

Sustainable exploitation of social species: a test and comparison of models

PHILIP A. STEPHENS*, FREDY FREY-ROOS†, WALTER ARNOLD† and
WILLIAM J. SUTHERLAND*

*School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK; and †Forschungsinstitut für
Wildtierkunde und Ökologie, Savoyenstrasse 1, A-1160 Wien, Austria

Summary

1. Overexploitation is a major threat to the persistence of many species. A wide variety of approaches to setting 'sustainable' quotas for exploitation exist but there are major discrepancies between theory and practice, and only limited integration between different branches of exploitation literature. Here, we bring together and compare the efficacy of a range of different approaches to estimating sustainability.

2. A simulated population of a social mammal was used to provide data for, and compare the recommendations of, 10 widely used estimators for setting levels of sustainable exploitation. Estimators tested included four methods for setting sustainable levels of constant-effort harvesting, two approaches to assessing the sustainability of constant-yield harvesting, and four systems for setting thresholds below which harvesting should cease.

3. The method used to fit catch per unit effort data to a stock dynamic model had an important influence on the variance of recommendations. Recommendations were also affected by the length of data set available and the frequency of changes in exploitation effort. Observation-error estimators were more consistent and more conservative than equilibrium, effort-averaging and process-error approaches. Harvesting at the point of maximum productivity was found to be unstable in a noisy system, suggesting the need for considerable caution when using any of these estimators.

4. Constant-yield indices, developed for use in the bush meat trade, overestimated the point at which exploitation was likely to become highly unsustainable. Sociality was an important factor underlying this finding and the assessment of sustainability in constant-yield systems should give consideration to the effects of different social systems.

5. Overall, threshold-harvesting systems provided the highest mean yields in relation to extinction risk. However, the introduction of error into these systems, particularly in the form of less frequent censuses, greatly increased both variance in yields and risk of extinction.

Key-words: alpine marmot, behaviour-based modelling, constant-yield harvesting, surplus production, threshold harvesting.

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Introduction

Overexploitation accounts for almost one-quarter of extinctions since 1600 for which the cause can be identified (Groombridge 1992), while hunting and international trade still contribute to the extinction risk of approximately one-third of the bird and mammal species listed as threatened by the World Conservation

Union (IUCN) (Mace & Reynolds 2001). Approximately half of the fisheries of Europe and the USA are believed to be overexploited (Rosenberg *et al.* 1993). Clearly, in spite of a long history of experience, conservationists and managers are still far from being able to ensure the sustainable exploitation of populations. Overexploitation occurs for a wide variety of reasons, including discounting, whereby it may be better to gain large profits in the short term rather than exploit sustainably and gain smaller profits continuously (Clark 1973; Lande, Engen & Sæther 1994), the 'tragedy of the commons', whereby competition among

Correspondence: Philip A. Stephens, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK (fax +44 1603 592250; e-mail philip.stephens@uea.ac.uk).

exploiters of a common resource promotes a lack of restraint by all (Hardin 1968), and multispecies exploitation, whereby uneconomic exploitation of species may be justified by the presence of other, more commercially viable, species (Reynolds *et al.* 2001). Such economic problems may only be tackled by appropriate regulatory institutions. By contrast, tackling the biological reasons for overexploitation, including a lack of necessary knowledge about the species exploited or the status of their populations, or a lack of understanding of the consequences of current systems of exploitation, is clearly within the ambit of ecology. Evidently, a key requirement for combating such deficiencies of knowledge is to determine the maximum safe level of exploitation that can be borne by populations without rendering them unacceptably vulnerable to extinction.

Methods of exploitation fall into only three distinct categories, or combinations of those same approaches. These are: constant-effort harvesting, in which the level of hunting pressure (days of hunting, number of traps, etc.) remains constant, while the yield varies as some function of exploitable population size; constant-yield harvesting, in which exploitation results in the removal of a set number of individuals from the population each year; and threshold harvesting, in which exploitation only occurs during years in which the population exceeds a given threshold, whereupon individuals are removed until the population reaches that threshold. The performance of these different approaches to exploitation has been compared with regard to a variety of management objectives including, for example, maximizing cumulative yields before extinction, minimizing the risk of extinction, maximizing economic returns and minimizing annual variance in yields (Lande, Engen & Sæther 1995; Lande, Sæther & Engen 2001; Milner-Gulland *et al.* 2001). However, despite early evidence that threshold harvesting was likely to provide the best method of meeting management objectives (Lande, Engen & Sæther 1995), exploitation is rarely conducted by this method and much exploitation remains unsustainable (Robinson & Bennett 2000). One reason for this lack of integration between theory and practice may be that exploitation occurs for a wide variety of reasons and in a wide variety of situations. Exploitation may include subsistence hunting, local market hunting, ranching or commercial harvest; it may be terrestrial, aquatic or marine based, and may range from highly developed and researched industries to small-scale opportunistic use. The most appropriate method in one combination of these circumstances may be completely unworkable in a different set of circumstances. For example, long-term records of sport hunting bags in relatively developed countries may enable the use of constant-effort systems in a way that would be unthinkable for subsistence or small-scale commercial hunting in remote, unstudied areas of less developed countries. A more pertinent question for many, therefore, concerns the relative merits of different

estimators available for determining the levels at which each method of exploitation may be carried out sustainably, i.e. estimating the appropriate amount of effort, size of yield or location of threshold, for use with each method.

In principle, levels for sustainable exploitation ought to be determined by an ongoing process of experimentation, learning and adaptation, the components of adaptive management (Holling 1978; Walters 1986). In practice, however, this approach is rarely used (Ludwig 2001; Sutherland 2001) and managers frequently rely on simpler estimators for making such decisions. A wide variety of estimators exists for determining levels appropriate for use with different types of exploitation. These range from highly sophisticated statistical techniques, primarily developed within the fisheries industry for use with constant-effort systems, to simple rules of thumb, available for managers and researchers examining the sustainability of exploitation in terrestrial systems. Comparing the recommendations of available estimators by experimentation on real populations presents a wide range of practical problems. Consequently, we conducted comparisons using a simulated population based on long-term field data, a technique that is increasingly used within fisheries research and has also been applied to terrestrial systems (Milner-Gulland *et al.* 2001).

