This is a preprint of an article published in *TRENDS in Ecology & Evolution* Vol.16 No.12 December 2001, pages 686-692.

Sustainability indices for exploited populations under uncertainty

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

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

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

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 very simple 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, however this is mathematically demanding. Red-listing of threatened species has to be carried out in very 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.

The hunting of wildlife for human consumption (BUSHMEAT 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 problem[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 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]. Despite 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 ex-

Soviet Central Asia has led to an 80% decline in population size since independence[4]. Overhunting of bushmeat species is for both subsistence and commercial use, 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 very low numbers or local extinction, then 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 biological data available, and the difficulty of collecting the data required for a full sustainability assessment. Hence the assessments are plagued with UNCERTAINTY.

Uncertainty is of three kinds; process uncertainty caused by the inherent variability of natural systems, model uncertainty which 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. Hence offtake levels should be assumed to be on the high side of the range of possible values, population sizes on the low side.

Bushmeat researchers have approached this uncertainty by developing quick and simple algorithms which provide crude estimates of sustainability. One such method was developed by Robinson and Redford[7] (Box 1) and has become the standard in the field[2, 8-11]. Despite 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 for 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 generating seriously misleading recommendations for conservation action by not using recently developed tools for estimating the sustainability of EXPLOITATION under uncertainty.

Here we review the methods used as standards 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, while remaining usable by practitioners in the field?

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 very simple 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 (Box 2, Eqn

1), but none of these parameters is straightforward to estimate, particularly for species that are poorly known and difficult to observe.

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 (the capture of species that are not the main target of the fishers)[14,16,17] is similar to that of Robinson and Redford, 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 which consistently underestimates it. Hence if an algorithm is to be useful for assessing the sustainability of hunting, the maximum sustainable level of offtake which it calculates should actually be sustainable in the long run. Given that we are dealing with an uncertain system, we define sustainability in terms of the probability of the population not falling below a given size over a given timeperiod.

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 the algorithms a number of considerations are involved:

- Is it possible to collect the data needed to parameterise the algorithm?
- How much uncertainty is likely to surround the estimates of the parameters collected?
- Under what circumstances is the algorithm likely to fail to detect over-exploitation when it is in fact occurring?
- Conversely, the algorithm should not be overly precautionary, given that bushmeat hunting is the livelihood of many people.

Although the algorithms have all been parameterised from field-collected data, little has been written concerning the practicalities of using them or on the likely uncertainties surrounding parameter estimation (but see Ref. 18 for discussion of the reasoning behind the U.S. National Marine Fisheries Service (NMFS) algorithm). The issues of failure to detect over-exploitation and giving overly precautionary results can be addressed using population models. It is particularly important to test algorithm performance for a range of life histories and incorporate both process uncertainty (e.g. demographic stochasticity) and observation uncertainty into the tests. Box 3 gives an example of the type of test that can be used. In this case, the accepted methods used for assessing the sustainability of bushmeat hunting did not perform well.

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 to 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 seems very 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 y^{-1} (Ref. 19). Generally, there is a trade-off between extinction risk and level of offtake. As the NMFS algorithm was developed for bycatch species, this trade-off was not a key consideration, hence it errs on the precautionary side. However this is a general problem for rules of thumb. Because bushmeat hunting encompasses such a wide range of taxonomic groups and there is a good deal of observational uncertainty, rules of thumb that lead to an acceptably low risk of over-exploitation for all species are also likely to entail substantial losses in offtake.

The potential of methods from other fields

Simple deterministic models of population dynamics are not a sound basis for decision-making 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 be near the estimated sustainable level, this 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, multi-species, involving many different biological and socio-economic factors, and is particularly rife in areas where the biological systems are very poorly known. Despite the severity of these obstacles to rigorous assessment, many of them also pertain to commercial fish stocks. Hence methods used in fisheries management that incorporate uncertainty explicitly, such as BAYESIAN statistics, may be very 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 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, while the assessments must be carried out in the field with only limited access to mathematical expertise, computational power and funding. An analogous situation is faced by IUCN - the World Conservation Union when compiling RED LISTS of species threatened with extinction[25]. Here too a full population viability analysis would be ideal, but most species have minimal data 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 may well be very 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 recognised as crucial to the sustainability of bushmeat hunting, is spatial heterogeneity[26-27]. Densities of hunted species may vary spatially naturally, or because of variations in HUNTING EFFORT. Effort is dependent on the cost of hunting. Costs include the distance 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].

