortality rates are low. Suggested values for *F* range from 0.2 for long-lived species (over ten years) to 0.6 for short-lived species (less than five years).

Robinson and Redford state that their method is a crude indication of sustainability and that any offtake level approaching *P* should cause concern. However, the method has been criticized for not explicitly including survival rates[c] and for using R_{max} instead of the actual population growth rate[d,e]. Both these problems lead to overestimation of *P*, which is contrary to the precautionary principle. The use of R_{max} is difficult because actual population growth rates are probably significantly lower than this because of density dependence. The mortality factor *F* addresses survival rates, but in a highly simplified way. It moderates the overestimation of *P*, with the greatest effect for longer lived species, which is good in conservation terms because these are often vulnerable. However, the original overestimation is probably more severe for shorter lived species[d].

To assess sustainability, *P* is compared to the number of individuals harvested from the area. However, if the population is already depleted to a low level, an apparently sustainable level of hunting can lead to overharvest and rapid extinction[d]. It is therefore important to supplement the assessment of sustainability with an independent check that the population density is above the level giving the maximum sustainable production.

References

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Methods for assessing bushmeat hunting sustainability

Many algorithms are used for the assessment of sustainability. We focus on three that were chosen for their simplicity and the degree of acceptance that they already command in the field (Table 1). In situations of uncertainty, such as generally exist for bushmeat hunting, the usual approach to assessing sustainability is to develop a highly simplified model of population dynamics with which to predict the effects of removing individuals through hunting. These models require parameters for the rate of population increase and abundance and an assumption about the effect of density dependence on population increase. There is much confusion in the literature about the definition of the rate of population increase (see Eqn I in Box 2), but none of these parameters is straightforward to estimate.

The Robinson and Redford[7] method uses the carrying capacity and the maximum rate of population increase (R_{max}) to calculate population PRODUCTION (Box 1). A conceptually similar model can be obtained using the deterministic discrete logistic equation, which also takes density dependence into account. A method developed by Bodmer[15] takes a rather different approach, based on calculating population production directly from fecundity rates rather than using R_{max}. A simple method developed for BYCATCH of marine mammals[14,16,17] is similar to that of Robinson and Redford[7], but with the crucial difference that uncertainty is taken into account by using a minimum estimate for abundance. All these methods involve the use of relatively arbitrary correction factors and assess sustainability by comparing actual offtake with a calculated threshold level above which offtake is deemed unsustainable.

An evaluation of methods for estimating sustainability

Following the PRECAUTIONARY PRINCIPLE, an algorithm that consistently overestimates the maximum sustainable offtake is less satisfactory than one that consistently underestimates it. If an algorithm is to be useful for assessing the sustainability of hunting, the maximum sustainable level of offtake that it calculates should actually be sustainable in the long term. Given that we are dealing with an uncertain system, we define sustainability in terms of the

Table 1. Algorithms used to assess the sustainability of bushmeat hunting and for cetacean bycatch

Name of algorithm	Algorithm[a]	Notes	Refs
Robinson and Redford	$P = 0.6\,K\,(R_{max}-1)\,F$	$F = 0.2$ for long-lived species, $F = 0.6$ for short-lived species	7
Bodmer A	$P = 0.5\,N\,\phi\,s$	$0.5\,N$ is an estimate of the density of the female component of the population. $s = 0.2$ for long-lived species, $s = 0.6$ for short-lived species	15
Bodmer B (altered version of Bodmer A)	$P = 0.5\,N\,\phi\,s$	s is the actual percentage of individuals surviving to the average age at reproduction	
NMFS	$P = 0.5\,N\,(R_{max}-1)\,F$	N is a minimum estimate. F varies between 0.1 and 1.0, depending on level of bias and uncertainty in the data. Here, $N = 0.9$ of the estimated value, $F = 0.5$	14
Deterministic discrete logistic	$P = 0.6K\left(\frac{R_{max}}{1+0.6(R_{max}-1)}-1\right)$	Assumes that the target population size is $0.6K$	36

[a]In each case: P, the sustainable level of production; R_{max}, maximum annual per capita rate of increase (Box 2); K, population density at carrying capacity; N, current population size; F, mortality or recovery factor. For Bodmer's method, s, female survival to the average reproductive age; ϕ, female fecundity.

probability of the population not falling below a given size over a given period of time.