The simulation model was based on the alpine marmot *Marmota marmota* (L.) population of Berchtesgaden National Park, southern Germany. Alpine marmots are large burrow-dwelling social sciurids, widely distributed throughout the mountainous regions of Europe. The Berchtesgaden population of alpine marmots was chosen for three principal reasons. First, this population has been the subject of intensive field research for more than 13 years (Arnold 1988, 1990a,b, 1995; Arnold & Dittami 1997; Frey-Roos 1998) and individual-based models of the population have been used to explore other applied issues affecting social mammals, such as the consequences of habitat loss for population persistence (Dorndorf 1999). The life history and population dynamics of the species are thus well understood, permitting the development of a full behavioural model. The model results in predictions of population dynamics that can be treated with considerable confidence (Stephens *et al.* 2002). Secondly, although alpine marmots are protected by law in Germany, they are widely hunted in many other parts of central Europe. Smaller, more isolated, populations, such as that found at Berchtesgaden, may be especially vulnerable to exploitation and, historically, many marmot populations have been locally extirpated throughout central Europe (Hediger 1948; Müller 1996; Preleuthner 1999). Finally, despite increasing awareness that social systems can affect vulnerability to exploitation (Dennis 1989; Greene *et al.* 1998; Stephens & Sutherland 2000), estimators for assessing sustainability rarely account explicitly for the social system of the exploited species. Ungulates

Table 1. Summary of sustainability models tested

Method of exploitation	Sustainability estimator	Reference
Constant-effort harvesting	Standard surplus production	Schaefer (1954)
	Effort averaging	Fox (1975)
	Process error	Quinn & Deriso (1999)
Constant-yield harvesting	Observation error	Walters & Hilborn (1976)
	Maximum potential productivity	Hilborn & Walters (1992)
	Actual productivity	Polacheck, Hilborn & Punt (1993)
Threshold harvesting	Logistic	Robinson & Redford (1991)
	Rule of thumb	Robinson & Bodmer (1999)
	The 75% rule	
	Maximum productivity	Roughgarden & Smith (1996)
		Fowler (1988)

and primates form the bulk of much terrestrial exploitation (Robinson & Bodmer 1999) and many species in these taxa display highly developed social systems. Using the alpine marmot as the basis for our comparisons may highlight issues that apply to social mammals in particular.

In this study, we contrasted different estimators available for determining sustainable levels of exploitation. The estimators tested are summarized in Table 1. The recommendations of each estimator were compared with regard to two principal criteria: the risk of extinction and the yields associated with the recommended levels of exploitation. The emphasis in this study was on identifying approaches to exploitation that maximize short-term yields while minimizing long-term extinction probabilities. Consequently, economic criteria, such as discounting of revenues, were not considered. We used these comparisons to address three main questions. First, given a certain method of hunting, how good are available estimators for determining sustainable levels of exploitation, and how do these estimators compare with one another? Secondly, do the findings associated with developments in fisheries exploitation apply equally well to a terrestrial species? Finally, how do the different approaches to exploitation compare when applied to our model system and how does this compare with the findings of other authors?

Methods

A population of alpine marmots was studied in Berchtesgaden National Park, southern Germany, between 1983 and 1996. During the field study, data were collected on the physical condition, behaviour, movement and survival of 654 individuals. The dispersal behaviour of 89 individuals (including 12 juveniles) fitted with radio-transmitters was monitored by telemetry. Data from this study were used to parameterize and validate an individually based behavioural simulation model of an alpine marmot population.

A detailed description of the model is given elsewhere (Stephens *et al.* 2002). The model was spatially explicit and environmentally stochastic, using winter lengths (number of days from the start of the year until territories were 75% free of snow cover, a critical determinant of overwinter mortality in the alpine marmot) drawn from a normal distribution, with a mean and standard deviation taken directly from the distribution of winter lengths measured during the field study. The model was also fully demographically stochastic, with litter sizes drawn from an empirically determined normal distribution, and mortality probabilities based entirely on the field data. Mean unexploited adult population size predicted by the model was 340 ± 32 (SD) and annual growth rate was maximized at an intermediate population size (approximately 180 adults), at an average of 7.3%. Negative density dependence was incorporated into the model through the restricted availability of breeding territories (Frey-Roos 1998), and positive density dependence was included, at a group level, by increased overwinter survival of juveniles and breeders in larger groups (Arnold 1988, 1990b). The dispersal behaviour of individuals within the model was based on a fitness-optimization function. Due to the relatively large life span of the marmots (up to 13 years in the field study) and the difficulties in collecting extensive data, model validation using a split data set was impractical. However, the model was shown to give accurate predictions of dispersal behaviours, group size distributions and overall population dynamics, when compared with data from the field study (for further details see Stephens *et al.* 2002).

An outline of the sustainability estimators used is given below. Further details of these estimators are given in the references in Table 1 and in relevant textbooks (Hilborn & Walters 1992; Quinn & Deriso 1999; Sutherland 2000; Jennings, Kaiser & Reynolds 2001). In all cases, only reproductively mature individuals were removed by hunting, always selected at random. All hunting took place in the later part of the marmots' above-ground period, after juveniles were

weaned but while individuals still had the opportunity to disperse.

CONSTANT-EFFORT HARVESTING

Surplus production estimators used to assess the sustainability of constant-effort harvesting require that data relating yield and effort are available from an already exploited population. The unit of effort used in this study was the hunter day (HD) and levels of effort were compared between years using hunter days per year (HD year^{-1}). Precision in simulating hunter behaviour is unnecessary for the purpose of comparing the performance of different estimators. However, the process of hunting in the model was loosely based on observations of the behaviour of hunters in other alpine marmot populations. Specifically, it was assumed that a hunter will spend 6 h actually hunting during 1 day. The number of marmots that are shot during this period depends on two components: the encounter time (time taken to locate or select a suitable target animal) and the handling time (time taken to reach a suitable vantage point, wait for an opportunity to shoot and then collect the carcass). Mean encounter time decreased with population density and was described by a function of the form:

$$T_E = \frac{\beta + N}{\alpha N}$$

where T_E = encounter time (h); N = population size (or density, given that the model population is closed) of animals aged 2 years or over; and α and β = parameters controlling the shape of the function. Based on practical experience of hunting marmots in Grisons, Switzerland, standard deviation of the encounter time was fixed at 0.2 h. Once an appropriate target was found, mean handling time was assumed to be independent of density and was fixed at 1 h $\pm$ 0.4 (SD). The values of α and β in the encounter time function were chosen so that in a high population (400 adults) the mean yield per HD was approximately four marmots (4.0 ± 0.7), dropping slowly at first with reducing density so that when there are 200 adults, mean yields are still almost 3.5 marmots HD^{-1} (3.4 ± 0.6). In depressed populations, mean yields are much lower, with a mean of just 1.1 $\text{HD}^{-1} \pm 0.3$ when the adult population is 40 individuals.