Terrestrial PROTECTED AREAS are often thought of as areas set aside principally for conservation. By contrast, recent interest in marine reserves has focussed on their potential for improving fishing yields, with 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 likely to be higher than in surrounding areas[33], it is less clearcut whether fishing yields in surrounding areas increase as a result of no-take areas; this depends on the dispersal characteristics of the hunted species[34]. The dispersal rate out of the area must low enough that fishing doesn't drain the no-take area, but high enough that a benefit is felt by fishers. 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 current concern, given the alarming population declines that are now being charted. Much financial and research effort is being put 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 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 likely to overestimate 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 cross-fertilisation between disciplines leading to improved assessment and management of hunted species.

Acknowledgements

This work was partly supported by the Center for Applied Biodiversity Science at Conservation International, as part of its Bushmeat Initiative. We thank Jim Cannon and Katriona Shea for their help and advice.

References

1 Bennett, E.L. and Robinson, J.G. (2000) *Hunting of Wildlife in Tropical Forests: Implications for Biodiversity and Forest Peoples.* World Bank Biodiversity Series - Impact Studies, Paper 76. World Bank

2 Robinson, J.G. and Bennett, E.L., eds (2000) *Hunting for Sustainability in Tropical Forests.* Columbia University Press

3 Oates, J.F. *et al* (2000) Extinction of a West African red colobus monkey. *Conserv. Biol.* 14, 1526-1532

4 Milner-Gulland, E.J. *et al* (in press) The current status of the saiga antelope. *Oryx*

5 Oates, J. (2000) *Myth and Reality in the Rain Forest: How Conservation Strategies are Failing in West Africa.* California University Press

6 Parma, A.M. *et al* (1998) What can adaptive management do for our fish, forests, food and biodiversity? *Integrative Biology, Issues, News and Reviews* 1, 16-26

7 Robinson, J.G. and Redford, K.H. (1991) Sustainable harvest of neo-tropical mammals. In: *Neo-tropical Wildlife Use and Conservation* (Robinson, J.G. and Redford, K.H., eds) pp. 415-429 Chicago University Press

8 Fa J.E. *et al.* (1995) Impact of market hunting on mammal species in Equatorial Guinea. *Conserv. Biol.* 9, 1107-1115

9 FitzGibbon C.D. *et al.* (1995) Subsistence hunting in Arabuko-Sokoke forest, Kenya and its effects on mammal populations. *Conserv. Biol.* 9, 1116-1126

10 Alvard M.S. *et al.* (1997) The sustainability of subsistence hunting in the Neotropics. *Conserv. Biol.* 11, 997-982

11 Muchaal P.K. and Ngangjui G. (1999) Impact of village hunting on wildlife populations in the Western Dja Reserve, Cameroon. *Conserv. Biol.* 13, 385-396

12 Hilborn, R. and Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data.* Princeton University Press

13 Cooke, J.G. (1995) The International Whaling Commission's Revised Management Procedure as an example of a new approach to fishery management. In: *Whales, seals, fish and man* (Blix, A.S. *et al.,* eds), pp 647-657, Elsevier Science

14 Johnston, D.W. *et al.* (2000) An evaluation of management objectives for Canada's commercial harp seal hunt, 1966-1998. *Conserv. Biol.* 14, 729-737

15 Robinson, J.G. and Bodmer R.E. (1999) Towards Wildlife Management in Tropical Forests. *J. Wildl. Manage.* 63, 1-13

16 NMFS (1994) *Annual Report to Congress Regarding Administration of the Marine Mammal Protection Act*, Office of Protected Resources, National Marine Fisheries Service

17 Wade, P.R. (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Mar. Mamm. Sci.* 14, 1-37

18 Taylor, B.L. *et al* (2000) Incorporating uncertainty into management models for marine mammals. *Conserv. Biol.* 14, 1243-1252

19 Fa, J.E. *et al.* (in press) Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conserv. Biol*

20 Hilborn, R. and Walters, C. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty,* Chapman & Hall

21 Engen, S. *et al.* (1997) Harvesting strategies for fluctuating populations based on uncertain population estimates. *J. Theor. Biol.* 186, 201-212