Because bushmeat hunting targets a wide range of species, from large mammals, such as primates, through to small birds, reptiles and insects, a wide range of life-history strategies is represented by the species to which these algorithms are applied. In evaluating the effectiveness of the algorithms, several important considerations must be addressed: (1) Is it possible to collect the data needed to parameterize the algorithm? (2) How much uncertainty is likely to surround the estimates of the parameters collected? (3) Under what circumstances is the algorithm likely to fail to detect over-exploitation? (4) The algorithm should not be too precautionary, because bushmeat hunting is the livelihood of many people.

Although the algorithms have all been parameterized from field-collected data, little has been published concerning the practicalities of using them or about the probable uncertainties surrounding parameter estimation [but see discussion of the reasoning behind the US National Marine Fisheries Service (NMFS) algorithm[18]]. The issues of failure to detect overexploitation and giving excessively precautionary results can be addressed using population models. It is particularly important to test algorithm performance for a range of life histories and to incorporate both process uncertainty (e.g. demographic stochasticity) and observation uncertainty into the tests (Box 3).

The main reason why the Robinson and Redford algorithm is unlikely to perform well under uncertainty is that it is insufficiently precautionary when populations are DEPLETED: it continues to allow offtake to occur when populations are small, which is not a problem when population dynamics are deterministic, but risks overhunting when there is uncertainty about the proportion of the population that the offtake represents. Bodmer's algorithm is unlikely to perform well because the factor s (a proxy for survival rates) is far too high: it is more robust when modified to include more realistic values for survival to the average reproductive age, tailored for individual species.

Even in the limited case study presented in Box 3, it is noticeable how much the performance of these algorithms varies with life-history strategy. Generally, the algorithms perform better for long-lived species with low annual fecundity. This is an effect of the values chosen for the correction factors s and F (the mortality or recovery factor): in long-lived species, the estimate of the sustainable level of production is reduced to 0.2 of the original estimate, compared with 0.6 for short-lived species. Thus, the algorithms are more precautionary for longer lived species, particularly if R_{max} is high. However, given that the range of life-history strategies of bushmeat species is so broad, it is important to find algorithms that are suitable for use for a wide range of species.

The NMFS method developed for cetacean bycatch appears to be highly promising in terms of its ability to reduce the risk of extinction to acceptably low levels. This was found both in the extensive simulation tests carried out by its developers[14,16–18], and in our case study (Box 3). However, another important consideration in controlling bushmeat hunting is that it is an important source of protein for many people living in and around forests. The estimated offtake of bushmeat from the Congo basin alone is 5 million tonnes yr^{-1} (Ref. 19). Generally, there is a tradeoff between extinction risk and level of offtake. As the NMFS algorithm was developed for bycatch species, this tradeoff was not a key consideration, so it errs on the precautionary side. However, this is a general problem for such rule-of-thumb algorithms. Because bushmeat hunting encompasses a wide range of taxonomic groups and there is a good deal of observational uncertainty, algorithms that lead to an acceptably low risk of overexploitation for all species also probably entail substantial losses in offtake.