To simulate the collection of sample data sets from a hunted population of marmots, the model was run through repeated simulations of 75 years duration. For the first 20 years, the population was allowed to stabilize without any exploitation. Following this, the population was subjected to light exploitation (1 or 2 HD year^{-1}) for a further 5 years, during which no data were collected. Following the 25th year, hunting pressure was allowed to change at intervals, either increasing by 1 HD year^{-1} (with probability = 0.7) or decreasing by 1 HD year^{-1} (with probability = 0.3). The 75-year simulations were repeated using both 2- and 3-year intervals between changes in hunting pressure. This ensured

relatively gradual changes between hunting pressures, characteristic in the absence of large changes in available technology and necessary for the utility of surplus production models. Changes every 2 to 3 years permitted a broad range of hunting pressures, without driving too many of the simulations to extinction. This regime continued until the 75th year of the simulation, with the hunting pressure constrained between 1 and 16 HD year^{-1} . Data on total yields and numbers of hunter days were collected from the 25th year until the end of the simulation, to provide 50-year data sets. Data sets that did not involve the extinction of the population and spanned a range of at least 3–13 HD year^{-1} were analysed to provide recommendations for sustainable levels of hunting. Twenty-five year data sets were also collected, using the same approach detailed above but running the simulation for only 50 years. To ensure that the population experienced a broad range of hunting pressures during this time, only 2-year intervals between changes in hunting pressure were used for these 25-year data sets.

A variety of functions are available to model population growth for surplus production models, with different assumptions regarding the nature of density dependence. However, indications from fisheries research are that the method used to fit surplus production models to exploitation data is much more important than the underlying choice of model (Polacheck, Hilborn & Punt 1993). As a result, only the simplest surplus production model (Schaefer 1954), assuming linear density dependence, was considered in this study. The standard Schaefer model is described below under 'equilibrium estimator'. Analyses were conducted using each of the estimators listed under constant-effort harvesting in Table 1. These are described further below.

Equilibrium estimator

The equilibrium estimator used was a surplus production model of the form described by Schaefer (1954). This requires that a regression line of the form:

$$U = a + bE \quad \text{eqn 1}$$

(where U = catch per unit effort; E = hunting effort; a and b are constants) is fitted to a graph of catch per unit effort against effort. This regression line is then used to predict the relationship between total catch, C , and effort, by multiplying both sides of the equation by E , such that:

$$C = aE + bE^2. \quad \text{eqn 2}$$

Total catch is predicted to peak at the inflexion point of this curve, i.e. where:

$$\frac{dC}{dE} = 0, \quad \text{or} \quad E_{MSY} = \frac{-a}{2b}.$$

E_{MSY} is assumed to be the level of effort required to keep the population at a size at which absolute productivity is highest, and hence sustainable offtake is also highest.

Effort averaging estimator

The standard equilibrium estimator described above assumes that the population was at equilibrium with its exploitation throughout the time series of available data. In practice, however, this is widely acknowledged to be rarely if ever true (Hilborn & Walters 1992). Effort averaging is an *ad hoc* approach to dealing with populations that are not at equilibrium with their exploitation (Quinn & Deriso 1999). Specifically, effort averaging acknowledges that previous hunting effort is also likely to have had an effect on current catches. Instead of regressing U against E , this model uses a weighted average of effort on the x axis (Fox 1975), calculated as follows:

$$\bar{E}_t = \frac{\sum_{i=0}^{k-1} (k-i)E_{t-i}}{\sum_{i=0}^{k-1} (k-i)} \quad \text{eqn 3}$$

where E_t = effort at time t and k is the number of age classes for which recruitment is thought to be affected by exploitation. For the marmots, all animals of 2 years or older are capable of breeding, and hunting discriminates between only three age classes: juveniles and yearlings, neither of which are hunted, and adults, which are hunted. Therefore, a value of $k = 3$ was used. Effort averaging then proceeds as in the standard equilibrium approach, only using $\bar{E}$ instead of E for the regression analyses.

Process-error estimator

Process-error estimation (Walters & Hilborn 1976) explicitly confronts non-equilibrium scenarios. Specifically, this approach is based on the principle that while catch per unit effort (U) may be an accurate index of population size, population size in any given year is unlikely to be precisely predictable from the size of the catch in the previous year. Analysis thus aims to determine more basic parameters enabling more accurate predictions. These parameters include the population growth rate, r , the unexploited population size, K , and the catchability coefficient of the hunted species, q . These are related as:

$$\frac{U_{t+1}}{U_t} - 1 = r - \frac{r}{qK}U_t - qE_t. \quad \text{eqn 4}$$

It is suggested that bias in this approach may be reduced by using U_{t+1} as the dependent variable (Hilborn & Walters 1992), and so the formula is often rearranged to give:

$$U_{t+1} = (1+r)U_t - \frac{r}{qK}U_t^2 - qC. \quad \text{eqn 5}$$

Multiple linear regression is then used to determine the values of r , K and q . These are substituted into the standard regression equation $U = a + bE$, using the relationships:

$$a = qK \quad \text{and} \quad b = -\frac{q^2K}{r}.$$

These values of a and b are then used in equation 2 in order to estimate E_{MSY} .

Observation-error estimator

Observation-error estimators take the opposite approach to that of process-error estimators in terms of where they assume error to occur in the catch size/stock relationship. Specifically, observation-error estimators are based on the principle that, while changes in population size are a direct result of the amount of hunting mortality in the previous year, it is unlikely that catch per unit effort is an exact index of population size in any year (Polacheck, Hilborn & Punt 1993). The approach is thus to determine the probability distribution for each data point, assuming log-normal multiplicative error in the relationship between population size and catch. Estimates of the model parameters are obtained by maximizing the likelihood function:

$$L = \prod \frac{\exp\{-\hat{v}_y^2/(2\hat{\sigma}_v^2)\}}{\sqrt{2\pi}\hat{\sigma}_v} \quad \text{eqn 6}$$

where the product includes all years (y) for which data on catch and effort are available.

This approach assumes a continuous distribution of catch data, a situation approximated by the very large potential catches available to fisheries. The components of the likelihood function are (Polacheck, Hilborn & Punt 1993):

$$\hat{v}_y = \log U_y - \log \hat{U}_y \quad \text{eqn 7}$$

$$\hat{\sigma}_v^2 = \sum \hat{v}_y^2/n \quad \text{eqn 8}$$

where $\hat{U}$ is the predicted catch per unit effort.