22 Milner-Gulland, E.J. *et al.* (2001) Competing harvesting strategies in a simulated population under uncertainty. *Anim. Conserv*., 4, 157-167

23 McAllister, M.K. and Kirkwood, G.P. (1998) Bayesian stock assessment: a review and example application using the logistic model. *ICES J. Mar. Sci.*, 55, 1031-1060

24 Spiegelhalter, D.J. *et al.* (1999) *WinBUGS Version 1.2 User Manual.* MRC Biostatistics Unit, Cambridge, UK

25 Hilton-Taylor, C., compiler (2000) *2000 IUCN Red List of Threatened Species.* IUCN, the World Conservation Union

26 Peres, C.A. (2000) Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. In: *Hunting for Sustainability in Tropical Forests* (Robinson, J.G. and Bennett, E.L., eds), pp 31-56, Columbia University Press

27 Hill, K. and Padwe, J. (2000) Sustainability of Ache hunting in the Mbaracayu Reserve, Paraguay. In: *Hunting for Sustainability in Tropical Forests.* (Robinson, J.G. and Bennett, E.L., eds), pp 79-105, Columbia University Press

28 Clayton, L. *et al.* (1997) Bringing home the bacon: A spatial model of wild pig harvesting in Sulawesi, Indonesia. *Ecol. Appl.* 7, 642-652

29 Hofer, H. *et al.* (2000) Modelling the spatial distribution of the economic costs and benefits of illegal game meat hunting in the Serengeti. *Nat. Res. Mod.* 13, 151-177

30 Tuck, G.N. and Possingham, H. P. (2000). Marine protected areas for spatially structured stock**.** *Mar. Ecol. Progr. Ser.* 192, 89-101

31 Mangel, M. (2000) Irreducible uncertainties, sustainable fisheries and marine reserves. *Evol. Ecol. Res.* 2, 547-557

32 Roberts, C. (1998) No-Take marine reserves: Unlocking the potential for fisheries. *Marine Environmental Management Review of 1997 and Future Trends* 5, 127 –132

33 Mosqueira, I. *et al* (2000) Conservation benefits of marine reserves for fish populations. *Anim. Conserv.* 3, 321-332

34 Sladek Nowlis, J., and Roberts, C. M. (1999) Predicted fisheries benefits and optimal marine fishery reserves design. *Fishery Bulletin* 97, 604 - 616

35 Lauck T. *et al* (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecol. Appl.* 8, S72-S78

36 Begon, M. *et al* (1996) *Population Ecology: A Unified Study of Animals and Plants (3rd Edn)* Blackwell Science

Glossary

Bushmeat: Meat from wildlife killed for human consumption. This includes all animal species that are eaten, particularly mammals, birds, insects and reptiles.

Sustainability: Ability to continue indefinitely. Defined here as the probability of the population staying above a given size over a given time period.

Offtake: The number (or biomass) of animals killed by bushmeat hunters in a given period.

Uncertainty: Inability to predict the future. There are three main types: process uncertainty caused by the inherent variability of natural systems, model uncertainty which reflects our ignorance about the system, and observational uncertainty arising from our attempts to obtain information about the system.

Exploitation: Killing of animals for any kind of use.

Production: The number (or biomass) of individuals added to the population in a given time period through births and immigration. If hunters remove the same number of individuals in this time period, the population remains stable. The maximum sustainable production is the largest number of individuals that can be added to the population each time period (hence that can be removed by hunters without causing population decline).

Bycatch: Species that are killed during fishing (or hunting) but are not the main target of the fishing vessels that catch them.

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.

Depleted: A population is depleted if it is well below its undisturbed 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 depleted.

Cetaceans: The order including whales, porpoises and dolphins.

Bayesian statistics: Named after its originator, a method that allows us to combine prior information about a parameter with observed data to produce an updated probability distribution for the parameter value (posterior probability).

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 IUCN - the World Conservation Union. The species are categorised according to the level of threat they face.

Fuzzy number: An uncertain number, i.e. one whose value is not precisely known even though it may in fact be fixed and unchanging (see Box 4 for examples). A fuzzy number generalizes an interval (which is characterized by a lower and an upper bound), and can be represented as a nested stack of intervals at infinitely many levels of confidence about uncertainty. These levels of confidence range between 0 (corresponding to the most conservative, widest interval) and 1 (the narrowest interval). The scale between 0 and 1 measures the possibility that a number is within the interval at a particular level.

