

5 • *Estimating Sustainability*

5.1 Introduction

Sustainability is a concept widely used in science and politics, and it has myriad different definitions. The idea of sustainability first emerged at the start of the eighteenth century when von Carlowitz (1713), in the first book on forest sciences, wrote that timber should be used with caution, balancing timber growth and use. Much later, the broadest political vision of sustainability was expressed in the Brundtland Commission, as ‘development that meets the needs of the present generation without compromising the ability of future generations to meet their own needs’ (Brundtland 1987). The idea that sustainability should encompass the maximum use for humans is expressed in Tivy and O’Hare’s (1981) description of sustainable yield as the ‘management of a resource for maximum continuing production, consistent with the maintenance of a constantly renewable stock’. Different definitions emphasize the ecological, sociopolitical and economic pillars of sustainability. Highlighting ecology and socioeconomics, the Convention on Biological Diversity (CBD), the international legal instrument for the protection of global biodiversity, defines sustainable wildlife management as ‘the sound management of wildlife species to sustain their populations and habitat over time, taking into account the socioeconomic needs of human populations’ (CBD 2018). Whilst there are many nuances in how sustainability is conceptualized and underpinned by a theoretical framework (e.g. in bioeconomics, Clark 2010), the concept is often very difficult to apply and measure. A poignant reminder is fisheries management, which is much more advanced compared to wild meat management, despite there being many cases of fisheries collapse, even with careful management planning focused on sustainability (Bavington 2011; Roughgarden & Smith 1996). The most prominent example of fishery collapse is the disintegration of the Newfoundland Atlantic cod stocks (Bavington 2011). These stocks, like in fisheries in general, were managed based on

the theory of maximum sustainable yield (MSY), which – under ideal conditions – can achieve the maximum possible harvest without depleting the species' stock over an indefinite period. This concept has limitations (see below); fisheries have now transitioned to ecosystems-based management, and in some parts of the world, at least, they seem to have achieved fisheries sustainability (e.g. Aswani *et al.* 2012; Pikitch *et al.* 2004; Section 5.7.1) It is the same concept that discussions of sustainability of wild meat hunting are currently emphasizing (Coad *et al.* 2019; Weinbaum *et al.* 2013), although more holistic concepts have recently emerged (Van Vliet *et al.* 2015b; Section 5.7.2). In this chapter, we introduce the different approaches and metrics that have been used or proposed to assess wild meat sustainability.

5.2 Growth Rate and Maximum Sustainable Yield

The MSY concept is based on a continuous time growth model according to which growth curves are density-dependent. The growth curve, that is, the recruitment that adds to a population, is parabolic, somewhat resembling an inverse U-shaped curve (Fig. 5.1). Growth rate is lowest at the two extremes of the possible densities of a population: at the carrying capacity, K , which is the maximum population size that the environment can support on a continuing basis and at very low population size. This means that the same levels of low sustainable yields exist when a population is unhunted, at K , as well as heavily hunted and close to extinction. Growth rate and, thus, sustainable yield increase when density either decreases from K or increases from very small values. The theoretical growth rate can be described with the following formula:

$$\begin{aligned} \text{growth rate} &= \text{change in population size over time } \Delta N / \Delta t \\ &= r \cdot N \cdot (1 - N/K) \end{aligned}$$

with N = population size, ΔN = change of N , Δt change of time, r = intrinsic rate of population increase and K = carrying capacity. The two crucial parameters are r and K , which are both inherently difficult, if not virtually impossible, to measure in wild populations. At a given population size, the maximum amount that can be removed from a population equals the growth rate at that population size. In other words, harvest rates that are equal or below the growth rate can theoretically achieve ecological sustainability as the resulting growth will not be smaller than zero. There is a clear exception, namely at very low population density, because

environmental, demographic and genetic stochasticity and possibly biological processes such as the Allee effect (Courchamp *et al.* 2008) lead to a high extinction probability – the ‘extinction vortex’ (Fagan & Holmes 2006). There is a point between the two extremes of K and population extinction, at $K/2$, where growth is maximum, and this point is where MSY occurs.

The effect of increases in the harvest rate depends on whether the density is smaller or larger than $K/2$. If it is larger than $K/2$, the hunted population will decline to a new equilibrium at a lower density (Fig. 5.1a and c). Consequently, a population decline does not necessarily mean unsustainability as it can mean that a declining population is on its way to a new equilibrium. If the density is equal to or smaller than $K/2$, however, then increase of hunting above the growth curve will eventually lead to population collapse because hunting takes away not only the surplus but also the stock itself (Fig. 5.1b). If the density is only slightly larger than $K/2$, an increase of hunting will decrease density towards $K/2$, but density can also swing below $K/2$ because of stochasticity, additional mortality or environmental variability (Fig. 5.1c). Any further increase of hunting, even when small, would then cause a population to

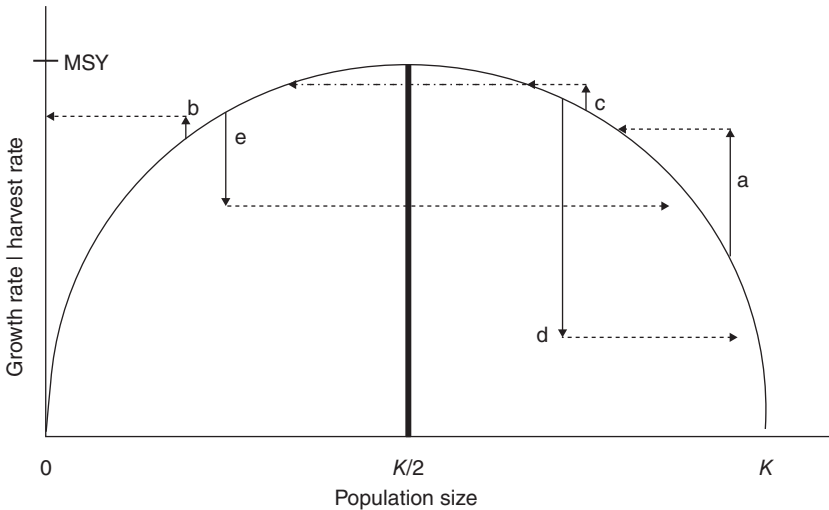


Figure 5.1 Parabolic relationship between population growth rate and population size derived from the logistic equation for population growth. When harvest rate equals growth rate, the population comes to an equilibrium at the associated population size. Changes in harvest result in new equilibrium sizes, indicated by the heavy black line. Further details in the text. Explanations of the letters are in the main text.

decline and collapse rather than achieve a new equilibrium. This applies when the harvest rate is constant. Once brought out of balance to the left side of $K/2$, the population is likely to crash except when hunting pressure is reduced; if hunting pressure is lowered, the population can grow until a new equilibrium above $K/2$ is reached (Fig. 5.1e and d; see also Clark 1976; Haddon 2011; Milner-Gulland & Mace 2009). When the harvest rate is proportional to the population size, then in principle any harvest rate is sustainable.

The CBD's (2018) definition of sustainable harvest implicitly points to MSY to balance ecological sustainability with socioeconomic sustainability to meet the needs of an increasing human population. Ecological sustainability could be at any point of the density-dependent continuum, but it must be stressed that at low population levels sustainability is unattainable (1) because of the potential for Allee effects (Courchamp *et al.* 2008) and the extinction vortex (Fagan & Holmes 2006) and (2) because the ecosystem may be disrupted as the species is no longer able to play its ecological role.

The most widely used method for assessing hunting sustainability – the Robinson & Redford (1991b) model – argues that sustainable harvesting should achieve the maximum possible level of extraction, which is a fraction of a species' maximum annual production, calculated from the carrying capacity and intrinsic population growth rate, whereby the fraction depends on the average lifespan of the species and an a priori precautionary factor (Section 5.4.2). Milner-Gulland and Akçakaya (2001) promote the full demographic harvesting model because it gives an accurate representation of the state of the population, unlike the Robinson and Redford (1991b) model, and is robust to uncertainty. It maximizes harvest whilst other simpler models incur substantial loss in offtake when estimating sustainable harvest levels. This means it is possible to hunt more without sending the population towards extinction but does not mean the maximum needs to be harvested.

Whilst the wild meat literature has introduced the MSY as an ideal to achieve (Coad *et al.* 2019), the suitability of MSY in fisheries management has long been rejected (Larkin 1977; Ludwig *et al.* 1993); the overwhelming criticisms against MSY were summarized by Larkin (1977). Even though the use of MSY approach has declined in fisheries, it has remained in use because it is a simple and easy-to-understand concept (Barber 1988). However, with the recent shift of the harvesting paradigm in fisheries towards ecosystem-based management (Section 5.7.1), MSY is now used as a reference point rather than as a target

(Mace 2001). In an analysis of managed fisheries collapses, Roughgarden and Smith (1996) stressed that the application of economic theory that aims to maximize sustainable harvest leads to an ecologically unstable equilibrium as ‘difficult as to balance a marble on top of a dome’. To facilitate population stability, the emphasis should be on ecological stability rather than maximizing harvests. The authors argue that ‘ecological stability is achieved if the target stock is above that producing maximum sustainable yield and harvested at less than the maximum sustainable yield’. In other words, the growth curve needs to stay on the right side of $K/2$. The apparent economic loss due to forfeiting MSY would act as a ‘natural insurance’ that is low in case of high productivity of the target species. However, this apparent economic loss under the MSY is not a loss under the concept of maximum economic yield (MEY), which is the long-term value of the largest positive difference between total revenues from fishing and total costs of fishing. Because it takes costs into account, MEY is almost always on the right-hand side of the parabola in Fig. 5.1, thus facilitating sustainability. Economists have argued that a fishery that maximizes its economic potential also usually will fulfil its conservation objectives. For example, Grafton *et al.* (2007) show that the biomass under MEY exceeds the biomass under MSY. However, to the best of our knowledge, the concept of MEY has not been applied as a management tool in wild meat hunting.

It is important to keep in mind that the logistic growth curve is an idealization. Real populations are more complex. This is because of demographic stochasticity, environmental variation, reproductive biases by age, sex and social structure, interdependence with other, often also hunted species (as in the case of predator–prey systems) and the influence of geographic structure, especially metapopulation dynamics and source–sink relationships. In the following sections, we introduce and critically discuss the commonly used methods to evaluate the sustainability of wildlife hunting. The selection of some of the benchmark example studies follows Weinbaum *et al.* (2013).

5.3 Indices Quantifying Population Trends over Time

Biological systems are multifaceted and are impacted by deterministic processes and stochastic events. There is usually also randomness and uncertainty in estimating population density and hunting pressure, not to mention complex biological parameters such as growth rate and reproductive parameters of prey species that are difficult to obtain from wild

populations (see Section 5.3.1). Thus, ultimately, a population can only be known to be sustainably harvested after there has been adequate time to observe if the population estimators are sufficiently precise, the predictions hold true and the system is stable. Therefore, indices quantifying population trends over time are, thus, the most practicable for evaluating sustainability. Although direct monitoring of prey populations may be the ‘golden standard’, there are a number of methods that continue to be used. We describe these, their advantages and disadvantages, as well as an example of each to demonstrate its application.

5.3.1 Direct Surveys of Population Density

In a review of sustainability indicators for wild meat hunting, Weinbaum *et al.* (2013) proposed monitoring of harvested populations through time as one of the gold standards in sustainability monitoring. The surveys provide indications whether a target population is stable, increasing or decreasing. For an overview of techniques to estimate absolute and relative densities, see Millner-Gulland and Rowcliffe (2007).

Pros: The advantage is that it is the only method that directly estimates sustainability. The method is very powerful if monitoring is continuous and the results are fed into adaptive harvesting strategies.