Where catches or yields are much smaller, as is the situation for our simulated population, the discrete nature of the raw data is unsuitable for this approach. One rough solution for this is to transform catch data to the mid-point of each discrete category by adding 0.5 to each catch. The likelihood function can then be used as is. The regression parameters (a and b in equation 1) that produce the maximum likelihood fit can then be used to estimate E_{MSY} , as for the previous methods.

CONSTANT-YIELD HARVESTING

In theory, all of the estimators described above for use with constant-effort harvesting could also be used to

determine C_{MSY} , the maximum sustainable number of individuals that could be removed from the population annually. In practice, however, it is unlikely that where such data are available for an effort-based system they would be used to determine a set yield, rather than a set level of effort. Two estimators that are widely used for determining sustainability of catches are described below.

Robinson and Redford's maximum potential productivity estimator

This estimator (Robinson & Redford 1991) has, at its core, the calculation of $r_{\max}$ (the maximum intrinsic growth rate) using Cole's equation (Cole 1954). This assumes that population growth rate will reach its maximum potential if females begin breeding at sexual maturity and continue to do so until the maximum age of reproduction, and takes the form:

$$1 = e^{-r_{\max}} + be^{-ar_{\max}} - be^{-(w+1)r_{\max}} \quad \text{eqn 9}$$

where a = age at first reproduction; b = annual birth rate of female offspring; and w = last age of reproduction. It must be solved for $r_{\max}$ by iteration. In practice, data on a , b and w are not always readily available. However, as this is a model population, these can be assigned values with complete confidence, ensuring the reliability of the Robinson and Redford method. The estimation approach assumes that population production (P) will be maximized when the population is at 60% of its unexploited size. For a long-lived species (with a life span of more than 10 years), such as the alpine marmot, Robinson and Redford suggest that no more than 20% of the maximum annual production can be removed sustainably each year.

Robinson and Bodmer's actual productivity estimator

Where data on birth rates are also available for the exploited species, estimates of production can be derived directly, without the need to make assumptions about the potential productivity of the species (Robinson & Bodmer 1999). Where both the average litter size, Y , and the annual frequency of pregnant females, g , are known, annual production is given by:

$$P = 0.5N \times Yg \quad \text{eqn 10}$$

where N is the adult population size (discounted by 50% under the assumption of an even sex ratio). As with the Robinson and Redford estimator, it is assumed that no more than 20% of this production can be harvested sustainably.

THRESHOLD HARVESTING

In threshold harvesting, it is assumed that a population can safely be harvested down to a certain level but that

no hunting should take place when the population is at, or below, this threshold. All estimators that aim to determine the size of the safe threshold are based on the negative relationship between population growth rate and population size. The simplest of these stems directly from the logistic equation, assuming linear density dependence. This suggests that absolute productivity will occur when a population is at half its unexploited size and, hence, that the threshold for harvesting should be $0.5K$, where K is the equilibrium unexploited population size. Bearing in mind that, for most vertebrates, density dependence is likely to be non-linear, with the point of maximum productivity closer to K (Fowler 1981; Sutherland & Gill 2001), one widely used rule of thumb recommends a threshold of $0.6K$. A second rule of thumb taking a more precautionary approach and thought likely to be highly stable (Roughgarden & Smith 1996) recommends $0.75K$. One approach deriving from more detailed knowledge of a species' life history is that based on the relationship between the population size giving maximum productivity and the rate of increase per generation (Fowler 1988). This relationship is given by:

$$R = 0.633 - 0.187 \times \ln(rT) \quad \text{eqn 11}$$

where R = the proportion of K at which productivity is maximized; r = the intrinsic growth rate of the species; and T = the generation time or mean age of all female parents of all offspring produced.

In total, 100 simulations of 125 years were run using each suggested threshold. In each simulation, the population was permitted to stabilize over 20 years. Following this, threshold harvesting was begun and, after a further 5 years, data on annual yields were collected each year for a total of 100 years.

Two variations on each estimator for threshold harvesting were also assessed. For the first of these, it was assumed that for many hunted systems it may be impractical or impossible to conduct an annual census. An accurate estimate of population size was thus made available only every 3 or 5 years, and quotas were set accordingly. The second variant acknowledged that censuses are unlikely to be entirely accurate. Annual censuses were thus subjected to error in the form of a coefficient of variation (CV) of 5%, 10% or 20%.

PROBABILITIES OF EXTINCTION

The probabilities of extinction associated with different levels of both fixed-effort and fixed-yield exploitation were also assessed. A total of 700 simulations, each of 120 years duration, was run for each level of constant-effort exploitation. For each level of constant-yield exploitation (which shows a clearer relationship between extinction risk and hunting pressure), 200 simulations of 120 years duration were run. As before, populations were allowed to stabilize over 20 years, following which exploitation at a set level (either a constant yield or constant level of