The potential of methods from other fields

Simple deterministic models of population dynamics are not a sound basis for making decisions about the sustainability of bushmeat hunting. The authors of current methods are well aware of both the crude nature of their algorithms and the need to treat them as upper limits: they state that if offtake is found to

Box 2. Parameters representing the intrinsic rate of population increase

The intrinsic rate of population increase is a difficult parameter, both conceptually and practically. It is best described as the maximum rate of increase that a population can achieve under natural conditions without significant intraspecific competition. Therefore, it is best measured as the rate of increase of an extremely small population [assuming that no DEPENSATION (see Box Glossary) occurs]. In most cases, it is not feasible to measure directly the intrinsic rate of population increase, which can be represented as Eqn I:

$$\frac{dN}{dt} = rN \text{ or } N_{t+1} = RN_t \qquad \text{[I]}$$

where N is the population size, t is time, r is the geometric rate of increase (measured in continuous time) and R is the finite rate of increase (measured in discrete time). The latter two are related as $R = e^r$. The appropriate time dimension for these parameters depends on the life history of the species; for many mammals, they are often measured over the course of one year.

The finite rate of increase is sometimes represented by λ, which is confusing because λ is frequently used as the eigenvalue of a matrix, implying age or stage structure and a stable distribution. Thus for clarity, we use R rather than λ to represent the population growth rate.

Another confusion exists because R, r and λ are used to refer both to actual population growth rates and to constants representing population- or species-specific maximum values of the growth rate. These two meanings diverge under density dependence, which is assumed by all the methods that we consider. Under density dependence, the growth rate is assumed to decrease as density increases. The maximum growth rate (at low density, assuming no depensation) is represented as R_{max}. Differences between R_{max} and observed growth rates could also be due to environmental fluctuations, demographic stochasticity, sampling errors and uneven sex ratios.

Robinson and Redford suggest that the growth rate can be estimated using Cole's equation[a]. The equation assumes no mortality in the population, which is a very strong assumption. It is also not ideal because the required data are often unobtainable, which introduces an estimation error. It might be better to estimate R_{max} using empirically derived allometries, which are relationships between growth rates and characteristics (e.g. body mass) of a group of similar species[b]. However, the uncertainty in such estimates can also be extremely high. Another possibility is observing the growth of unhunted populations that are far below their carrying capacities, for example, populations in areas recently closed to hunting.

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Box Glossary

Depensation: also known as the Allee effect. The population growth rate increases as population size increases. This can occur at very low population sizes. By comparison, under normal density dependence, growth rate decreases with population size and so is at a maximum at low population sizes.

be near the estimated sustainable level, it should be a cause for concern[7].

Much recent progress has been made with research into sustainable exploitation under uncertainty, both in fisheries management and in theoretical ecology[20–22]. It would be highly beneficial if those working to bring the bushmeat hunting crisis under control could adopt some of the methods that have been developed in these other research fields.

The bushmeat problem is complex, involves many species and many different biological and socio-economic factors, and is particularly rife in areas where the biological systems affected are extremely poorly known. In spite of the severity of these obstacles to rigorous assessment, many of them also pertain to commercial fish stocks. Hence, methods used in fisheries management that explicitly incorporate uncertainty, such as BAYESIAN STATISTICS, could be useful[23]. Bayesian methods incorporate the uncertainty surrounding a parameter by representing it as a RANDOMLY DISTRIBUTED VARIABLE. They also provide a flexible framework for evaluating alternative hypotheses about the system. Results are given in the form of probability distributions, so that sustainability assessments are accompanied by a measure of the degree of certainty surrounding them. A high degree of mathematical sophistication is required, although this is becoming less of a constraint as software packages for Bayesian analysis are developed (such as WinBUGS)[24].

The data available for assessing the sustainability of bushmeat hunting are often patchy and short term, and the assessments have to be carried out in the field with only limited access to mathematical expertise, computational power and funding. An analogous situation is faced by the World Conservation Union (IUCN), when compiling RED LISTS of species threatened with extinction[25]. Here, a full population viability analysis would also be ideal, but, for most species, there are minimal data available from which a threat assessment must nonetheless be made. FUZZY NUMBERS have been used to place poorly known species into threat categories (Box 4). This approach is simple and intuitive enough to be used without mathematical training and could well be extremely useful for assessments of the sustainability of bushmeat hunting.