Cons: The major caution is that changes in population abundance are difficult to interpret if estimates of associated species (e.g. predator–prey systems), harvesting and external factors (e.g. habitat change or climate change) are not simultaneously estimated, or if spatial scales are too small to detect source–sink patterns. Time frames need to be sufficiently long to allow distinguishing stochastic change from systematic change, albeit sudden declines in population density can act as early warning systems to trigger more intensive monitoring. The major disadvantage is that it is time intensive and expensive, especially when remote, tropical locations are concerned. Whilst intensive monitoring is more likely for those species in logistically easy-to-monitor habitats (e.g. savannahs), where animals can be directly observed or trapped, monitoring prey populations in dense vegetation environments (e.g. tropical forests) is more difficult.

Example: Weinbaum *et al.* (2013) describe the earliest textbook example of this method as Larivière *et al.*'s (2000) grey wolf monitoring study in southern Québec, Canada. Here, wolves are found in a mosaic of wildlife reserves, where

hunting is controlled by quotas on hunting licenses, unlike public and private lands where harvests are less restricted. Over a 15-year time period, starting with the onset of wolf trapping in the reserves, the study monitored wolf densities in nine wildlife reserves by a combination of questionnaires distributed to moose hunters and the usage of radio-tracking wolves. Aerial surveys were used to monitor moose densities. Pelt sales and tanning records for each trapping district were employed to quantify wolf harvest. Over the study period, although wolf densities fluctuated widely in seven reserves, these showed no indication of long-term declines. By contrast, wolf populations in two reserves declined steadily. Without continuous monitoring, estimates of sustainability would have been highly biased. Population variability was negatively correlated with reserve size, indicating that wolf populations in smaller reserves were more unstable than those in larger reserves. In the two smallest reserves, however, harvesting frequently exceeded wolf densities but without population decline. This points to the presence of a source–sink system in which wolves from adjacent reserves repopulated the smaller reserves. Previously it was thought that these reserves acted as sources for the surrounding public and private lands, but the Larivière *et al.* (2000) study showed the contrary. These results demonstrate the importance of investing in continuous population density surveys to provide information to local wildlife managers to ensure conservation of the target species alongside their exploitation. As mentioned above, population monitoring of species such as the grey wolf is possible because the target species is generally visible to the observer (and therefore can be counted using direct methods) or their numbers can be inferred indirectly from records of hunted animals.

5.3.2 Catch Per Unit Effort over Time

The yield or number of animals removed by hunting, H , depends on catchability, q , hunting effort, E , and population size, N :

$$H = q \cdot E \cdot N$$

The parameter q is a species-specific constant quantifying how difficult or easy it is to hunt the species. If the effort is independent of the yield and population density, then changes in H/E translate in variations in N . This is the catch per unit effort (CPUE) – the ratio of yield to the effort expended to achieve the yield. Hunting effort can be measured as duration of hunts that result in H hunted animals, number of hunted animals per trip, number of snares set or amount of ammunition used. Using interviews and hunting returns, Vickers (1994) was the first to estimate population density trajectories, but without calling it CPUE, for Siona-Secoya hunters in the northwest Amazonian Peru. More recently,

Rist *et al.* (2010) investigated the methodology in more detail by comparing data collected by hunters with more direct information gathered by accompanying hunters on hunting trips. By applying simulations, Rist *et al.* (2010) assessed the accuracy, power and resolution of the method.

Pros: CPUE values can be obtained directly from hunters, which is easier and cheaper than monitoring populations in the field. Hunters require little training for data recording.

Cons: Estimates resulting from CPUE data are unable to determine population density and thus yield. CPUE needs to be monitored over time to reliably identify whether it increases, decreases or stays stable. It requires an adequate and representative sample of hunters per area/region to account for differences in their hunting efficiencies and strategies and geographic substructure such as contrasts between villages. The sample must be sufficiently large to distinguish between measurement errors and stochasticity from 'true' changes in CPUE. Studies need to demonstrate this, for example by subsampling and modelling (Rist *et al.* 2010). Selecting a sufficiently large number of monitored hunters can be a challenge, especially where hunting is illegal (e.g. protected areas), or where specific hunting methods are prohibited (e.g. snares). Moreover, if CPUE is used for management of hunting quotas, reductions in quota will likely erode the hunters' willingness to participate and compromise the trustworthiness of the data provided. Rist *et al.* (2010) modelled CPUEs assuming a statistical power of only 80% and $\alpha = 0.05$ reporting that information on 1,000 hunts had to be collected to allow the detection of a 20% density change. As many as 3,000 hunts were required for a detection of a 10% change. The method relies on trust between all participants where trust-building is time consuming. Reported values must be unbiased, but experience from fisheries has shown that there is over-reporting of both catch and effort in some fisheries (Lunn & Dearden 2006). A crucial component of the equation is that yield is directly proportional to both effort and population size. CPUE assumes that no density-dependent changes occur in hunter effort, such as change in technology or strategy. However, hunters might change to night hunting with flashlights when densities decline, which would bias CPUE and might even result in a stable CPUE despite population declines (Bowler *et al.* 2019). Similarly, hunting yield needs to be proportional to density. Even the assumption that catchability is a

constant might not hold for many species, for example, when animals respond behaviourally to the presence of humans as a reaction to hunting pressure and, thus, bias the yield (Keane *et al.* 2011; Papworth *et al.* 2013a). Aggregation behaviour, the tendency for animals to group together in flocks or herds as seen in many bird and ungulate species can result in similar hunter effort independent of whether density is stable or declining. This is because it is easier to hunt gregarious species than solitary, territorial ones and because aggregations occur despite changes in density. Finally, the same caveats apply to the interpretation of inferred population decline as for the direct surveys of population density.

Example: Hill *et al.* (2003) recorded harvest-rate data for 5,526 Aché hunter days during seven years in the Mbaracayu Reserve, Paraguay. CPUE, expressed as animals killed per hunting day, was seen to decline in seven of the ten prey species, which jointly contributed 95% of all individuals and 96% of biomass harvested. Only the drop in capuchin monkeys was significant but high variability in monthly harvest rates may have masked the negative trends. To be able to interpret the complexities of the observed fluctuations in CPUE, 7,535 km of diurnal random line transect surveys were conducted by teams of five observers. Encounter rates from the line transects showed negative trends in nine of the ten species, with four species exhibiting significant declines (Fig. 5.2). However, these four species did not include the capuchin monkey. The 95% confidence interval (CI) of the estimated maximum harvest rate was lower than 1% of the standing stock for six species including the capuchin monkey and was lower than 3.7% for the remaining four species. Overall, the declining CPUE and encounter rates of most species caused concern, but there was little evidence that hunting pressure by Aché hunters was the main cause of these observed decreases. However, there was support for considerable poaching by non-Aché hunters, which could explain the observed patterns. Regarding the capuchin monkey, CPUE was possibly misleading as the observed significant declines may have been caused by changes in hunting effort E , but possibly not in N . During the study, Aché hunters appeared to refocus their attention to peccaries rather than capuchin monkey, thus changing E for the species involved. Finally, the results demonstrate that the applicability and interpretability of the CPUE index in the study was limited without the inclusion of direct surveys of population density.

5.4 Indices Based on Full Demographic Models

Modelling populations based on their life history traits and demographic parameters allows us to determine how much additional mortality is

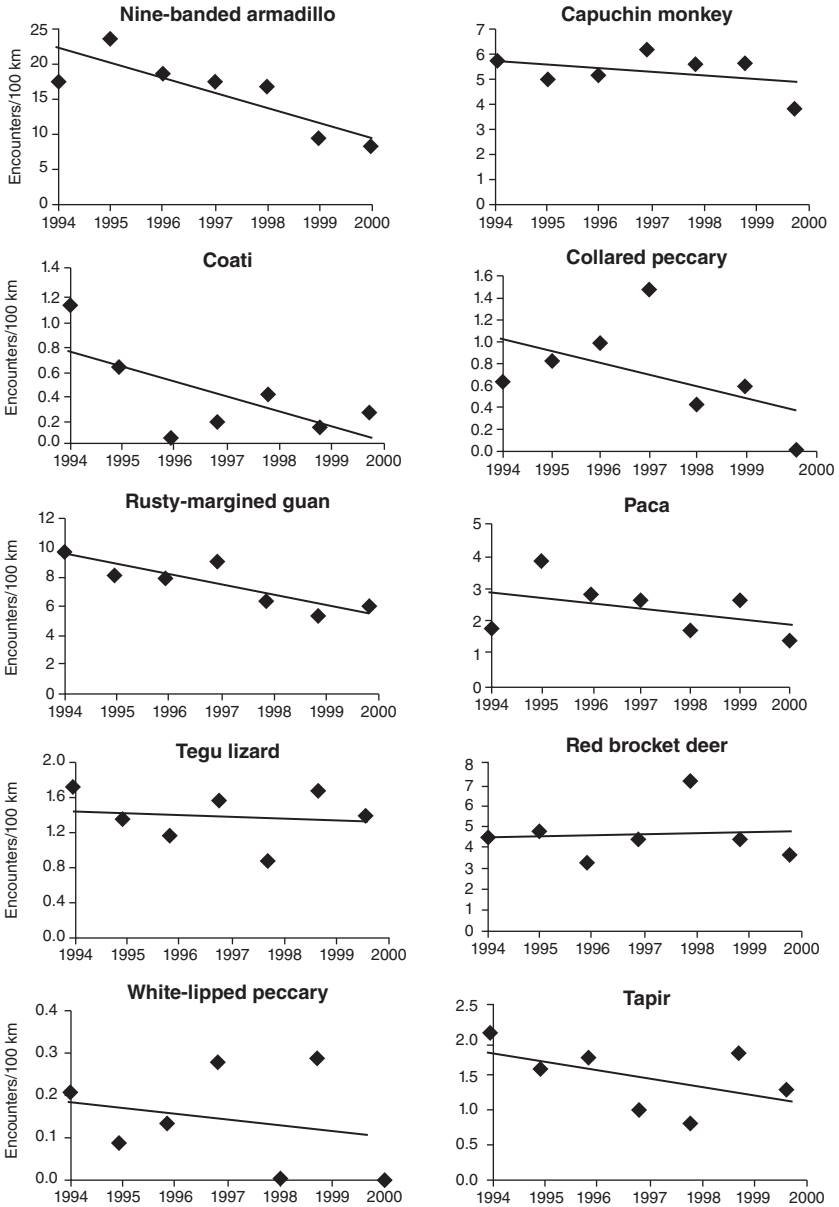


Figure 5.2 Crude encounter rates/100 km of ten important hunted species. Encounter rates were calculated as total encounters divided by total kilometres of transect walked in each 12-month period of the study. (From Hill *et al.* 2003; adapted with permission from John Wiley & Sons.)

compatible with population persistence. This can then be compared with the actual harvest. Milner-Gulland and Akçakaya (2001) introduced the full demographic harvesting model based on realistic demographic parameters and proportional harvest rates for each age class. Populations were simulated using RAMAS Metapop, a software package to analyse population viability (Akçakaya & Root 2002), under different demographic scenarios and then compared with simulations using different simple demographic algorithms (Section 5.4). The target was population persistence of 200 individuals during a 50-year period, with a likelihood of over 95%. Simulations indicated that the full demographic model outperformed all other models in population persistence and maximum harvest rates. It dramatically outperformed the Bodmer B method (Section 5.4.2), which was the next best performing model in terms of harvest, by a 7% greater harvest and a 95% lower risk of population collapse. It also outperformed the National Marine Fisheries Service algorithm (Section 5.4.3), which was the next-best performing model in terms of population persistence, by a 62% greater harvest.

Pros: Full models allow maximization of extraction rates whilst keeping extinction probabilities low. They allow the simulation of ranges of reasonable population parameters and, thus, make it possible to conduct sensitivity analyses. Population viability analysis (PVA) permits not only the modelling of deterministic parameters but also demographic, environmental and genetic stochastic events, which are of particular importance in small populations.