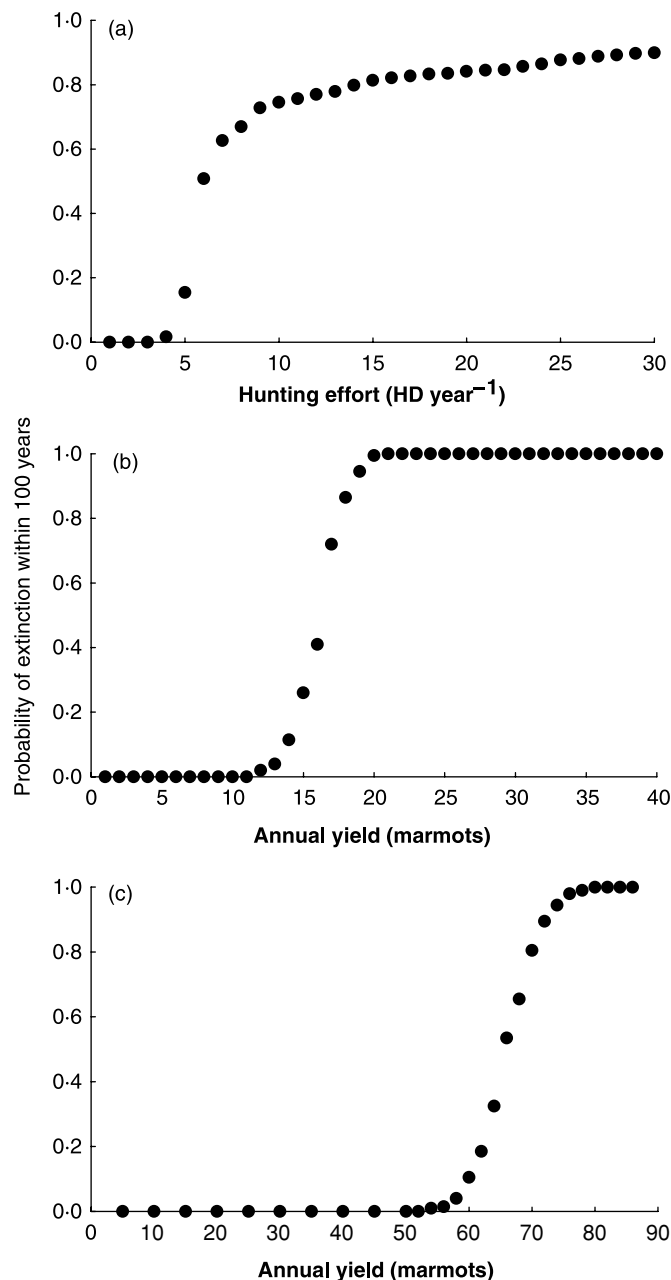


Fig. 1. Probabilities of extinction associated with different levels of (a) constant-effort and (b) constant-yield harvesting for the standard model population (equilibrium adult population = 340 ± 32), and (c) constant-yield harvesting of a larger population (equilibrium adult population = 1160 ± 65). Each data point represents the proportion of (a) 700 and (b and c) 200 simulations, during which extinction occurred within 100 years of harvesting at the given level.

effort) was initiated, and the population was assessed each year for a further 100 years. The proportions of simulations that led to extinction under each level of exploitation were used as an indicator of the extinction risk associated with that level of exploitation.

To determine the degree to which results were influenced by the relatively small population considered by the standard population model, probabilities of extinction under constant-yield harvesting were also determined using a population with four times as much available habitat. In the absence of exploitation, the equilibrium adult population size in this larger population model was 1160 ± 65 (SD).

Results

PROBABILITIES OF EXTINCTION

The probabilities of extinction associated with both constant-effort and constant-yield harvesting are shown in Fig. 1. Probabilities of extinction referred to hereafter are taken directly from the data in Fig. 1a,b. Probabilities of extinction are sharply non-linear. Due to the stochastic nature of harvest under constant-effort regimes (Fig. 1a), non-linearity in extinction probabilities is less pronounced in this case than when constant-yield harvesting is used (Fig. 1b). The

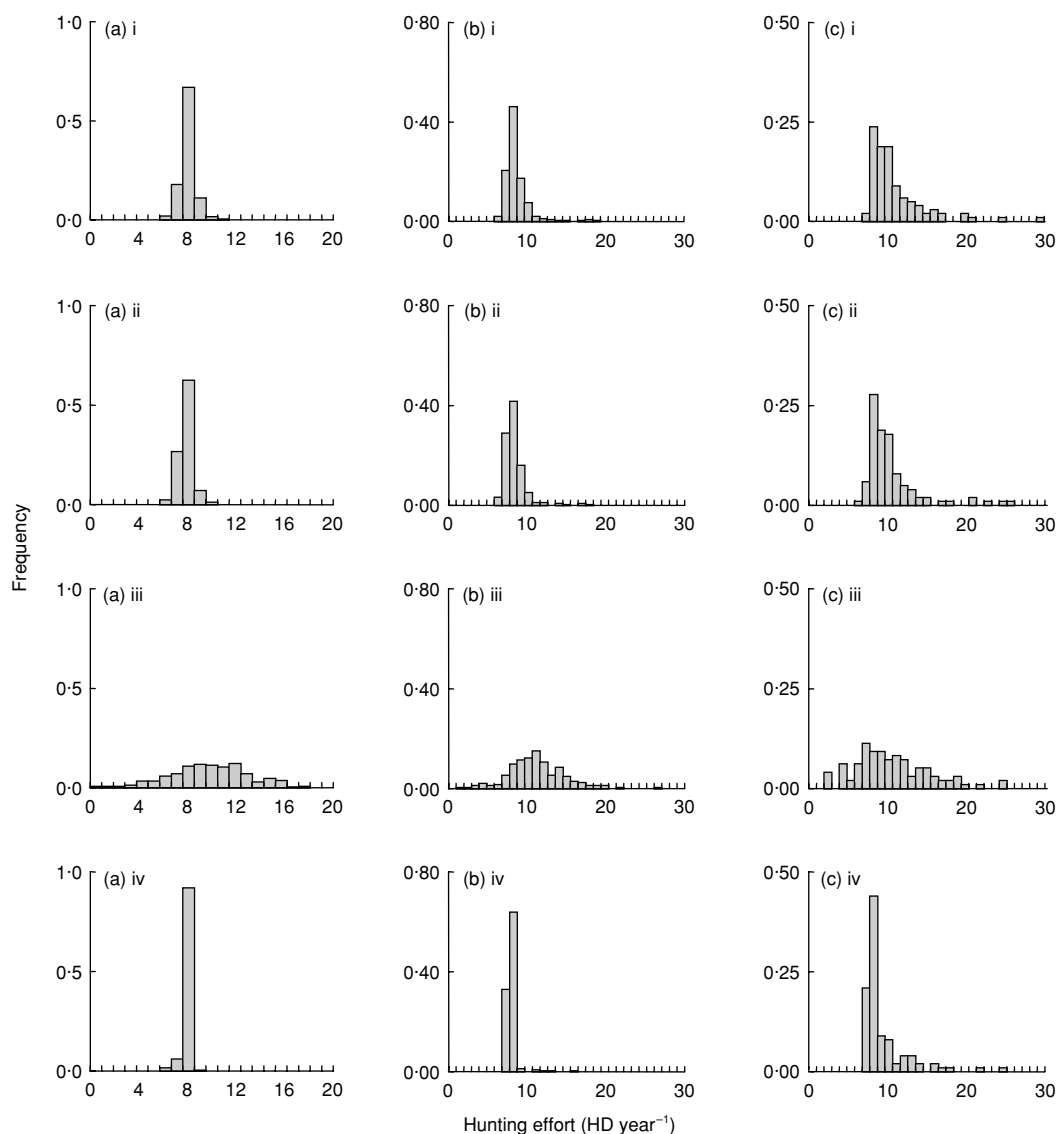


Fig. 2. Frequency distributions of recommendations for constant-effort harvesting, based on simulations of (a) 50-year data sets with pressure changes at 3-year intervals ($N = 250$), (b) 50-year data sets with pressure changes at 2-year intervals ($N = 250$), and (c) 25-year data sets with pressure changes at 2-year intervals ($N = 100$), using (i) equilibrium, (ii) effort-averaging, (iii) process-error and (iv) observation-error estimators. Note different axes scales. For the process-error estimators, negative recommendations (comprising 4–5% of recommendations) were excluded from the analysis.

non-linearity is not attributable to the small size of the population but rather is equally a feature of larger populations (Fig. 1c).