Spatial heterogeneity

One issue that is difficult to address with simple models, but which is increasingly recognized as being crucial for the sustainability of bushmeat hunting, is spatial heterogeneity[26,27]. Densities of hunted species might vary spatially either naturally or because of variations in HUNTING EFFORT. Effort is dependent on the cost of hunting. Costs include the distance that hunters must travel to catch or sell bushmeat, or in the case of illegal hunting, the risk of being caught in a PROTECTED AREA or with a protected species[28,29].

Box 3. An example of comparing the sustainability of the offtake obtained under various algorithms

Table I. Scenarios tested for each of the algorithms[a]

Life history[b]	Initial N[c]	K trend[d]	R_{max}	CV[e]	Bias[f]
Fast	K	1.0	1.05	0.1	1.0
Slow	0.2K	0.95	1.15	0.2	1.1

[a]1000 simulations of 50 years were run for each of the 64 combinations of scenarios for each algorithm.
[b]The slow life-history strategy has six age classes, first reproduction in age class 5, 2.05 daughters born to an average female each year, adult survival of 0.8, juvenile survival of 0.4885. The fast life-history strategy has four age classes, first reproduction in age class 1, 6.89 daughters born to an average female each year, adult survival of 0.4, juvenile survival of 0.3049. Density dependence is contest-type (i.e. following the Beverton–Holt equation) and affects fecundities.
[c]The carrying capacity, K, is set at 10 000 individuals. The two scenarios represent an unhunted population (initial population size, N, = K) and a depleted population (N = 0.2K).
[d]Carrying capacity either remains stable over time, or it is reduced by 5% each year, simulating the effects of habitat destruction.
[e]Variability is simulated by varying both survival and fecundity annually according to lognormal distributions with coefficients of variation (CVs) of 0.1 or 0.2.
[f]Bias in estimating parameters is either assumed not to exist (Bias = 1.0) or is assumed to inflate estimates of all parameter values by 10%.

Table II. Results of the comparison of algorithms[a,b]

Scenario		noH	Bod A	Bod B	Logistic	R&R	NMFS
Fast, R_{max} = 1.05	Base	0[b]	XXX	0	0	X	0
	CV = 0.2	0	XXX	X	XX	XXX	0
	Bias	–	XXX	X	XXX	XXX	0
	K trend	0	XXX	0	XXX	XXX	0
	Depleted	0	XXX	X	XXX	XXX	0
	All	0	XXX	XX	XXX	XXX	XX
Slow, R_{max} = 1.05	Base	0	XXX	0	0	0	0
	CV = 0.2	X	XXX	X	XX	XX	X
	Bias	–	XXX	0	XXX	XXX	0
	K trend	0	XXX	0	XXX	0	0
	Depleted	0	XXX	0	XXX	X	0
	All	XX	XXX	XX	XXX	XXX	XX
Fast, R_{max} = 1.15	Base	0	XXX	0	X	XXX	0
	CV = 0.2	0	XXX	XX	XX	XXX	0
	Bias	–	XXX	XX	XXX	XXX	0
	K trend	0	XXX	XXX	XXX	XXX	0
	Depleted	0	XXX	XX	XXX	XXX	0
	All	0	XXX	XXX	XXX	XXX	0
Slow, R_{max} = 1.15	Base	0	0	0	X	0	0
	CV = 0.2	0	XX	0	XXX	XX	0
	Bias	–	XXX	0	XXX	XXX	0
	K trend	0	XX	0	XXX	XXX	0
	Depleted	0	X	0	XXX	X	0
	All	X	XXX	X	XXX	XXX	XX