Cons: Full models are data-intensive, requiring life history information and knowledge of the many processes affecting populations. Attainment of such level of detail and precision is often not possible for most tropical, hunted species. Because such robust biological information is not available – even for well-studied species – such models do not adequately account for demographic complexities, in particular density-dependence. For example, in a study of sustainable harvest rates of the European hare, Marboutin *et al.* (2003) chose a simplified life cycle with three age classes and density-independence because of the lack of adequate data, despite the fact that sustained harvesting might indicate density-dependence. The absence of realistic reproductive and demographic data from wild populations has been pointed out as a major problem in applying sustainability models, even for widely hunted species. As a consequence, reproductive parameters are often taken from captive populations, which

can be crude, biased towards *ex situ* conditions and in many cases outdated (Mayor *et al.* 2017; Van Vliet & Nasi 2018; see Chapter 8). For example, reproductive data used in sustainable hunting models (see Robinson & Redford 1986) for woolly monkeys, the Amazon's most hunted primates, have come primarily from captive populations for the 1960s, when they rarely reproduced, and before a major taxonomic revision split one supposed species into five different ones (Bowler *et al.* 2014). It is therefore essential not just to verify the suitability of demographic parameters from captivity for sustainability analysis, otherwise 'population modelling is based largely on guesswork' (Bowler *et al.* 2014). A relatively new approach is to utilize a citizen science approach with hunters themselves supplying the genitalia of prey animals to more precisely determine reproductive parameters of these species (see Section 8.2.1). Independent of data quality, computational issues can limit the reliability of the simulation outcomes. Diverse software packages and sometimes different versions of the same package may implement the modelling differently, sometimes producing results that are not concordant (Brook *et al.* 1999). Consequently, results from several modelling packages should be compared, albeit something rarely done in the literature. Modelling requires expertise in software applications and species biology and 'must be a collaborative, trans-disciplinary and social process' (Lacy 2019).

5.4.1 Estimation of the Population Growth Rate

Another approach to using full demographic information is the modelling of net recruitment rates. Rather than modelling the likelihood of a population to persist as in the VORTEX software approach, the population growth rate λ , is estimated from the data including harvest whereby $\lambda \geq 1$ implies sustainability and $\lambda < 1$ unsustainability. Simulations allow us to evaluate the sensitivity of λ to the effects of parameter variations (Combreau *et al.* 2001; Marboutin *et al.* 2003).

Example: Lofroth and Ott (2007) assessed the sustainability of wolverine harvests across the Canadian province of British Columbia. Demographic parameters – survivorship estimates of juvenile, subadult and adult age classes and reproductive rates – were taken from the literature. The authors emphasized the caveats that reproductive output data are rare and that demographic parameters are not necessarily constant between habitats that differ in quality. But because

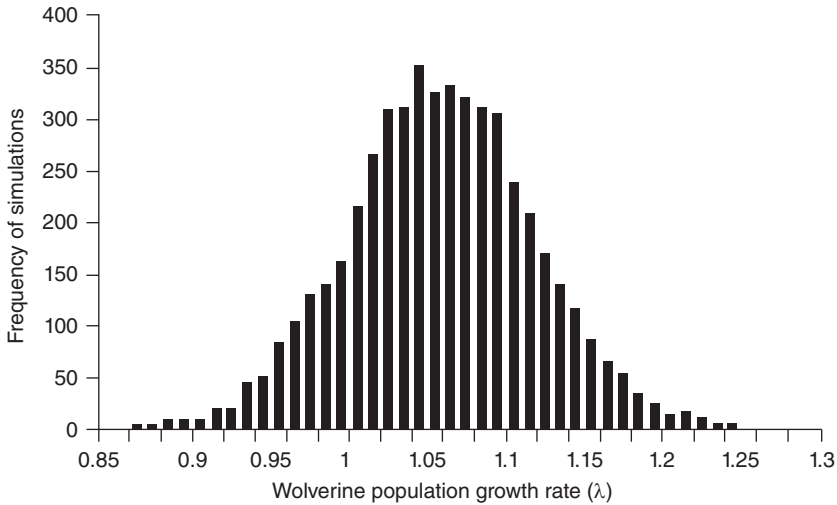


Figure 5.3 Frequency distribution of estimated wolverine population growth rate (λ) using simulation, British Columbia, Canada for 2007 (from Lofroth and Ott 2007; adapted with permission from John Wiley & Sons).

of lack of data, no density-dependence was modelled. Assuming an underlying normal distribution for all demographic parameters 5,000 estimates of population sizes were simulated by randomly drawing parameter values from their normal distributions. Subsequently, λ was mathematically calculated, resulting in a normal distribution with a mean \pm SE of 1.06 ± 0.06 (Fig. 5.3). Using spatially explicit density estimates and harvest rates from the province's 71 population units, annual net recruitment rates for the period 1985–2004 were then calculated. In 16% of simulations, net recruitment was negative, and 15 population units had negative net recruitment in more than half of the simulations, indicating unsustainable harvests. Overall, the simulations showed that the whole province was sustainably harvested between 1984 and 2004 despite the occurrence of 15 unsustainably harvested population units, emphasizing the importance of the spatial dimension of harvest for the assessment of sustainability. The study suggests the use of an adaptive management approach which advises wildlife managers to monitor mean harvest and recruitment rate for individual population units and then intervene when consecutive years of harvest are unsustainable. For a well-studied species such as the wolverine, monitoring recruitment might well be feasible, but it is information that is highly challenging to collect, particularly for many wild meat species. It is possible to estimate the reproductive status of harvested females, but this is still labour intensive and may not be a good guide to recruitment into the population if there is density-dependent juvenile mortality.

5.4.2 Population Viability Analysis and the Madingley General Ecosystem Model

Several software PVA packages are available, which can produce different results. These include GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX. The most often used software for PVA is VORTEX, an individual-based simulation of population demography (Lacy 1993, 2000). VORTEX is the PVA model of choice for use to simulate the fate of small populations threatened by extinction vortices and for complex models that include individual variation, spatial and metapopulation structure, and complex feedback between demography and genetics (Lacy 2019). Although hunting can be incorporated alongside other additional types of mortality, PVA's are essentially designed for single-species systems and are difficult to apply for multi-species ones, such as wild meat hunting. For multi-species systems, Barychka *et al.* (2020a) recently used a new approach, the Madingley General Ecosystem model, which allows simulation of ecosystem dynamics with multi-species harvesting. In computer simulations for duikers, the most heavily hunted species in sub-Saharan Africa (Chapter 1), the model adequately predicts yields, species extinction rates and ecosystem-level harvesting impacts compared to single-species models. Barychka *et al.* (2020a) suggest that this method should be used more widely for management, but so far it awaits implementation on the ground.

Example: Combreau *et al.* (2001) assessed the mortality rate of migrant Asian houbara bustards using VORTEX PVA modelling based on demographic data obtained from ringing, satellite tracking and a three-year study on the bird's breeding success (Combreau *et al.* 2002). The results of the PVA model demonstrated that the houbara population would become extinct within 50 years (with a probability of 94%) if current levels of hunting and poaching persisted.

5.5 Quantitative Indices Based on Surplus Production Models

Sustainability models that are able to use basic information of prey species' life-history traits are comparatively more accessible than those that depend on large amounts of population data being collected in the field. Since in situations where monitoring levels are minimal, and not long-term, less ambitious methods can still be useful in estimating sustainable production levels. These models employ the information available on life-history traits

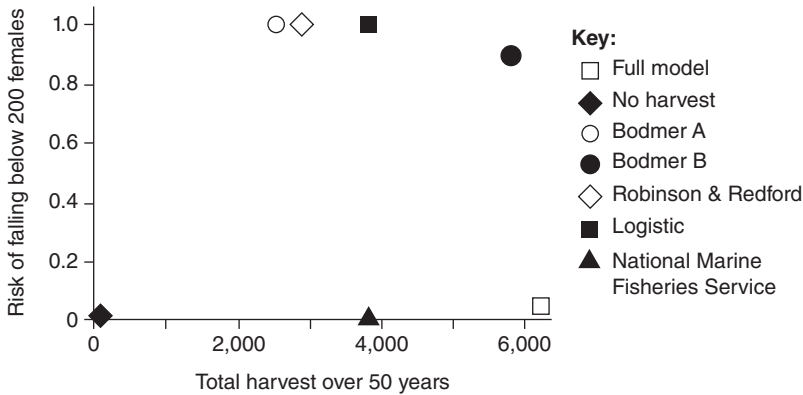


Figure 5.4 The trade-off between the risk of population decline and the number of individuals hunted, shown for a species with fast life history, high growth rate, depleted population, declining habitat and high variability (from Milner-Gulland and Akçakaya 2001; adapted with permission from Elsevier).

of the hunted species and take into account their average lifespan as a good index to which harvest takes the animals that would have died anyway. The proportion of animals that can be hunted will depend on whether the species is long or short-lived. Comparisons between the calculated sustainable production levels and the measured levels of hunting and additional mortality can then be used to point to whether a specific population is sustainably harvested or not. Perhaps the best exponent is the Robinson and Redford equation (Section 5.4.2) (see Weinbaum *et al.* 2013). Depending on the method, the underpinning calculation for the sustainable level of production, P , includes carrying capacity K , maximum rate of population increase (r_{\max}), current population size, N , mortality or recovery factor, F , female survival to the average reproductive age, s , and female fecundity, ϕ . Milner-Gulland and Akçakaya (2001) simulated populations under a range of scenarios for two contrasting life histories and calculated the probability of falling below the threshold population size of 200 individuals when applying different models. For all scenarios, the simulations resulted in vastly differing model performances depending on the model used (example in Fig. 5.4).

Pros: These methods have been widely used as fallback when species are data-deficient as only a few parameters, not a full population model, are needed. The equations are easy to calculate and do not need modelling or specific software packages. Typically, the required

life-history parameters are taken from the literature from *in situ* or *ex situ* populations, thus not requiring additional field work. By contrast to the Robinson and Redford method, the US National Marine Fisheries Service equation has been rarely used (Weinbaum *et al.* 2013) despite it being shown to generate robust, conservative estimates in simulation modelling (Milner-Gulland & Akçakaya 2001).

Cons: All algorithms use rudimentary sets of simplified parameters for life history traits because of the general paucity of the data available (Van Vliet & Nasi 2018; Weinbaum *et al.* 2013). General life history parameters taken from published lists (e.g. Robinson & Redford 1986) often do not adequately represent the populations under study (Bowler *et al.* 2014; Mayor *et al.* 2017; Van Vliet & Nasi 2018). Results from different sites are not comparable even when calculated with the same algorithm as a variety of methods can be used to calculate the parameters of the same model and each of the methods has different sources of error (Van Vliet & Nasi 2008b). The US National Marine Fisheries Service equation has been criticized as being too precautionary, and thus not facilitating maximum harvest, whereas other methods have been criticized because they are not precautionary enough (Milner-Gulland & Akçakaya 2001; Weinbaum *et al.* 2013).

5.5.1 Maximum Sustainable Yield Model

The standard logistic growth rate model introduced in Section 5.1 allows the calculation of maximum sustainable yield (MSY) as

$$MSY = (r \cdot K)/4$$

and a maximum sustainable harvest rate, (MHR), of

$$MHR = r/2$$

Whenever an observed harvest is larger than MSY, it is considered unsustainable. However, a harvest that is smaller or equal to MSY is not necessarily sustainable as we do not know whether the harvest yield is on the left side or the right side of the parabola; in case of the first, it would be unsustainable (see Fig. 5.1). This model is mainly used in fisheries (Weinbaum *et al.* 2013).

Example: Brook and Whitehead (2005) estimated r and the associated MHR using published information on fecundity and credible estimates of survival in

magpie geese in northern Australia. They show that the range of reasonable r estimates is from $r = 0.035$, derived under the assumption of ‘average environmental conditions’, to $r = 0.498$, where all reproductive rates and survival rates are at maximum capacity. This range corresponds to MHR that spans from 2% to 25%. This assessment demonstrated that the previous estimate of $r = 0.78$ and MHR = 39% from a time-series analysis of aerial count data, before the best information was available, was not plausible and constituted a gross overestimate of the possible sustainable harvest. Instead, the authors argued that the overestimate of r constituted an example of ‘extravagant claims of population resilience, and correspondingly excessive levels of exploitation’. They suggested an MHR of no more than 5–14% of total population size per annum for magpie geese.