CONSTANT-EFFORT HARVESTING

Frequency distributions for the recommended sustainable levels of hunting produced by each of the four estimators are given in Fig. 2. A small proportion of both 50- and 25-year data sets (13 of 250, 3 of 250 and 4 of 100, for a, b and c, respectively) yielded recommendations for negative harvests when subjected to analysis using process-error estimation. Rather than highlighting errors in the method, as suggested by some authors, such results are indicative of the fact that there is little useable information in the data set

(Hilborn & Walters 1992). Clearly, such results would not be considered as worthwhile recommendations and these data were thus excluded from further analyses. Mean and modal recommendations and their associated probabilities of extinction are summarized in Table 2.

CONSTANT-YIELD HARVESTING

Robinson and Redford estimator

The parameter values required to solve Cole's equation for the Robinson and Redford estimator are inherent in the model design. The age at first reproduction (a) is 2 and the age at last reproduction (w) is 12. The annual birth rate of female offspring (b) can be calculated as:

Table 2. Extinction probabilities associated with recommendations for sustainable constant effort hunting

Estimator	Length of data set (years)	Recommendations (HD year ⁻¹)			
		Mean $\pm$ SD	Probability of extinction*	Mode	Probability of extinction*
Equilibrium	25†	11.5 $\pm$ 6.9	0.76	8	0.67
	50†	8.0 $\pm$ 0.6	0.67	8	0.67
Effort averaging	25	10.7 $\pm$ 5.1	0.75	8	0.67
	50	7.8 $\pm$ 0.6	0.66	8	0.67
Process error	25	10.4 $\pm$ 4.9	0.75	7	0.63
	50	9.8 $\pm$ 3.3	0.74	12	0.77
Observation error	25	9.5 $\pm$ 4.5	0.74	8	0.67
	50	7.9 $\pm$ 0.4	0.67	8	0.67

*Probabilities of extinction are derived from the analysis shown in Fig. 1a. Probabilities associated with non-integer harvest recommendations were derived by linear interpolation.

†Extinction probabilities associated with the best- and worst-case scenarios considered in Fig. 2a,c are shown here, i.e. 50-year data sets with 3-year intervals between changes in hunting pressure, and 25-year data sets with 2-year intervals between changes in hunting pressure.

$$\begin{aligned}
 b &= \text{annual probability of reproduction} \times \\
 &\quad \text{female sex ratio} \times \text{average litter size} \\
 &= 0.64 \times 0.42 \times 3.47 = 0.93
 \end{aligned}$$

These values yield a prediction of $r_{\max} = 0.46$, suggesting that the maximum production of the adult population is:

$$P_{\max} = 0.46 \times 0.6 \times 340 = 94$$

As stated above, in applying this method it is assumed that no more than 20% of this maximum annual production can be removed safely each year, giving a recommended maximum quota of 19 marmots per annum.

Robinson and Bodmer estimator

The annual quota recommended by this estimator is produced by using equation 10 to calculate the maximum production of the population:

$$\begin{aligned}
 P &= 0.5N \times Yg \\
 &= 0.5 \times 340 \times 3.47 \times 0.26 \\
 &= 153
 \end{aligned}$$

Again, the assumption of Robinson & Bodmer (1999) is that no more than 20% of this production can be removed each year, giving a recommended maximum annual quota of 30 marmots.

The extinction probabilities associated with the maximum quotas recommended by the Robinson & Redford (1991) and Robinson & Bodmer (1999) estimators are 0.95 and 1, respectively (Fig. 1b).

THRESHOLD HARVESTING

Three of the estimators for threshold harvesting set known thresholds at 0.5K, 0.6K and 0.75K. The fourth estimator, based on Fowler (1988), was calculated

using equation 11 and suggested that population productivity would be maximized at 0.48K. As this was so close to the threshold suggested by the logistic model, further analysis was conducted using only the first three estimators.

The results of threshold harvesting are summarized in Table 3. When censusing was conducted annually, this approach was associated with no risk of extinction within 100 years, even when census estimates were prone to substantial errors with a CV of up to 20%. Mean yields tended to be highest when the threshold was set at 0.6K (typically between 15 and 17 marmots per year) but variance in yields was high and the proportion of years in which hunting was not possible was also high (between 13% and 65%). Reducing the frequency of censuses greatly increased the risk of extinction, particularly when combined with census error. For triennial censusing, the best yields and lowest extinction risks were produced using a threshold of 0.75K but the proportion of years in which no hunting could occur was greater than one in two. A frequency of only one census every 5 years was always associated with high risks of extinction, even when the censuses were entirely accurate.

Discussion

The results show that a relatively small fluctuating population, such as that of the marmots in Berchtesgaden National Park, would be very prone to extinction when subjected to even quite low levels of regular hunting (e.g. the annual removal of numbers equivalent to 5% of the equilibrium adult population). Furthermore, due to the nature of density dependence in this species, the probability of extinction increases very abruptly, so that a difference in annual quotas of only a few individuals could be the difference between a very low probability of population extinction and what is almost a certainty of extinction. This sharp non-linearity in extinction risks is not a product of small population