[a]The results are shown for all the algorithms discussed in Table 1, as well as for a situation without hunting (noH). Bod A = Bodmer A, Bod B = Bodmer B, R&R = Robinson and Redford, NMFS = National Marine Fisheries Service algorithm. The results are shown for four different life history strategies (Fast or Slow, with R_{max} = 1.05 or R_{max} = 1.15, see Table I for details), for a base case scenario (Base, the coefficient of variation of survival and fecundity rates is 10%, no bias in parameter estimates, no trend in carrying capacity, population is initially unhunted). The effect of increasing realism is shown for each of these factors in turn (CV = 0.2, the coefficients of variation (CVs) of survival and fecundity rates are 20%; Bias, 10% upwards bias in all parameter estimates; K trend, carrying capacity reduces by 5% a year; Depleted, initial population is depleted to 20% of carrying capacity), as well as for all of them together (All).
[b]The probability of falling below the threshold population size of 200 individuals within the 50-year simulation period is shown as: XXX, P>0.5; XX, 0.5 ≥ P>0.2; X, 0.2 ≥ P>0.05; 0, P≤0.05.

To show how algorithms might be compared, we used RAMAS Metapop[a] to simulate algorithm performance under a range of scenarios for two contrasting life histories (Table I). These represent a broad range of conditions under which bushmeat hunting occurs. The parameter values are reasonable for mammals. The levels of bias and uncertainty tested are relatively low. In reality, sustainability assessments probably occur under even more challenging conditions.

The maximum sustainable offtake predicted by an algorithm was taken from the population each year, and performance evaluated in terms of the risk of going below a threshold population size of 200 individuals (2% of carrying capacity) at some point in the 50-year simulation period (Table II). The Robinson and Redford, Bodmer A, and Logistic algorithms performed extremely poorly under realistic conditions of uncertainty, the Bodmer B algorithm (with actual values for survivorship) performed much better, except for high productivity species (fast life-history, R_{max} = 1.15). The NMFS algorithm performed well in all tests.

The results of the Logistic algorithm illustrate why it is important not to limit tests to best guess parameter values, but to ensure a broad range of scenarios are tested: it performed reasonably well in the base case scenario but extremely poorly under more demanding conditions. The test results also show how useful it is to get results from several algorithms when making sustainability assessments, rather than just using one.

If instead of using simple algorithms, we maximize proportional harvest rates on each age class (under the constraint that the risk of falling below a threshold population size of 200 individuals stays below 5%), the average offtake over a 50-year simulation is 62% higher than under the best-performing rule of thumb (the NMFS algorithm, Fig. I). Thus, a substantial loss of offtake is incurred by using a simple algorithm to estimate sustainable offtake levels, rather than a full harvesting model.

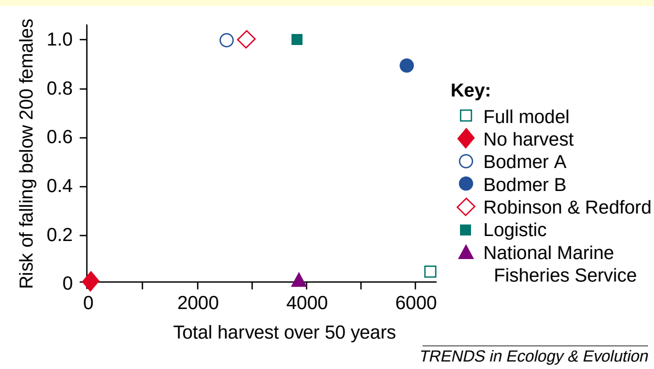

Fig. I. The tradeoff between the risk of population decline and the number of individuals hunted, shown for a species with fast life history, high growth rate, depleted population, declining habitat and high variability (the row Fast, R_{max} = 1.15, All in Table II). The optimal harvest method has low risk and maximum harvest (i.e. it would be in the lower right corner with the worst method in the upper left corner). The Full model involves maximizing proportional harvest rates on each age class, under the constraint that the risk of falling below a threshold population size of 200 individuals during a 50-year period stays <5%. For this life history, the full model gives a 7% greater harvest and a 95% lower risk than does the Bodmer B method (which has the next highest harvest), and a 62% greater harvest than does the NMFS method (which has the next highest harvest with minimal extinction risk).