5.5.2 Robinson and Redford Index

This algorithm has been the most widely used for wild meat species in tropical settings, despite some concerns being raised about its application (Weinbaum *et al.* 2013). The index is relatively easy to calculate according to the equation:

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

with an ad hoc mortality factor F dependent on the species’ life history ($F = 0.2$ for long-lived species whose age of last reproduction is over 10 years, $F = 0.4$ for short-lived species whose age of last reproduction is between 5 and 10 years and $F = 0.6$ for short-lived species whose age of last reproduction is less than five years). The value of $0.6K$ is merely a precautionary factor that stems from the assumption that the maximum produced would be achieved when population density (N_i) was at 60% of carrying capacity K . This is a subjective percentage and could be adjusted according to density estimates and knowledge of the population. To assess the species’ intrinsic rate of increase Robinson and Redford (1991b) use Cole’s (1954) equation to calculate r_{\max} from the age at first reproduction, the age at last reproduction and the annual birth rate of female offspring, b :

$$1 = -e^{-r_{\max}} + b \cdot e^{-r_{\max}(\text{age at first reproduction})} - b \cdot e^{-r_{\max}(\text{age at last reproduction} + 1)}$$

This equation does not consider mortality, ‘which is a very strong assumption’ (Milner-Gulland & Akçakaya 2001). Estimates of these reproductive parameters are available for many commonly hunted forest species (e.g. Robinson & Redford 1986) but vary in their accuracy depending on their origin (see above). For example, in a comparison

between published ex situ data and empirical in situ information for the ten most-hunted Amazonian mammal species, the authors found concordance, underestimation and overestimation of species' r_{\max} values, resulting in different biases for those studies that used the various estimates (Mayor *et al.* 2017). The discrepancies can be so wide that new assessments of these parameters which relate to various ecological conditions are urgently needed (Van Vliet & Nasi 2018). According to Milner-Gulland and Akçakaya's (2001) the index performed rather badly under realistic conditions simulation experiments (Section 6.3). Population persistence of 200 individuals during a 50-year period was never achieved and harvest was less than half of that of the best performing model, the National Marine Fisheries Service algorithm. Weinbaum *et al.* (2013) identified five publications which calculated the Robinson and Redford index alongside at least one other index. From 86 population comparisons, 23 (27%) resulted in divergent conclusions of sustainability.

Example: Zapata-Ríos *et al.* (2009) assessed the sustainability of mammal hunting by the Shuar within a 243 km² hunting catchment area in the Ecuadorian Amazon. The authors assessed sustainability of hunting of mammals by comparing the Robinson and Redford model, the Bodmer B model (Section 5.4.2) and the MSY index (Section 5.4.3). Harvest rates were obtained from hunter interviews and hunter self-monitoring data, animal density data from line-transects, and r_{\max} and fecundity rates (litter size and gestations per year) were derived from the literature (Robinson & Redford 1986). Of the 21 mammal species hunted there were sufficient data to assess 15, 12 of which were hunted above maximum sustainable levels. All three methods produced the same conclusions.

5.5.3 Bodmer A and B Indices

The equation for the two Bodmer indices (Bodmer 1994a), also called the 'unified harvest model', is the same:

$$P = 0.5 \cdot N \cdot \phi \cdot s$$

and requires information on the female part of the population, $0.5 \cdot N$, female fecundity, ϕ , and female survival to the average reproductive age, s . The latter is either estimated as $s = 0.2$ for long-lived species and $s = 0.6$ for short-lived species in case of the Bodmer A model or estimated from actual data in case of the Bodmer B model. Fecundity is typically estimated from ex situ populations that have the same associated

problems, as already discussed for the Robinson and Redford index. Sustainability is achieved if the observed harvest is smaller or equal to the estimated P (Weinbaum *et al.* 2013). In Milner-Gulland and Akçakaya's (2001) simulation experiments, the Bodmer B model performed better in terms of yield, but led almost as often to a high risk (approx. 90%) of the population falling below 200 individuals during a 50-year period as the Bodmer A model (100%).

Example: Altrichter (2005) investigated the sustainability of collared, white-lipped and Chacoan peccary hunting in the Argentine Chaco by contrasting results from the Bodmer B model with comparisons of population densities in hunted versus unhunted sites (Section 5.5). Harvest data was obtained from hunter interviews, estimates of peccary density from transect counts and from published data from similar sites in the Chaco. Reproductive parameters for the three species were obtained by examining genitalia of hunted animals and from published data. Results showed the collared peccary was harvested sustainably according to both algorithms but findings were ambiguous for the Chacoan peccary. Estimates for the latter species showed that major differences appeared when density and reproductive parameters are based on field and published data resulting in an estimate of 74% versus 18% of production taken, which is either unsustainable or sustainable. Comparing unhunted with hunted sites showed that peccary populations were unsustainably harvested if density in hunted sites was only 35% of the unharvested density. For the white-lipped peccary, results were also ambiguous as the percent production taken in Bodmer B was below 50%, that is 'sustainable' according to Weinbaum's (2013), and according to Altrichter's (2005) cut-off point. However, the comparison of unhunted with hunted sites suggested unsustainability as the density of the harvested population was only 32% of the unharvested one. In conclusion, the study demonstrates, first, that there is no agreement how the Bodmer B method is interpreted and, second, that the discrepancies of the interpretations between the two methods stipulates the need for additional monitoring and refined reproductive parameter estimates for the site.

5.5.4 US National Marine Fisheries Service Index

The algorithm, also called the potential biological removal index (PBR), was developed for cetacean bycatch (Wade 1998):

$$\text{PBR} = N_{\min} \cdot 0.5 \cdot r_{\max} \cdot F_{\text{R}}$$

with N_{\min} = minimum population estimate, F_{R} = recovery factor between 0.1 and 1, and r_{\max} = maximum rate of population increase.

The index specifically calls for the minimum population estimate rather than a mean estimate, thus accounting for uncertainty of density estimates. This is one of the main strengths of the index. The recovery factor allows for the implementation of different management strategies but needs to be assigned with care. Importantly, current knowledge of the species in general and the targeted population in particular, conservation goals, harvesting requests and the feasibility of further monitoring the population, need to be taken into consideration. The smallest value of $F_R = 0.1$ allows a population to be maintained close to its carrying capacity, to minimize extinction risk for depleted and small populations, or to delay the recovery of a depleted population only slightly. The largest value of $F_R = 1$ allows a healthy population to be maintained at its maximum net productivity at the MSY density. A recovery factor of $F_R = 0.5$ accounts for unknown bias or estimation problems such as overestimating r_{\max} or underestimating mortality.

The risk of extinction is low in simulations and the algorithm performs best amongst the indices based on surplus production models. In Milner-Gulland and Akçakaya's (2001) simulation experiments, the algorithm performed best in its ability to have a no risk of the population falling below 200 individuals during a 50-year period. Total harvest was lower than the full demographic model (Section 6.3) because of its precautionary approach, which has been listed as a potential disadvantage since the algorithm is not designed to maximize yield (Weinbaum *et al.* 2013). Notwithstanding the favourable performance of this index and its popularity in fisheries and marine mammal, turtle and seabird bycatch studies, the approach remains very rarely used, despite its potential favourability over the Robinson and Redford and the Bodmer indices (Weinbaum *et al.* 2013).

Example: Dillingham and Fletcher (2008) compared the US National Marine Fisheries Service index with demographic models in two well-studied birds, the greater snow goose and the magpie goose. Both methods performed similarly giving comparable results for both species, further validating the algorithm. The authors also explored the sustainability of high mortality rates of the white-chinned petrel as bycatch in fisheries; a species with limited demographic information to apply demographic modelling. Because of data deficiency and history of high losses of this bird due to fisheries, the authors suggested the application of a F_R value between 0.1 and 0.3. The resulting PBR was lower than the known mortality from fisheries at $F_R = 0.1$ and possibly $F_R = 0.3$. Considering that mortality is strongly biased towards males, which constitute 80% of the bycatch, male-specific PBR was lower than male mortality at both F_R levels, suggesting unsustainable mortality. The high sex bias in bycatch of the

white-chinned petrel highlights that the index might need to be adapted if applied to other life-histories other than the species it was designed for, namely cetaceans and pinnipeds, which are characterized by long life, delayed maturity and low fecundity.

5.5.5 Modelling Parameter Uncertainty

Barychka *et al.*'s (2020b) model allows the implementation of parameter uncertainty, which is pertinent in all field situations for the planning of sustainable hunting. The model centres on the Beverton–Holt population model which is widely used in fisheries (Beverton & Holt 1957):

$$N_{t+1} = r_t N_t / (1 + [(r_t - 1)/K]N_t)$$

with N_t and N_{t+1} = the population densities at time t and the following time step, respectively; K = the equilibrium population size without harvesting; r_t = the density-independent intrinsic rate of natural increase (i.e., the balance of births and deaths) for year t . Uncertainty for the parameters r_t and K are modelled based on prior belief. The prior belief is ideally based on field data for the studies populations and, failing that, on expert judgement. Barychka *et al.* (2020b) implemented two harvesting strategies at a constant rate, set either as a quota or proportional to the population size, N_t .

Example: Barychka *et al.* (2020b) simulated harvesting over a 25-year harvest period for three hypothetical duiker populations. Duikers are relatively well studied but population estimates vary considerably between localities (Van Vliet & Nasi 2008b), emphasizing the importance of modelling parameter uncertainty to assess sustainable harvesting. Figure 5.5 compares the modelled quota-based harvest yields and population survival probabilities for the blue duiker under scenarios without and with consideration of parameter uncertainties. At a harvesting level of four animals/km²/year the survival probability was 100% over 25 years and the median yield was between 3 and 5 when no parameter uncertainty was considered, but survival probabilities (50% to 80%) and yield were markedly smaller (1–5) when parameter uncertainty was modelled. Thus, modelling uncertainty revealed a trade-off between yield and extinction probability whereas ignoring uncertainty implies higher yields and lower extinction probabilities that are unrealistic under field conditions where parameter uncertainty prevails (Van Vliet & Nasi 2008b). Moreover, with uncertainty there was no target quota that resulted in 100% survival probability in the investigated case. No such trade-off between yield and survival probability was evident for the blue duiker when a proportional harvesting strategy was implemented. However, such a proportional strategy is much more difficult to implement as

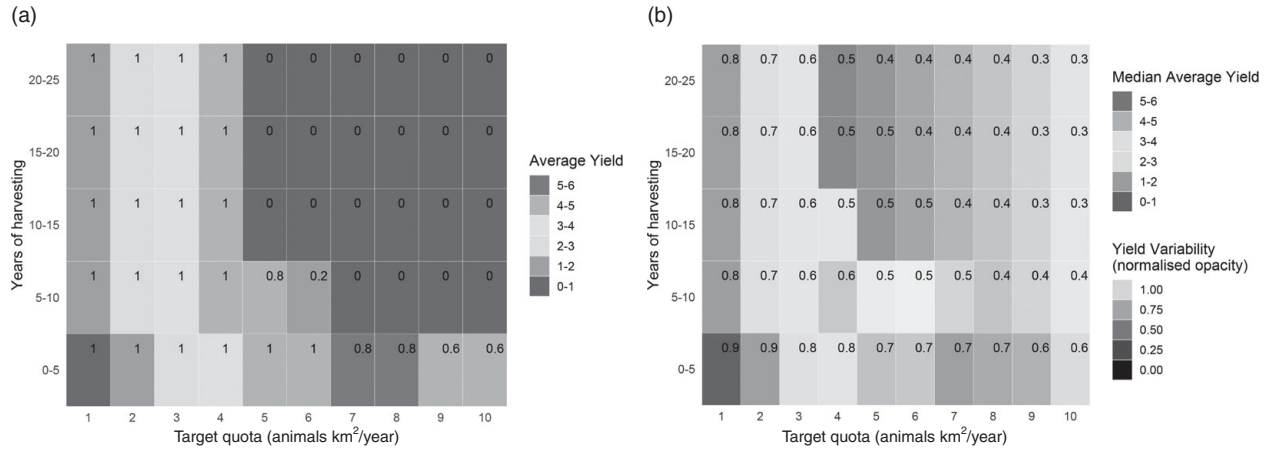


Figure 5.5 Estimated yields (animals/km²/year) from quota-based harvesting of blue duiker without (a) and with (b) parameter uncertainty. Yields are estimated over 25 years in 5-year increments. The survival probabilities are shown in top-right corner of each rectangle. (From Barychka *et al.* 2020b; reprinted with permission from PLOS ONE.)

it requires yearly field-based estimates of population size. The model demonstrates that considering model uncertainty is crucial to develop sustainable harvesting strategies.