Table 3. Yields and extinction risks from threshold harvesting

Conditions		Results of threshold harvesting of the simulated population compared by threshold size*								
Census interval	CV of estimates (%)	Mean yield† ± SD			Years with zero yield/%‡			Probability of extinction§		
		0.5K	0.6K	0.75K	0.5K	0.6K	0.75K	0.5K	0.6K	0.75K
1 year	0	15.5 ± 11.5	17.1 ± 12.9	14.8 ± 14.2	13.4	14.3	25.8	0.00	0.00	0.00
	5	15.2 ± 15.0	16.9 ± 16.6	14.8 ± 17.9	25.5	26.0	37.9	0.00	0.00	0.00
	10	14.1 ± 18.7	16.7 ± 21.5	14.7 ± 22.3	42.7	41.6	51.4	0.00	0.00	0.00
	20	12.5 ± 23.5	14.8 ± 27.2	15.3 ± 30.0	63.0	62.4	65.3	0.00	0.00	0.00
3 years	0	5.0 ± 13.0	7.9 ± 16.8	13.6 ± 21.6	91.4	78.5	57.3	0.64	0.29	0.01
	5	4.4 ± 12.8	8.4 ± 16.3	14.1 ± 22.3	91.7	75.9	55.4	0.59	0.25	0.00
	10	4.1 ± 12.0	8.2 ± 16.7	13.8 ± 22.3	93.6	77.6	57.7	0.69	0.29	0.02
	20	5.5 ± 17.6	7.7 ± 23.1	9.8 ± 27.2	94.2	91.7	87.5	0.78	0.60	0.53
5 years	0	15.4 ± 40.3	18.3 ± 42.0	12.9 ± 27.4	99.0	98.2	86.7	0.99	0.99	0.67
	5	17.5 ± 42.4	14.3 ± 35.9	12.8 ± 27.3	98.4	97.4	86.4	0.98	0.94	0.62
	10	30.1 ± 62.9	16.2 ± 37.8	13.0 ± 27.8	99.7	96.9	88.1	1.00	0.94	0.71
	20	24.1 ± 54.0	20.7 ± 43.4	13.8 ± 29.5	99.1	98.4	89.1	0.98	0.98	0.77

*Threshold size is given as a proportion of the equilibrium adult population size in the absence of hunting (K).

†Calculations of mean yields exclude years following extinction but include years with zero yield prior to extinction.

‡Shows the proportion of years in which the population was estimated to be at, or below, the threshold and no hunting was possible. If extinction occurred, years following extinction are included as years in which no hunting could occur.

§Probability of extinction is calculated as the proportion of all 100 simulations during which the population went extinct within 100 years of the stated hunting regime.

size; the same phenomenon is apparent for a population of approximately four times the size. The result of this is that all of the estimators tested for regular fixed hunting regimes (either constant effort or constant yield) suggest quotas that are too high to sustain over long periods. In keeping with other authors (Lande, Engen & Sæther 1995), the results of this study suggest that the safest way to exploit this fluctuating population is to use a threshold-harvesting approach. However, the results also show that a threshold approach to exploitation is associated with highly variable yields and a high proportion of years in which no hunting is possible, neither of which is likely to be acceptable in the majority of exploitative systems. Furthermore, reducing the frequency of censuses and, to a lesser extent, introducing census error, can greatly reduce the safety of threshold exploitation, leading to high risks of population extinction. These results are discussed in light of the three questions posed in the introduction.

In terms of estimating the level of effort required to maximize total yields, the constant-effort estimators were extremely dependent on both the length and quality of the data set. When 50-year data sets were available, at least three of the estimators were relatively consistent in their recommendations. By contrast, shorter data sets and shorter intervals between changes in hunting pressure led to considerably greater variation in the recommendations of all estimators. Larger intervals between changes in pressure increase the chance that the population will equilibrate with its exploitation. It is also likely that over 50 years there is a greater chance of an exploited population showing the effects of over-exploitation and, thus, longer data sets will produce

more conservative recommendations with greater consistency. Even so, managers benefiting from 25-year data sets would be in a position of considerable privilege, and many of the classic examples of surplus yield models rely on considerably less data (often of less than 20 years), frequently collected during periods over which means of assessing effort and yield changed. This finding highlights the need for caution when making use of data sets involving stochasticity in both population growth and hunting success. Nevertheless, the modal recommendations of all but the 50-year process-error estimators were remarkably accurate at estimating the level of effort required to produce the greatest annual yields. Figure 3 shows the results of collating every year's data from all of the 50-year data sets with 3-year intervals between changes in hunting pressure. Evidently a level of effort of 8 or 9 HD year⁻¹ is optimal for producing the highest annual yields and, from this point of view, the constant-effort estimators performed well.

By the other major criterion considered here, however, the constant-effort estimators performed very poorly. All recommended levels of effort were associated with high probabilities of extinction within 100 years, typically of 60–75%. The problem is exactly that identified by Roughgarden & Smith (1996): the point of optimal harvest is an unstable equilibrium. For a fluctuating population, if stochastic events drive it below the point of maximum production, then harvest will be likely to exceed production and the stock will decline to extinction. The solution suggested by Roughgarden & Smith (1996) is to exercise caution and harvest below the point of optimal harvest. Harvesting at a rate of 4 HD year⁻¹ (50% of the modal recommendations of most of

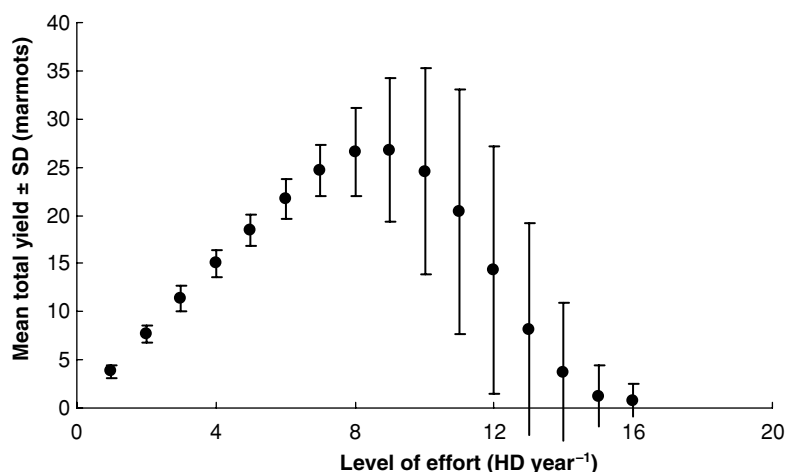


Fig. 3. Mean annual yields against hunting effort for all years used in the 50-year data set analysis (total number of years = 12 500).

the estimators, and very roughly equivalent to Roughgarden and Smith's 75% rule) would be associated with a very low (< 2%) risk of extinction. Such an approach buffers against fluctuations upsetting the stability of exploitation and is thus considerably more stable.

Overall, the observation-error estimator produced the most conservative recommendations with the least variance. This result is in keeping with the findings of Polacheck, Hilborn & Punt (1993), who compared these techniques when applied to three sets of data from fisheries. It is widely acknowledged in the fisheries literature that equilibrium estimators should never be used (Hilborn & Walters 1992; Jennings, Kaiser & Reynolds 2001). In addition, Polacheck, Hilborn & Punt (1993) suggested that bias in the effort-averaging approach and the wide variance of process-error estimates should preclude the use of either of these in isolation. Our results support these findings, confirming the greater reliability of observation-error techniques. However, the results also suggest that these should be applied to widely fluctuating populations only with great caution.