Hunting effort: The input that a hunter puts into hunting. This can be expressed as the number of snares set, the number of days spent hunting, the number of hunters in an area etc. For a given population size, offtake increases as hunting effort increases.

Protected area: Any area that has some legal or customary conservation status. This covers a very broad range of designations, including nature reserves, sacred areas etc.

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.

Depensation: Also called the Allee effect. The population growth rate increases as population size increases. This may 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.

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 obtainable, 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 to actual data on offtakes. The parameters are:

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 (see Box 2).

3) Density at which maximum production occurs (MSY level).

4) Maximum production (P). Production is defined as all additions to the population (births, immigrations) in a given time period. 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:

$$P = 0.6\ K\ (R_{max}-1)\ F$$

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. Hence hunters can 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 (>10 years) to 0.6 for short-lived species (<5 years).

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

To assess sustainability, P is compared to the 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]. Hence it is important to supplement the assessment of sustainability with an independent check that the population density is above the level giving the maximum sustainable production.

a Robinson, J.G. and Redford, K.H. (1991) Sustainable harvest of neo-tropical mammals. In: *Neo-tropical Wildlife Use and Conservation* (Robinson, J.G. and Redford, K.H., eds) pp. 415-429 Chicago University Press

b Fowler, C.W. (1981) Comparative population dynamics in large mammals. In: *Dynamics of Large Mammal Populations*. (C.W. Fowler and T.D. Smith, eds) pp 437-455. John Wiley

c Slade, N.A. *et al* (1998) Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. *Conserv. Biol.* 12, 148-155

d Milner-Gulland, E.J. (2000) Assessing the sustainability of hunting: insights from bioeconomic modelling. In: *Bushmeat hunting in the African Rain Forest*, Advances in Applied Biodiversity Science series, Centre for Applied Biodiversity Science

e Sutherland, W.J. (2000) *The Conservation Handbook: Research, Management and Policy.* Blackwell Science

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 intra-specific competition. Therefore it is best measured as the rate of increase of a very small population (assuming that no DEPENSATION occurs, i.e. that the population growth rate always decreases as population size increases and so is at a maximum at low population sizes). It is unfeasible to measure it directly in most cases. It can be represented by Eqn 1:

$$\frac{dN}{dt} = rN \text{ or } N_{t+1} = RN_t \quad (1)$$

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). They are related as $R = e^r$. The appropriate time dimension for these parameters depends on a species' life-history; for many mammal species, they are often measured over 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 occurs 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 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 data required are often not obtainable, 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 very high. Another possibility is observing the growth of unhunted populations that are far below their carrying capacities, e.g. populations in areas recently closed to hunting.

a Robinson, J.G. and Redford, K.H. (1991) Sustainable harvest of neo-tropical mammals. In: *Neo-tropical Wildlife Use and Conservation* (Robinson, J.G. and Redford, K.H., eds) pp. 415-429 Chicago University Press

b Fenchel, T. (1974) Intrinsic rate of natural increase: the relationship with body size. *Oecologia*, 14, 317-326

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

As an example of how algorithms can be compared, we used RAMAS Metapop[a] to simulate algorithm performance under a range of scenarios for 2 contrasting life-histories (Table I). These scenarios represent a broad range of conditions under which bushmeat hunting occurs. The parameter values are reasonable for mammal species. The levels of bias and uncertainty we test are relatively low. In reality, sustainability assessments are likely to 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 shows the results; the Robinson and Redford, Bodmer A, and Logistic algorithms performed very 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 very 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 quite well in the base case scenario but disastrously 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 maximise 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 there is a substantial loss of offtake incurred as a cost of using a simple rule of thumb to estimate sustainable offtake levels, rather than a full harvesting model.