Reference

a Akçakaya, H.R. (1998) *RAMAS Metapop: Viability Analysis for Stage-structured Metapopulations (version 3.0)*, Applied Biomathematics

Box 4. An example of the use of fuzzy numbers for assessing the threat of species extinction[a]

The World Conservation Union threatened species criteria[b] use both numerical variables (e.g. past population reduction), and Boolean (true/false) variables (e.g. whether there is continuing decline). The criteria compare numerical variables to fixed thresholds, and combine such comparisons (and the Boolean variables) with the logical operators AND OR. For example, one criterion can be summarized as: (past reduction ≥80%) OR (future reduction ≥80%).

When such variables are uncertain, they can be represented as fuzzy numbers (Fig. I). The simplest way to do this is to specify a best estimate and a range of plausible values. The uncertainty expressed in fuzzy numbers is propagated[a,c] through the IUCN criteria using the fuzzy number equivalents of operations such as division, comparison (e.g. 'greater than or equal to'), conjunction (AND) and disjunction (OR). When uncertainty is propagated using these functions, the threat category that results from applying the criteria might itself become a fuzzy number. When presenting and interpreting these uncertain (fuzzy) results, attitudes toward risk and uncertainty might play an important role. Attitudes have two components. Risk tolerance ranges from a precautionary (risk averse) to an evidentiary (risk prone) attitude. Dispute tolerance ranges from including the full range of plausible values (and thereby avoiding dispute), through excluding extreme values from consideration, to using only the best estimates (and thereby minimizing uncertainty in the results)[a].

An assessment using point estimates (i.e. single numerical values) for all variables leads to a single Red List category. However, when a plausible range for each parameter is used to evaluate the criteria, the result might also include a range of plausible categories, reflecting the uncertainties in the data (Fig. II)[c].

A similar approach can be used in assessing the sustainability of hunting, by representing all input parameters (such as population size) as fuzzy numbers or simple intervals. The result can then be expressed in the form a tradeoff between offtake and risk of extinction or decline (as in Box 3, Fig. I), with intervals (instead of points) representing different strategies or levels of hunting. Another alternative is to express the result as a range of plausible values for production, which is then compared to the recorded offtake (which could itself be represented either as a fuzzy number or scalar). Such a comparison would indicate whether the offtake levels are safe (similar to Fig. II), given the uncertain data and the attitudes of the assessors towards risk and uncertainty.

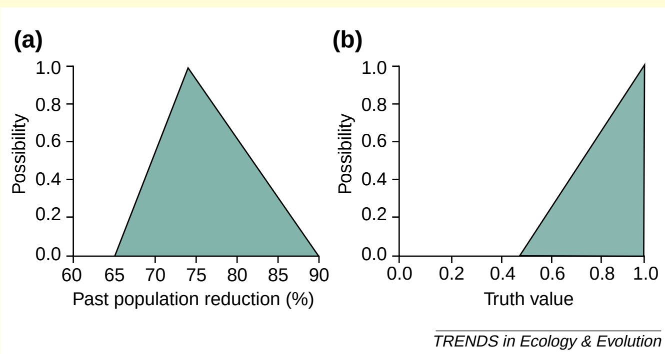

Fig. I. Examples of fuzzy numbers representing (a) past population reduction and (b) whether there is continuing decline, for which the truth value ranges from zero (false) to unity (true). In (a), the best guess is that the past population reduction is 75%, but the range of plausible values is 65% to 90%. The range of values used in the analysis (i.e. how far up the y-axis the range is taken) depends on the assessor's dispute tolerance.

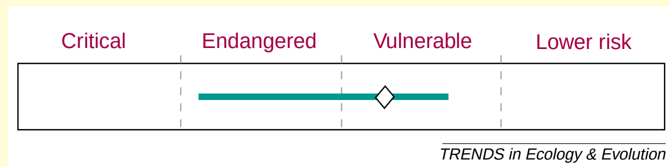

Fig. II. An example of the result of using uncertain variables in assessing the World Conservation Union (IUCN) threat category of a species[a,c]. Although the most plausible threat category is Vulnerable, the range of categories includes Endangered. The final threat category chosen for the species depends on the assessor's risk tolerance.