Both of the constant-yield estimators used suggest maximum annual quotas associated with very high probabilities of extinction, despite the fact that neither predicted unrealistic levels of population production. The predictions of Cole's equation as presented above, are that the maximum possible growth rate of the population is less than 5% per annum. In fact, our analyses suggest that our model population has a maximum growth rate (at approximately 0.55–0.6K) of over 7% (Stephens *et al.* 2002) and, thus, the Robinson & Redford (1991) approach actually underestimates population growth. The Robinson & Bodmer (1999) method for calculating production of the unexploited population is parameterized using data from the model and is entirely accurate in predicting the mean annual production. Why then, do these methods predict unsustainable harvest rates? The answer must lie in the extreme sociality of the alpine marmot, a factor that cannot be captured by the simplistic population models

underlying the Robinson and Redford and Robinson and Bodmer approaches. Alpine marmots are among the most social of sciurids and an important factor underlying this sociality is their need for social thermoregulation during winter. Marmots live at high elevations and hibernate throughout the long harsh winters. Survival of juveniles and lone animals is low, but juvenile survival can be greatly increased by hibernating with larger numbers of adults (Arnold 1988, 1990b, 1993, 1995; Arnold *et al.* 1991). Due to the importance of social thermoregulation, the removal of relatively few adults late in the year becomes critical. The majority of dispersal in alpine marmots occurs early in the year. It is possible that hunting would lead to increased perturbation and increased dispersal later in the year. Culling of badgers *Meles meles* has been demonstrated to lead to higher rates of dispersal (Tuytens *et al.* 2000) and might be expected to have similar effects in other social mammals. If this were to occur, the population would be more robust to the effects of exploitation (Fig. 4). However, in the absence of evidence that this is the case, the analyses presented here do not incorporate these effects of increased perturbation.

The need for social thermoregulation in marmots is just one example of a behavioural mechanism that underlies the importance of group living in many social mammals. Many primate species are very dependent on sociality for a variety of reasons, including energetic constraints (Sussman & Garber 1987), predator detection (van Schaik & van Hooff 1983; van Schaik *et al.* 1983) and interspecific resource defence (Clutton-Brock 1974). The effects of losing adult members and falling below a minimum group size have been shown to be critical in some primates (Young & Isbell 1994). Vigilance (Lipetz & Bekoff 1982), anti-predator defence (Berger 1979; Bowyer 1987) and other behavioural mechanisms (Mooring & Hart 1992) can also have a negative effect on the fitness of ungulates when group sizes are depleted. The constant-yield estimators assessed in this paper were designed specifically for use

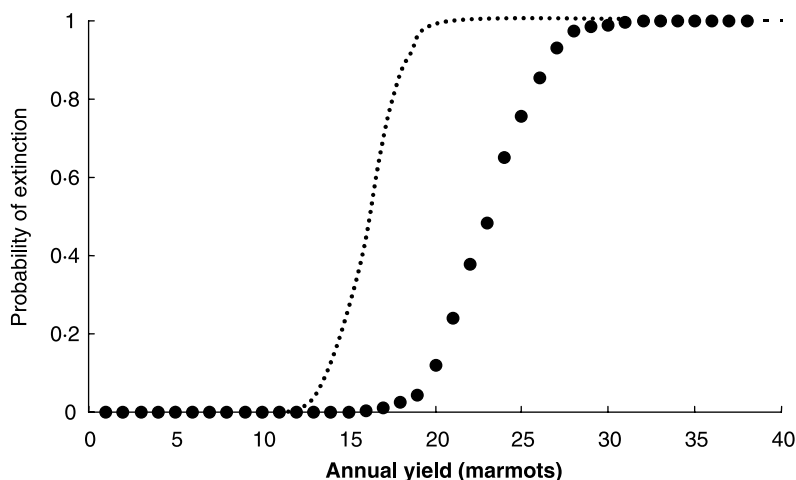


Fig. 4. Probabilities of extinction in the standard model associated with different levels of constant-yield harvesting, when hunting induces social perturbations and increases the frequency of late autumn dispersal. Filled circles show the proportion of 200 simulations during which extinction occurred within 100 years of harvesting when all potential dispersers in the population were allowed a second opportunity to disperse at the end of the year, following hunting mortalities. For comparison, the dotted line shows the extinction profile given in Fig. 1b, which assumes no perturbation and no increase in late dispersal.

with the bush meat trade, a large component of which is based on hunting primates and ungulates. The authors of these estimators stress that they indicate only the level above which hunting is definitely unsustainable and do not suggest that hunting would be sustainable at or below the calculated annual yield. However, in view of the results of this study, it may also be important to stress the importance of social system in relation to these estimators and it is recommended that indices of unsustainability are markedly reduced for species dependent on sociality.

As stated previously, threshold harvesting proved to be the safest way to exploit the population, in keeping with the findings of Lande, Engen & Sæther (1995). These authors also suggested that where census error was a factor, a more cautious approach of proportional threshold harvesting, where only a proportion of the individuals above the threshold were killed, was preferable (Engen, Lande & Sæther 1997). In our study, extinction risk remained low even with a CV of 20% in population estimates, as long as the population was censused annually. However, proportional threshold harvesting may reduce variance in yields in these cases and may also greatly reduce extinction risks when censuses occur less frequently (Lande, Sæther & Engen 2001). In general, threshold harvesting with a threshold of 0.6K performed better than either of the other thresholds tested. This is to be expected, given (as observed above) that population growth peaks at about this size. Nevertheless, in scenarios of reduced certainty, particularly when population estimates are infrequent, a more conservative threshold (such as the 75% threshold) is likely to minimize extinction risks.

Milner-Gulland *et al.* (2001) found that the best strategies were simple, involving harvesting a 'small proportion' of the population size each year, i.e. that a constant-effort system based on a low level of effort is

the optimal approach. If variance in yields is to be reduced, it is likely that our results would concur with this and that a level of 3 HD year⁻¹ would be recommended, corresponding to a mean annual yield of 10–12 marmots from this population. Nevertheless, for most stock managers, the problem remains: what is a 'small proportion' of the population, how does this vary among species, and how should it be estimated? Our findings suggest that for fluctuating populations, especially of a social species, a 'small proportion' is considerably less than would be predicted by available estimators for constant-effort harvesting and that such estimators should be treated with considerable caution.

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