5.6 Early Warning Systems

Several measurements indicate, but cannot demonstrate, whether wild meat hunting is sustainable or not. However, collecting these data is important in data-deficient situations as they act as early warning systems, identifying situations where more detailed monitoring is urgently advisable. Such indicators can use the comparison of population density and/or population structure between sites subjected to different hunting pressure, changes in harvest characteristics and or changes in number of carcasses appearing in markets. The reasons underpinning the observed differences or changes can be problematic to interpret because hunter and animal populations are multivariate, dynamic and complex systems, which these indices do not measure or can take into account. The most realistic outcome is that the differences and changes obtained can be used as early warning systems which can trigger further monitoring and analysis.

5.6.1 Comparing Populations between Sites

The comparison of population density and/or population structure, especially age and sex, between hunted and non-hunted or lightly hunted sites has been used to assess harvesting sustainability. It is assumed that significant differences in density or age and sex composition can be interpreted as the result of unsustainable harvest in the exploited area.

Pro: Population density can be relatively easily estimated using line transects or camera traps for some species (Milner-Gulland & Rowcliffe 2007). Age and sex structure can be determined from direct observations of the hunted carcasses brought back by the hunters and requires little training. Differences can be statistically tested.

Cons: In dense tropical and subtropical habitats, the estimation of population density and age and sex structure can be challenging. Sites must be ecologically comparable, but that can often be verified only by intensive field work. Even when differences are significant and large, the data indicate only local depletion, but not sustainability. As indicated in Fig. 5.1, sustainable harvesting is possible in a large

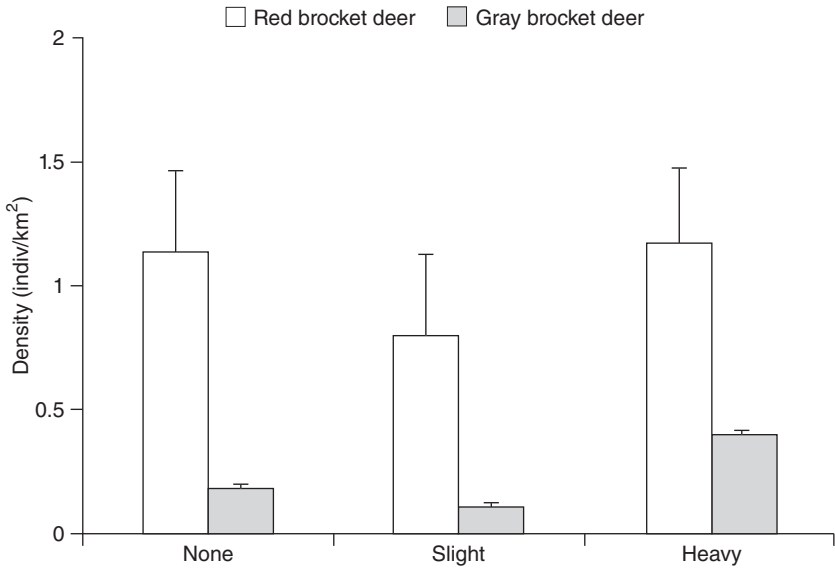


Figure 5.6 Densities of red and gray brocket deer according to different hunting pressures in the study site. Densities were estimated by line transect surveys. (From Hurtado-Gonzales and Bodmer 2004; adapted with permission from Elsevier.)

range of population densities. Thus, differences in population density per se do not prove unsustainability. Also, differences in sex and age structure per se do not prove unsustainability but the absence of differences does not demonstrate sustainability either. For example, Fitzgibbon *et al.* (1995) observed significant differences in density estimates in hunted versus unhunted areas in four-toed elephant shrews, squirrels and Syke's monkeys, but not for yellow baboons. Conversely, comparing current harvest levels reported by hunters with the estimated maximum potential sustainable harvest rates according to the Robinson and Redford (1991b) model (Section 5.4.2) indicated non-sustainability of yellow baboons and Syke's monkeys but not the other species.

Example: Hurtado-Gonzales and Bodmer (2004) assessed the sustainability of red and gray brocket deer hunting in unhunted, slightly hunted and heavily hunted sites in Peru. For the two species, gross productivity was higher in the heavily hunted site compared to the unhunted site as measured by the number of foetuses recorded per female. The heavily hunted area had a higher density of gray brocket deer compared to the non-hunted area (Fig. 5.6) but differences in

age structure were not tested. No significant differences in density and age structure were found for red brocket deer. To solve this ambiguity, the Bodmer B algorithm (Section 5.4.2) was applied revealing that the harvest of both species was sustainable.

5.6.2 Differences in Harvest Characteristics

Changes in the characteristics of harvest data over time or differences between the characteristics of harvest data between ecologically similar sites might indicate depletion of populations or overharvesting. Such changes may encompass changes in hunting pressure, that is, number of animals killed per area, increasing distances required to reach profitable hunting grounds, and changes of species composition over time (Albrechtsen *et al.* 2007; Hurtado-Gonzales & Bodmer 2004; Smith 2008).

Pros: Data directly from hunters can be used, thus, relatively easy to obtain.

Cons: As discussed for CPUE (Section 5.2.2) the application of this method requires an adequate and representative sample of hunters involved in data generation. This may be a challenge in some situations, especially if hunting is illegal. Moreover, the sample obtained may be biased if offtake differs by age or sex of the hunter, or if hunting is for subsistence rather than for trade, factors often overlooked in harvest studies (Ingram *et al.* 2015). Moreover, hunters may under-report or fail to report the hunting of protected species. A suite of different factors can impact the system, other than hunting. These could include biological factors, such as climate or vegetation structure, and anthropogenic impacts, such as logging or road development, hunting motivations, hunting technology, market supply and demand, or law enforcement. There are neither standardizations nor any quantitative or even qualitative generalized guidelines or agreement on how to accept or reject the hypothesis of sustainability.

Example: Smith (2008) mapped the spatial patterns of hunting yields in Panama within a community of Indigenous Buglé and Ngöbe hunters. Kill sites were concentrated within just 2 km of the hunters' homes; nearly 90% of the total harvest originated here (Fig. 5.7). Hunting at larger distances occurred less often and depends on the availability of firearms, whereas other methods including slingshots and bow and arrow are more common near the settlements. While most species were killed near settlements, other species, in particular the

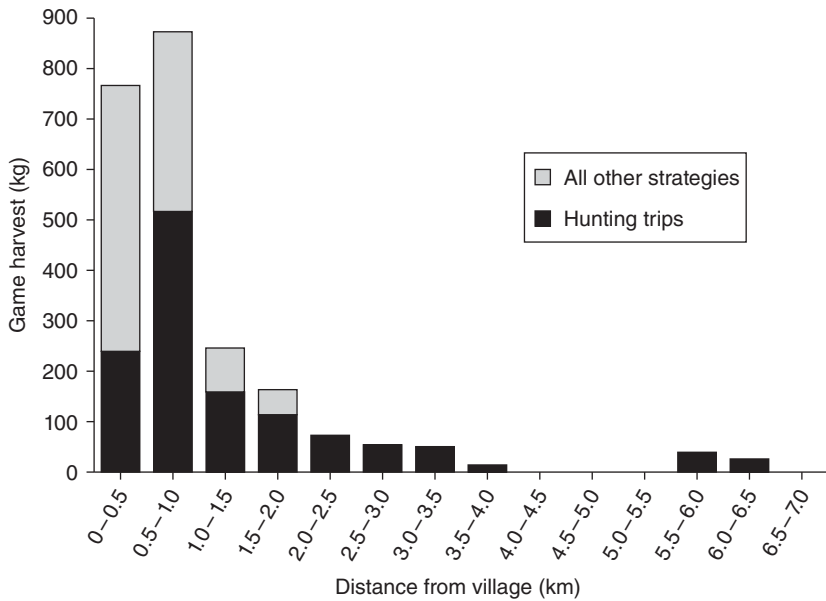


Figure 5.7 Hunting yields as a function of distance from hunters' primary residences in 500-m intervals. (From Smith 2008; adapted with permission from Elsevier.)

black-handed spider monkey, were hunted only further away. Smith (2008) argues that this pattern suggests that some degree of localized depletion may have occurred due to overhunting close to human settlements. Based on the local ecological knowledge of rural hunters, population depletion of hunted forest wildlife close to villages has been clearly demonstrated by Parry and Peres (2015) in the Brazilian Amazon. Similarly, mammal and bird population densities declined with their proximity to infrastructure such as roads (Benítez-López *et al.* 2010). For example, abundance of several species including duikers, situngas and forest elephants in Central Africa were depressed by the presence of roads. (Laurance *et al.* 2006)

The special case of duikers. Duikers (genera *Philantomba* and *Cephalophus*) are amongst the most hunted mammals for wild meat throughout the Congo Basin (Fa *et al.* 2016; Kingdon *et al.* 2013; Wilkie & Carpenter 1999; Yasuoka 2006b). Thus, there is a much interest in ascertaining the hunting sustainability for these species. Yasuoka *et al.* (2015) suggested that the catch ratio between the smaller blue duikers and the larger duikers, especially red duikers, could be used as an indicator of depletion in a site; higher numbers of red duikers

denoting a less-affected system. The different duiker species respond distinctly to increased hunting pressure with the smaller blue duiker being less affected at a population level. This is because this species reaches reproductive age earlier than medium-sized duikers and have, thus, a higher reproductive output. The other reason is that they are more tolerant to and thrive in human-modified landscapes (Hart 1999). These predictions were fulfilled in Yasuoka *et al.*'s (2015) study on duiker densities in southeastern Cameroon. However, duiker densities in central African forests can vary from 3.5 to 59.8 individuals/km² for blue duikers and 2.6 to 64.5 individuals/km² for red duikers but explanations for these differences are likely to be related to a combination of habitat type, hunting history and hunting pressure factors (Breuer *et al.* 2021). Since the interactions of these factors has not been adequately determined in African forests, unlike studies for the Amazon for other species (see Peres 1999a), trends of the few studied duiker populations have been shown to decline with increases in hunting pressure (Grande-Vega *et al.* 2016; Hart 1999) but the impact of habitat or hunting history is unknown. Moreover, hunting methods can impact small- and medium-sized duikers differently with gun hunting, especially at night, making blue duiker easier prey than the medium-sized red duikers (Yasuoka *et al.* 2015). However, the large variance of the blue to red duiker ratios ranged from 0.39 to 22.5 ($n = 5$, median = 1.33) in hunted areas and from 0.23 to 1.66 ($n = 4$, median = 1.4) for unhunted areas. Breuer *et al.* (2021) suggest to use them only with precaution as an indicator of hunting pressure or habitat type. Thus, the catch ratio as a means to estimate sustainability remains uncertain and for the time inapplicable.