References

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Terrestrial protected areas are often thought of as areas set aside principally for conservation. By contrast, recent interest in marine reserves has focused on their potential for improving fishing yields, protecting habitat and vulnerable species as a side effect[30–32]. Areas that have sustainable use as their prime objective are often called NO-TAKE AREAS, to distinguish them from areas that are protected with other purposes primarily in mind. Although it is well established that fish population sizes in marine no-take areas are probably higher than in surrounding areas[33], it is less clear cut whether fishing yields in surrounding areas increase as a result of no-take areas: this depends on the dispersal characteristics of the exploited species[34]. The dispersal rate out of the area must be low enough that fishing does not drain the no-take area, but high enough that fishers notice a benefit. No-take areas are particularly promising management tools for situations with a high level of uncertainty, especially about what proportion of the current population size a given level of offtake represents[31,35].

The way forward

The conservation of species that are being overexploited for the bushmeat trade is of urgent concern, given the alarming population declines that are being charted. Much financial and research effort is being channelled into understanding and alleviating unsustainable hunting. Here, we have concentrated on the first step of this process – how to tell whether hunting is sustainable. However, methods used to determine

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Glossary

Bayesian statistics: a method that allows the combination of existing knowledge about a parameter with observed data to produce an updated probability distribution for the parameter value (posterior probability).
Bushmeat: meat from wildlife killed for human consumption.
Bycatch: species killed during fishing (or hunting) that are not the main target.
Depleted: a population is depleted if it is well below its exploited size. A common fisheries definition is that a population is depleted if it is below 35% of carrying capacity, but any population below its point of maximum sustainable production can be considered to be depleted.
Exploitation: killing of animals for any kind of use.
Fuzzy number: an uncertain number, that is, one whose value is not precisely known even though it might be constant (Box 4). A fuzzy number generalizes an interval (which is characterized by a lower and an upper boundary), and can be represented as a nested stack of intervals at infinitely many levels of confidence about uncertainty. These levels of confidence range between zero (the most conservative, widest interval) and unity (the narrowest interval). This scale measures the possibility that a number is within the interval at a particular level.
Hunting effort: the input that a hunter puts into hunting: expressed as the number of snares set, the number of days spent hunting, etc. For a given population size, offtake is positively correlated with hunting effort.
No-take area: an area within which hunting or fishing is not allowed. Generally thought of as a management measure for increasing the sustainability of exploitation, rather than as a pure conservation measure.
Offtake: the number (or biomass) of animals killed by bushmeat hunters in a given period of time.
Precautionary principle: the principle that if there is uncertainty about the outcome of an action, the benefit of the doubt should be given to the species to be conserved. The main argument for using the precautionary principle is that species extinction is irreversible.
Production: the number (or biomass) of individuals added to the population in a given period of time through births and immigration. If hunters remove the same number of individuals in this period, the population size remains stable. The maximum sustainable production is the greatest number of individuals that can be added to the population in any period (and hence that can be removed by hunters without causing a population decline).
Protected area: any area that has some legal or customary conservation status.
Randomly distributed variable: a variable expressed as a probability distribution rather than as a point value.
Red lists: lists of species threatened with extinction, produced by the World Conservation Union. Species are categorized according to the level of threat that they face.
Sustainability: ability to continue indefinitely. Defined here as the probability of the population staying above a given size over a given period of time.

sustainability can also be used within the management process once hunting is controlled. The methods currently used for assessing the sustainability of bushmeat hunting are not precautionary, and are prone to overestimating the sustainable level of offtake. Instead, we suggest that it is vital to use methods that explicitly incorporate uncertainty. Such methods are being developed in the fisheries literature and for the red listing of threatened species. Thus there is the possibility of crossfertilization between disciplines, leading to improved assessment and management of hunted species.

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