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

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

The IUCN 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 logical operators AND and OR. For example, one criterion can be summarized as:

(Past reduction $\geq$ 80%) OR (Future reduction $\geq$ 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 may itself become a fuzzy number. When presenting and interpreting these uncertain (fuzzy) results, attitudes toward risk and uncertainty may 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 may 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 a 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.

a Akçakaya, H.R. *et al.* (2000) Making consistent IUCN classifications under uncertainty. *Cons. Biol.* 14, 1001-1013.

b IUCN (1994) *International Union for the Conservation of Nature Red List Categories.* IUCN Species Survival Commission

c Akçakaya, H. R. & Ferson, S. (1999) *RAMAS Red List: Threatened Species Classifications Under Uncertainty. User Manual for Version 1.0.* Applied Biomathematics

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

Name of Algorithm	**Algorithm**[a]	**Notes**
Robinson & Redford	$P = 0.6\ K\ (R_{max}-1)\ F$	$F = 0.2$ for long-lived species, $F = 0.6$ for short-lived species
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
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, $F = 0.5$ (following Wade[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 $0.6K$

a. In each case, P, the sustainable level of production; R_{max}, maximum annual per capita rate of increase (see 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.

Source references: Robinson & Redford - Ref. 7, Bodmer - Ref 15, NMFS - Ref 14. Logistic - Ref. 36.

Box 3, 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. 1,000 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 10000 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%.

Box 3, Table II Results of the comparison of algorithms.

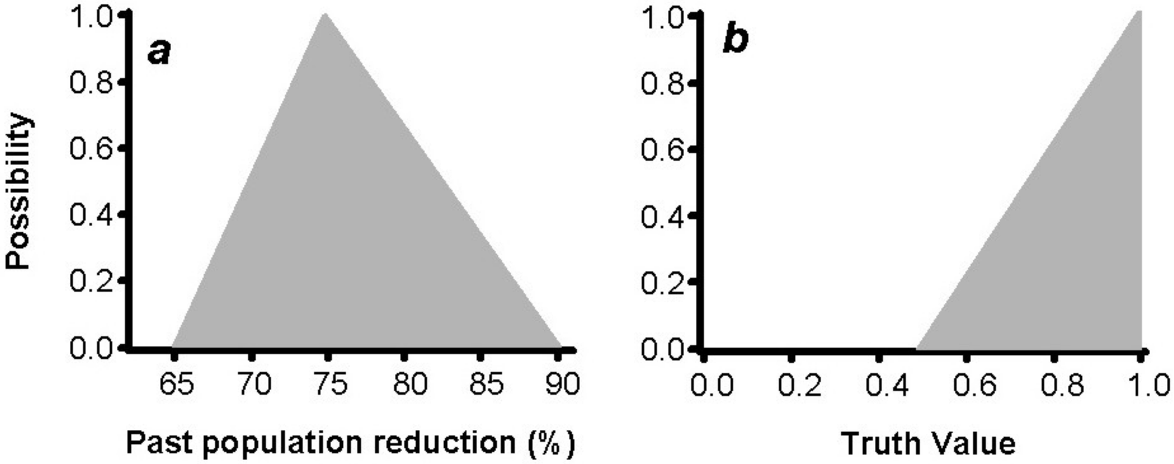
Scenario[a]		noH	Bod A	Bod B	Logistic	R&R	NMFS
Fast, R_{max} = 1.05	Base	0[b]	XXX	0	0	X	0
	CV=0.2	0	XXX	X	XX	XXX	0
	Bias	-	XXX	X	XXX	XXX	0
	K trend	0	XXX	0	XXX	XXX	0
	Depleted	0	XXX	X	XXX	XXX	0
	All	0	XXX	XX	XXX	XXX	XX
Slow, R_{max} = 1.05	Base	0	XXX	0	0	0	0
	CV=0.2	X	XXX	X	XX	XX	X
	Bias	-	XXX	0	XXX	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 the text (Table 1), as well as for a situation without hunting (noH). Bod A = Bodmer A, Bod B = Bodmer B, R&R = Robinson & 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, $0.5 \geq P > 0.2$; X, $0.2 \geq P > 0.05$; 0, $P \leq 0.05$.

Box 3, 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 would have low risk and maximum harvest (i.e. it would be in the lower right corner; the worst method would be in the upper left corner). The Full model involves maximising 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%. The other models are: No Harvest; Bod A, Bodmer A; Bod B, Bodmer B; R&R, Robinson & Redford; NMFS, National Marine Fisheries Service (see Table 1). For this life history, the full model gives 7% more harvest and 95% less risk than the Bodmer B method (which has the next highest harvest), or 62% more harvest than the NMFS method (which has the next highest harvest with minimal risk).

Box 4, 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 0 (false) to 1 (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.



Box 4, Fig. II. An example of the result of using uncertain variables in assessing the IUCN threat category a species falls into[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.