5.6.3 Changes in Body Mass

A drop in the mean body mass of harvested species in a site can be used as an indicator of depletion. Trends in species composition and the average size of prey have been used in monitoring fish exploitation, a phenomenon known as 'fishing down marine food webs' (Pauly 1998) where fisheries increasingly rely on the smaller, short-lived fishes as the larger ones are depleted. This phenomenon has been measured by the large fish indicator (LFI), which captures changes over time in the contribution of biomass from large fish to the catch (Greenstreet *et al.* 2011; Shephard *et al.* 2011). The mean body mass of hunted terrestrial prey within each sample can also be used as a proxy of species composition, where a drop from larger to smaller species may indicate a process of defaunation of a

habitat (Dirzo *et al.* 2014). In hunted terrestrial systems, the decrease in mean body mass of prey can reflect the increase in the proportion of small-bodied species over time, either because large-bodied species were extirpated, or more small-bodied species are being harvested. Based on these premises, Ingram *et al.* (2015) used the mean body mass indicator (MBMI) to integrate taxonomically, spatially and temporally disparate data collated from multiple sources over a period of 40 years. The MBMI can be used to offer insights into wildlife exploitation dynamics and is useful in understanding trends in hunted wildlife. In addition to the MBMI, Ingram *et al.* (2015) used an index of hunting pressure, the offtake pressure indicator (OPI) providing a measure of relative change in the number of harvested individuals indexed across multiple sites and species.

Pros: As suggested by Ingram *et al.* (2015), these two indicators offer potentially useful approaches to assess wildlife offtake in the absence of comprehensive monitoring schemes, especially once further calibrated. For example, because each index is calculated differently, with the former employing an arithmetic mean and the latter a geometric mean, MBMI will change more rapidly compared to the OPI. With more time series at multiple sites available, it would be possible to calculate both indicators for the same sites and compare them. However, identifying causal links between changes in pressure on and the state of wild animal populations is often difficult. Wild animal offtake indicators have the potential to establish such linkages when combined with indicators of state to potentially estimate sustainable exploitation.

Cons: Long-term data are required, which are rarely collected. As discussed for CPUE (Section 5.2.2) and for monitoring changes in harvest characteristics (Section 5.2.2), recruitment of hunters can be a challenge, especially when long-term monitoring is involved, as required here.

Example: Using data available for West and Central African mammals and birds, Ingram *et al.* (2015) demonstrated the indexed number of individuals harvested, OPI, of both mammals and birds increased dramatically between 1998 and 2010, indicating increasing hunting pressure (Fig. 5.8). During the same time span average body mass of harvested mammals declined significantly between 1966 and 2010, whereas that of birds increased between 1975 and

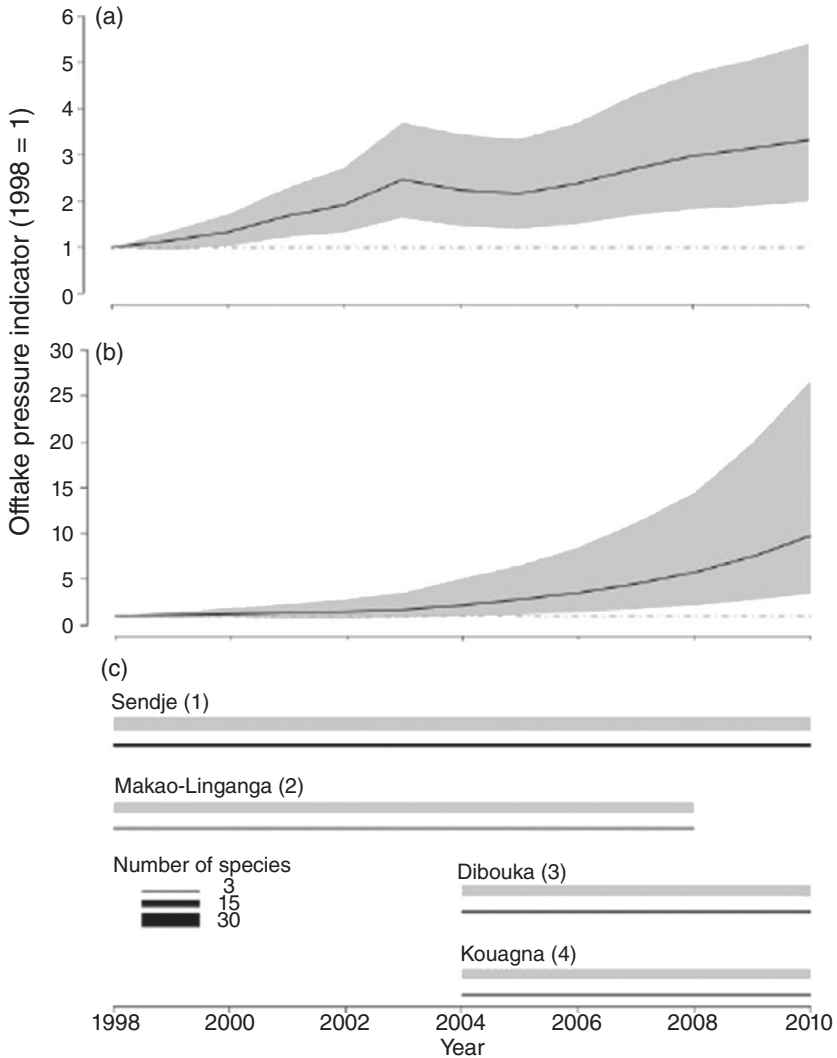


Figure 5.8 Offtake pressure indicator for (a) mammals and (b) birds in Central Africa and (c) the distribution of time-series data at four sites. The indicator is set to 1 in the first year for which data were available (dotted horizontal line). Shading (a and b) represents $\pm 95\%$ confidence intervals generated with 1,000 bootstrap replicates. Width of bars (c) represents the number of mammal (grey) and bird (black) species sampled at four sites. (From Ingram *et al.* 2015; reprinted with permission from the Resilience Alliance.)

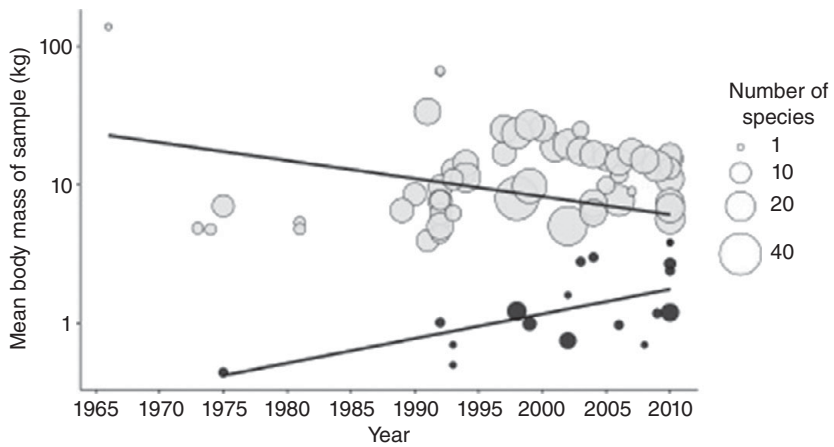


Figure 5.9 Mean body mass indicator for mammals (grey circles) and birds (black circles) in West and Central Africa. Circles represent offtake samples and are scaled by the number of species harvested within each sample; lines are fitted using linear mixed effects models. Samples are plotted on a logarithmic scale. (From Ingram *et al.* 2015; reprinted with permission from the Resilience Alliance.)

2010, indicating changed compositions of hunting bags (Fig. 5.9). This difference may indicate that whilst mammal prey were being depleted, in birds larger species were progressively being targeted, reflecting either the change in the demand for larger birds and their bills, such as the black-casqued hornbill, or in response to the decline in mammalian prey, although these effects are difficult to determine. The latter difficulty emphasizes that the trends in MBMI and OPI need careful interpretation because species might be hunted because of differing demands, for example, subsistence *versus* trophy hunting.

5.6.4 Market Indices

Among all different types of data required for sustainability assessments, market data are the easiest to collect. Surveys of wild meat markets over time allow monitoring of different aspects that might indicate unsustainability: price trends, quantity of species available, species composition and wildlife source distance. It is considered unsustainable whenever prices increase, quantity of available species decrease, species composition change and the distance where wildlife is sourced increase (Albrechtsen *et al.* 2007; Cowlshaw *et al.* 2005; Damania *et al.* 2005; Milner-Gulland & Clayton 2002; Rowcliffe *et al.* 2003). The hypothesis is that the composition of species for sale in wild meat markets, as influenced by

hunting history in their catchment areas (Cowlshaw *et al.* 2005), will indicate the level of exploitation in the supply areas since vulnerable taxa (slow reproducers such as large ungulates and primates) are depleted first and are replaced by smaller-bodied robust taxa (fast reproducers), such as rodents and small antelopes. Consequently, there is increased prominence of species with high reproductive potential (as defined by their intrinsic rate of natural increase r_{\max}) sold in markets characterizes heavily exploited catchments as shown in Dupain *et al.* (2012).

Pros: Requires monitoring of market stalls that sell wild meat, which is more easily conducted by local people than any other method of surveying sustainability. Changes can be statistically tested.

Cons: Data collection is not advised for foreigners in many settings because of safety concerns. Supply and demand of traded wild meat are impacted by a complex mixture of factors, such as taste preferences, tradition, economic settings, supply, demand and price of domestic meat and fish, environmental changes or law enforcements. There are neither standardizations nor any quantitative or even qualitative generalized guidelines or agreement on how to accept or reject the hypothesis of sustainability. The difficulties in interpreting the data make these changes more an early warning system than a decision-making system on sustainability.

Example: Albrechtsen *et al.* (2007) explored market data at the main wild meat market in Bioko Island, Equatorial Guinea, in 1996 and 1998. There was an increase in price, a significant decline in total and individual animal group carcass volumes, the species composition differed, and the diversity indices changed. Whilst the first three parameters indicate overhunting, the diversity index changed towards more diversity, which is surprising as the classic depletion model predicts the decrease of diversity. The authors argue that this is a transient phase and will be followed by a decrease of diversity once only the more resilient species are left as shown elsewhere in Bioko (Fa *et al.* 2000). Subsequent, independent market surveys showed that the numbers of these animals entering the market have not increased (BBPP 2006; Reid *et al.* 2005), thus indicating a sustained vulnerability of animal populations to extensive hunting.

The study by Fa *et al.* (2015a) shows a clear relationship between anthropogenic pressures in catchment areas and the profile of species appearing in wild meat markets from data for 79 markets (covering 30,000 km²) in the Cross-Sanaga region in Nigeria and Cameroon (Fa *et al.* 2006; Macdonald *et al.* 2011, 2012). The hypothesis tested was that the

percentage composition of various mammal groups (ungulates, rodents, primates and carnivores) in a market can be a crude measure of depleted faunas of the areas supplying that market. Results indeed confirmed that markets in heavily exploited areas (defined by indirect anthropogenic metrics such as high human population densities), the percentage contribution of larger-bodied prey (slow-reproducing species), especially ungulates and primates, to markets was characteristically lower than the percentage contribution of smaller fast-reproducing prey, such as rodents. Carnivores (mostly smaller taxa) become more numerous in markets as areas become more depleted of wild meat. Research from other sites in Central Africa are consistent with these results, especially the observation that species hitherto unimportant in the wild meat trade gain prominence when ungulates become scarce (Ingram *et al.* 2015; Wilkie 1989). In lightly hunted rural sites, duikers and other antelopes are the more common prey (Lahm 1993; Noss 1998a). Although factors, such as habitat quality and human pressures, will jointly impact the wildlife supplying markets (Fa & Brown 2009), the most parsimonious interpretation of the composition of traded species in wild meat markets in the Fa *et al.* (2015a) study was the contrasting ability of ungulate and rodent populations to recover from hunting. Thus, at sites where larger species have been severely depleted, hunters would extract fewer of the preferred larger red and blue duikers and more of the smaller species such as the Emin's and the African giant pouched rats or the cane rat. In most continental sites in Africa (unlike Bioko Island, see Fa *et al.* 2000), rodents only become important prey items in disturbed areas (Eves & Ruggiero 1999). Therefore, increases in rodents hunted suggest reductions in the availability of more preferred wild meat species. The relative proportions of ungulates and rodents in the offtake can be used as indicators of site over-exploitation. Fa *et al.* (2015a) showed that the relationship between ungulates and rodents was related to a number of prominent anthropogenic factors, rather than environmental variables *per se*. Higher road densities were linked to reduced abundance of a number of mammal species due to higher hunting pressure. Heavily populated and accessible areas have fewer duikers, forest buffalos and red river hogs (Laurance *et al.* 2006). Moreover, using an index of game depletion (GDI) for each market (the sum of the total number of carcasses traded per annum and species, weighted by the intrinsic rate of natural increase (r_{\max}) of each species, divided by individuals traded in a market), Fa *et al.* (2015a) showed that this index increased as the proportion of fast-reproducing species (highest r_{\max}) rose and as the representation of species with lowest

r_{\max} (slow-reproducing) declined. The GDI is akin to indicators used for fishery catches and, as noted for the MBMI and OPI, can be used as a framework for discerning the status of hunted prey (particularly mammals) in a catchment area from observations of the composition of species for sale in markets (Section 5.5.3).

5.7 Ecosystem-Based Management

5.7.1 Ecosystem-Based Fisheries Management

The harvesting of any wildlife resource, whether wild meat and fisheries, should strive for the sustainable use of exploited species on land and in the sea. Because of the much longer history of industrial exploitation of marine life, and accompanying research on how to achieve sustainable exploitation of marine fish and stop fisheries collapses (Pauly *et al.* 2002), lessons learnt in fisheries can be applied to wild meat (Section 5.4.4; Milner-Gulland & Akçakaya 2001). Given this, we briefly describe some of the latest developments in fisheries management that are relevant to wild meat.

The failure of several fisheries, such as the notorious collapse of the Newfoundland Atlantic cod fishery (Bavington 2011), has led to the recognition that traditional management has failed to lead to sustainable exploitation of marine resources. These have caused a clear paradigm shift in fisheries research leading to a change in focus from a single species and MSY approach towards ecosystem-based management (EBM) (Lidström & Johnson 2020; Pikitch *et al.* 2004; Townsend *et al.* 2019). EBM has been defined by the FAO as aiming ‘to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries’ (FAO Fisheries Department 2003). Similarly, the United States’ National Oceanic and Atmospheric Administration (NOAA), has adopted ecosystem-based fisheries management (EBFM), as the agency’s strategic policy. NOAA defines EBFM as: ‘a systematic approach to fisheries management in a geographically specified area that contributes to the resilience and sustainability of the ecosystem; recognizes the physical, biological, economic, and social interactions among the affected fishery-related components of the ecosystem, including humans; and seeks to optimize benefits among a diverse set of societal goals’ (NOAA 2016).

EBM and EBFM differ from the conventional management of single species by describing management strategies for entire ecosystems, to explicitly achieve not only sustainability of target species but ensure the ecological sustainability of the species' ecosystems, including economic and social sustainability. These holistic approaches take into account natural marine resources' interactions with their environment as well as human interactions with these resources and the environment. The implementation of policies reflecting these new approaches must necessarily rely on the support of ecosystem science, continuing population monitoring, modelling and analysis and crucially the collaboration and consultation between scientists, policy makers, stakeholders and the public. Despite these encouraging innovations, there is still little practical advice on how to better select specific management measures to achieve EBFM goals. The main operational problems with implementing EBM/EBFM are: (1) defining proper long-term ecosystem related objectives, (2) identifying meaningful indicators and reference values for sustainable use and (3) developing appropriate data collection, analytical tools and models (Cury *et al.* 2005). As a response to these issues, Levin *et al.* (2009) suggested the adoption of integrated ecosystem assessments (IEAs), as a framework of 'formal synthesis and quantitative analysis of information on relevant natural and socioeconomic factors, in relation to specified ecosystem management objectives'. This framework is a looping workflow composed of scoping, indicator development, risk analysis, management strategy evaluation and ecosystem assessment repeated in an adaptive manner (Fig. 5.10). Importantly, the mechanistic indicators and estimators for population sustainability discussed in this chapter still remain important in indicator development, embedded in this adaptive management loop. Several example cases exist of successful implementation of the IEA framework under the EBFM policy, in particular outside the tropics (Townsend *et al.* 2019). In these cases, such as the Gulf of Alaska Pacific cod harvest, the use of ecosystem models in a management process has improved the health or status of particular fish stocks or habitats. These examples highlight the importance of collaboration between modellers, stakeholders and resource managers to ensure sustainable management. For fisheries in the tropics, however, an additional series of challenges and problems exist, resulting from undeveloped or inappropriate governance structures, poor science, lack of political will in many cases and often economic development overriding biodiversity protection (Aswani *et al.* 2012). Moreover, many developing countries have property rights which do not grant local coastal communities any legal rights to establish and enforce control over the coastal resources.

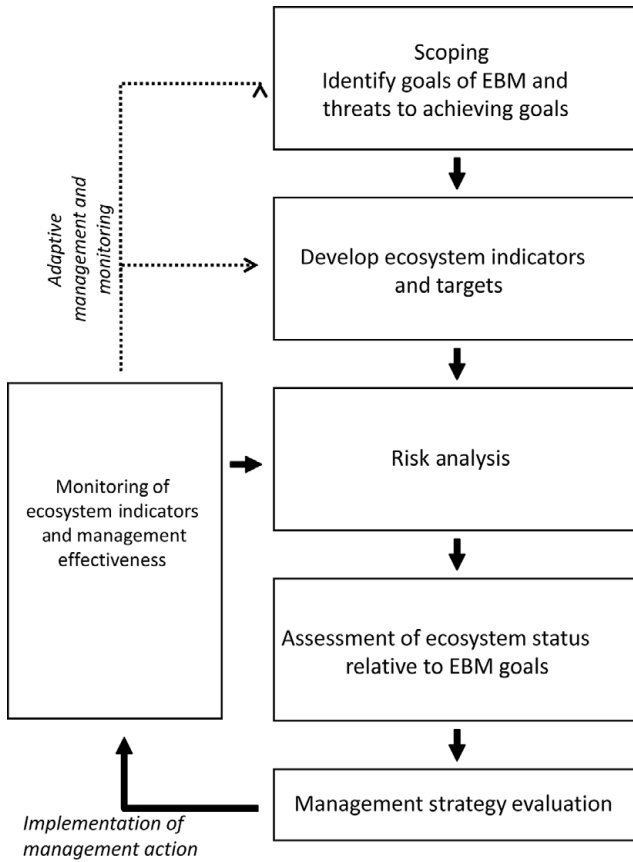


Figure 5.10 The Five-Step Process of Integrated Ecosystem Assessment. It begins with a scoping process to identify key management objectives and constraints of the ecosystem-based management, identifies appropriate indicators and management thresholds, determines the risk that indicators will fall below management targets and combines risk assessments of individual indicators into a determination of overall ecosystem status. The potential of different management strategies to alter ecosystem status is evaluated, and then management actions are implemented, and their effectiveness monitored. The cycle is repeated in an adaptive manner. (From Levin *et al.* 2009; adapted with permission from PLOS Biology.)

Problems associated with the implementation of EBM approaches to fisheries in tropical countries also apply to wild meat hunting. A holistic system such as EBM can be the gold standard for wild meat, but we are still far from pursuing this goal. Data-deficiency for most wild-meat-producing areas is not necessarily a limiting factor in implementing EBM

because in such situations natural history and general knowledge can be used to develop precautionary safety margins as a starting point for more comprehensive EBM in the future (Pikitch *et al.* 2004). However, economic underdevelopment and local poverty can prevent the implementation of more sophisticated monitoring, modelling and management systems. For example, solid frameworks of population assessments and monitoring which are the foundation of EBM, are exceedingly rare in the tropics and subtropics. In fact, in many tropical countries, monitoring programmes are often short-lived, largely research projects limited by funds and unable to be extended over longer time periods. Even the basic acknowledgement of the need for monitoring is often missing at local, regional and national levels. Nevertheless, the idea of managing wildlife populations within a clear ecosystem and social context has been raised by some authors (Van Vliet *et al.* 2015b).

5.7.2 Shifting from Biological Indicators to Resilience Analysis for Wild Meat

In line with the EBM approach, Van Vliet *et al.* (2015b) have argued that wild meat hunting must be considered as a social-ecological system, and by so doing managers must move towards resilience analysis, adaptive resource management and participatory governance. Although this notion has been critiqued by Sirén (2015) who argues that MSY is seldom, if ever, the goal, most approaches to resolving wild meat hunting systems have been caught up in assessing rather achieving sustainability, as we show in Section 5.8. Because hunting systems involve human actions and include social structures, as well as biological processes (prey species, ecosystems), the distinction between the social and the natural is arbitrary (Berkes *et al.* 2002); hence a social-ecological system. Van Vliet *et al.* (2015b) argue that the emphasis should move away from just assessing stocks of prey populations, to considering the complex and dynamic relationships between the hunting ground, its resources, the stakeholders in play and the different exogenous drivers of change affecting the system. This new way of looking at hunting systems incorporates uncertainty and stochasticity inherent to complex systems. It also recognizes that systems evolve over time, adapt and transform.

The main implication of changing the theoretical understanding of hunting systems is that one-off biological indicators are not useful for the estimation of sustainability. Other methodologies that integrate complexity, for example, theoretical models, such as agent-based models,

companion modelling approaches, fuzzy cognitive mapping, and resilience analysis tools, among others, are advantageous. Spatially explicit multi-agent-based models are particularly adapted to understanding wild meat hunting sustainability (Bousquet *et al.* 2001; Iwamura *et al.* 2013; Van Vliet *et al.* 2010a). Agent-based models are a class of computational models for simulating the actions and interactions of autonomous agents, both individual and collective entities such as organizations or groups, with a view to assessing their effects on the system as a whole. These models combine elements of game theory, complex systems, emergence, computational sociology, multi-agent systems and evolutionary programming (Grimm *et al.* 2005).

A number of methods are available for use in addressing the complexity of social-ecological systems. Firstly, collective decision-making processes in complex situations can be better understood with the application of participatory models (Barreteau *et al.* 2014). This approach facilitates collective decision-making processes by making more explicit the various points of view and subjective criteria to which the different stakeholders refer implicitly. As demonstrated in past research (Funtowicz *et al.* 1998; Mermet 1992; Ostrom *et al.* 1994), when a complex situation exists, the decision-making process is evolving, iterative and continuous. This process always produces imperfect ‘decision acts’, but by following each iteration they are less imperfect and more shared. Participatory scenario planning allows the description of how the future might unfold on the basis of coherent assumptions about the relations among drivers of change and key aspects of the system. The method also allows the participation of a great diversity of stakeholders.

Graphical stock-and-flow modelling, such as fuzzy-logic cognitive mapping (FCM), is a simple and easy method that allows groups to share and negotiate knowledge collaboratively and build semi-quantitative conceptual models. Fuzzy-logic cognitive mapping facilitates the explicit representation of group assumptions about a system being modelled through parameterized cognitive mapping (Gray *et al.* 2014). Specifically, FCM allows cognitive maps to be constructed by defining the most relevant variables that constitute a system, the dynamic relationships between these variables and the degree of influence, either positive or negative, that one variable can have on another. In group settings, FCM models are constructed based on combining group beliefs in a similar format as individuals share their experiences and understanding (Gray *et al.* 2014). The strength of using FCM in this context is the ability to extract, combine and represent group knowledge in a sensitive

situation for comparison between or among groups. Nyaki *et al.* (2014) used FCM to understand the drivers of wild meat trade in four Tanzanian villages bordering Serengeti National Park.

Resilience analysis explicitly allows for sustainable use options (Box 5.1). Traditional one-off biological models applied to hunting

Box 5.1 *The Resilience Assessment Workbook*

The resilience assessment workbook (Resilience Alliance 2010) may also be useful to provide insight into developing strategies for buffering both known and unexpected change in hunting systems. The workbook was developed by Resilience Alliance to apply resilience thinking (Walker *et al.* 2002). It operationalizes resilience for practitioners and following its first release in 2007, it has been applied in multiple contexts around the world (Resilience Alliance 2021) primarily in natural resource management contexts (Bennett *et al.* 2005; Biggs *et al.* 2012; Peterson *et al.* 2003) and more recently in urban planning (Sellberg *et al.* 2015). The workbook guides researchers and practitioners in identifying the focal social-ecological system, describing threats and the impacts of those threats, and identifying the current and new strategies to strengthen the resilience of the system. It also guides the identification of potential thresholds that represent a breakpoint between two alternative system states and helps reveal what is contributing to or eroding system resilience.

As Van Vliet *et al.* (2015b) have further suggested, the resilience approach introduces the need to adopt an adaptive management process, which embraces uncertainties. In more classic forms of management, precautionary principles are put forward, interpreting precaution as the need to avoid impacts until wild meat stocks are estimated with precision and risks are measured. In fisheries, the practical challenge of giving advice when evidence is uncertain was solved by moving toward a better quantification of uncertainty (Getz & Bergh 1988). Recent experiences of adaptive management in temperate hunting systems can also provide inspiration for the sustainable use of wild meat in tropical areas (Brown *et al.* 2015; Carter *et al.* 2014; Fiorini *et al.* 2011; Hunt 2013). Weinbaum *et al.* (2013) suggest that learning how to manage under uncertainty is fundamental to achieving sustainable wild meat hunting and requires putting in place efficient monitoring processes. The creation of participatory monitoring systems

often triggers a process of collective action (e.g. in Amazonian communities, see El Bizri *et al.* 2020a; Mayor *et al.* 2017) which can be included in any strategic action aimed at managing wild meat resources (Garcia & Lescuyer 2008). The hypothesis stating that the information generated by the system is inserted into the decision-making process so as to approach sustainability is only possible when resource management is completely decentralized and when a direct link is established between the monitoring results and the management decisions taken (Garcia & Lescuyer 2008).

Strategies for improving forecasts about the behaviour of hunted systems will require a combination of tools but under the assumption that sufficiently thorough understanding of ecosystems is needed to reduce deep uncertainties is probably not achievable. Therefore, as suggested by Schindler and Hilborn (2015), research should integrate more closely with policy development to identify the range of alternative plausible futures and develop strategies that are robust across these scenarios and can respond adequately to unpredictable ecosystem dynamics. Moving away from the assumption that developing richer mechanistic appreciation of ecological interactions will improve forecasts is now fundamental, and hunting sustainability models as described above, are heuristic tools for communication and for developing new ideas on how hunted systems respond. Managing ecosystems for multiple ecosystem services and balancing the well-being of diverse stakeholders will involve the development of multiple systems that also contain different kinds of trade-offs (Daw *et al.* 2015). Such trade-offs involve non-economic and difficult-to-evaluate values, such as cultural identity, employment, the well-being of poor people, or particular species or ecosystem structures. Management and policy decisions demand approaches that can explicitly acknowledge and evaluate diverse information flows, that take science into account but that involve more than this.

systems, which were based on a binary yes/no question, do not allow the system to be brought back to sustainability in case of a ‘no’ answer. In such cases, the response would be to ban hunting, reinforcing the protection of wildlife by prohibiting its use through legal prohibitions. In contrast, the resilience focus provides the opportunity for identifying strategies that strengthen resilience when the system is close to a given

threshold. By recognizing the benefits that wild meat use generates for people, especially indigenous and local people who live with wildlife, and therefore bear associated costs (e.g. danger to life, damage to crops, restrictions on land use), the resilience approach can incorporate the diverse views and value systems of stakeholders, as well as different knowledge sources, including experimental or scientific knowledge and experiential or local ecological knowledge (Cooney & Abensperg-Traun 2013). As a result, resilience approaches recognize multiple objectives, design mechanisms for incorporating them, weigh trade-offs and establish conflict resolution mechanisms that are fair to all parties. Identifying areas of agreement and disagreement between actors helps in understanding and overcoming obstacles between them (Biggs *et al.* 2011).

5.8 Putting the Theory into Practice

The importance of developing reliable methods for evaluating the sustainability of wildlife offtake and assessing the status of hunted wildlife populations is unquestioned (Milner-Gulland & Akçakaya 2001; Robinson & Redford 1994; Sutherland 2001). Indices and models are available that provide a preliminary measurement of hunting sustainability in tropical forest systems. These allow the determination of whether the population production exceeds or is less than harvest demand at a given moment in time. These assessments do not imply that the harvest will continue to be sustainable over the long term, since the relationship between game population density and game harvest is a dynamic one. Hunting is sustainable in the long term only if the harvest is both biologically and socioeconomically sustainable (Robinson 1993). One of the main challenges is how to obtain realistic and timely information to adequately describe the basic components of demography of the hunted species as well as hunting effort. Even if this is possible, most assessments of sustainability for hunted species are still based on a posteriori comparison of actual *versus* estimated sustainable offtake. For example, Weinbaum *et al.* (2013) reviewed 750 separate evaluations of harvest sustainability of mostly mammal populations (but also birds and some reptiles) and found that all assessments measured the sustainability of harvests in theory. In other words, the conclusion that a large proportion of all reviewed studies were deemed sustainable by the authors may have depended on the model used but more importantly were not used in real time to guide the efforts of hunters to exploit wildlife more sustainably. So, even though in the literature the importance of theory

informing data collection and management planning is frequently advocated, the reality is that because the methods for determining sustainable exploitation are highly sophisticated, most hunting schemes are based on limited science and data. This is the case even for resource management agencies in developed countries. For example, even though wildlife agencies in the USA and Canada commonly defend controversial policy by claiming adherence to science-based approaches, Artelle *et al.* (2018) provided limited support for the assumption that wildlife management in 62 US state and Canadian provincial and territorial agencies across 667 management systems were guided by science. Most management systems lacked indications of the basic elements of a scientific approach to management.

Even if a framework that provides guidance for adopting a science-based approach is adopted as suggested by Artelle *et al.* (2018), there is a case for arguing that for very many species simple methods that can be applied by non-specialists will be the most practical. Pretending that hunting communities in the tropics have the time and resources to compile prey population data so as to populate full demographic models, which incidentally are not even regularly applied by agencies in developed countries, is unrealistic. Assessing effort or demographic components such as density dependence or population growth rates are often too difficult to provide estimates that are sufficient to form the basis for sufficiently accurate exploitation. Milner-Gulland and Rowcliffe (2007) may have argued that long-term population monitoring programmes are the most informative approach to provide baseline information against which any hunting effects and/or conservation interventions can be monitored. But, although scientifically interesting and useful to understand exploitation processes, indicators of sustainability are the most realistic way forward to ensure practical management of wildlife populations will have to be based on sustainability indicators. This may mean that resource management by communities in the tropics will have to be based on perhaps less scientifically robust data, especially in countries where investment in research is limited. Community-led monitoring systems of hunting are becoming more common (see El Bizri *et al.* 2020a). These schemes may shorten decision-making time frames while promoting local autonomy in resource management and strengthen community resource rights (Brook & McLachlan 2008; Danielsen *et al.* 2014).

Participatory, adaptive management of wildlife use requires efficient monitoring systems designed to address impacts at appropriate temporal and spatial scales, while involving both scientific experts and local

resource users (Luzar *et al.* 2011). Ideally, metrics that allow conservation managers or communities themselves to understand patterns, track changes, and revise and update regulations affecting hunting, are fundamental. However, collecting data on spatial and temporal changes in hunting offtake to assist a community to regulate their impact on prey numbers can be demanding if hunters are required to provide daily data on hunter effort and number of animals killed. The difficulty of convincing hunters to partake in self-monitoring activities is exemplified by a study of hunters in five communities in the Piagaçu-Purus Sustainable Development Reserve in Brazil in which only 37 out of 74 (50%) potential monitors, and 36% of initially interested families, participated (de Mattos Vieira *et al.* 2015). If monitoring of hunters is to be assisted by researchers (e.g. Coad *et al.* 2013) the costs of this would increase dramatically, especially if hunter follows are undertaken. Data on each hunting event, such as time dedicated to hunting and location of hunt, are more time-consuming to collect for every hunter especially if long-term trends are required. Thus, more cost-effective means of recording and using data on hunter offtake are required for hunting monitoring systems to be maintained over long periods. A practical way forward may comprise describing hunting offtake by gathering data that are simpler to collect, pertaining to animals hunted (number of animals taken by species, sex and relative age of animals) and hunter identity within a village or camp. In a study of three villages in Cameroon, Avila *et al.* (2019) argued that even though these types of data are imperfect, indicators such as catch per hunter per day (CPHD) and MBMI can be used alongside more basic hunter interviews at different intervals to ascertain whether hunters are increasing their hunting effort by using indirect methods such as those employed by Parry and Peres (2016). Testing how much the coarser CPHD index differs from the more costly to obtain CPUE measures may provide the information required to allow practitioners and communities to sustainably manage their wildlife resources. As Sutherland (2001) suggests, the simplest method is probably often the best method. Nowhere is this more urgent than in the places where people rely directly on wildlife meat for protein, calories, micro-nutrients and livelihoods. In such regions, the precautionary principle alone will not be sufficient to balance the needs of wildlife species and the people who depend on them; therefore, efforts to maximize harvests and the persistence of harvested populations must be improved.

5.9 Final Considerations

Quite a number of approaches exist to evaluate sustainability of wild meat hunting. All have their unique parameter requirements and assumptions and their own advantages and disadvantages. All methods require careful parameter selection and data interpretation. Ideally, studies employ two or more methods alongside each other. With the exception of the defaunation index, which quantifies the effects of any parameter on population and species survival, none of the methods explicitly considers the effects of animal predation and competition on population dynamics and hunting sustainability. The competition/predation release of smaller species when larger species are hunted down, for example, smaller duikers or monkeys, might actually increase in density when larger antelopes or carnivores are depleted (e.g. Prins 2016). Moreover, whilst the estimators for sustainability are a tool to assist wildlife management, they are not tools to assist the setting of management policies. Even the very term ‘sustainability’ has different meanings ranging from any level of exploitation that does not endanger population survival, as in the Brundtland (1987) definition, to aiming at maximum sustainable exploitation, as in the Tivy and O’Hare (1981) definition. Diametrically opposite is a conservation approach characterized by the total exclusion of humans from protected areas rejecting any notion of sustainable wildlife utilization, so-called ‘forest conservation’ (e.g. Adams & Hutton 2007; Brockington 2002; Pemunta 2019). For example, the expansion of protected area networks in Cameroon caused the eviction, displacement and widespread multiple human rights violations from armed guards/forest protection forces on the traditional way of life – hunting and gathering – of indigenous Baka people (Pemunta 2014, 2019). Only recently, the Rainforest Foundation UK (2020) voiced concerns that the Conference of Parties to the Convention on Biodiversity (CBD) is set to agree in 2021 on a new conservation target to place at least 30% of the earth’s surface into conservation status by 2030, which could ‘dispossess millions’. Although many in the conservation and sustainable development communities have diametrically opposite and mutually exclusive approaches to values of wildlife in general and sustainable hunting in particular, this apparent conflict is solvable as many examples of successful community conservation, for example in the Amazon Basin, have demonstrated (Kothari *et al.* 2013; Redpath *et al.* 2013). We outline these issues further in Chapter 8.