

INSIGHTS FROM THE BIO-ECONOMIC MODELLING OF BUSHMEAT HUNTING

A report to the Conservation International Foundation
as part of their Bushmeat Initiative

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1 INTRODUCTION

Sustainable hunting has two sides; the economic side (in which the profits from hunting are such that the exploiters of a population continue to hunt at the same rate in perpetuity) and the biological side (in which the population growth rate matches the offtake so that the population remains stable in perpetuity). In this review I will analyse both sides of this equation, starting first in section 2 with an analysis of how to assess whether a given level of hunting will lead to the population stabilising. Then in section 3 I discuss how to predict the level of hunting that will actually occur when there is no manager to set a hunting level, but instead individuals decide how many animals to kill. This involves assessing the economics of hunting. In both sections, I discuss some of the complications that can arise in the assessment of sustainability, and how they can be addressed.

However, first it is necessary to consider what is meant by sustainability. Sustainability cannot be attained, inasmuch as it implies an equilibrium situation **in perpetuity**. All biological and economic systems are unpredictable. Thus although models can suggest that a system is likely to move towards extinction of the exploited population, or towards that population being maintained at a given size, this should not be taken as a prediction. Deterministic models produce a simple result; the offtake level will be X and the population size Y. However, if more realistic stochastic models are used to assess sustainability, including natural variability in population dynamics, measurement errors in estimating model parameters and variation in the actual hunting mortalities imposed on a population, then the way in which sustainability is expressed is as a probability of a population remaining above a given size within a stated time period. This is a much more appropriate output of an assessment than a simple statement that hunting is or is not sustainable in a particular situation (Mangel, in press, Ludwig et al 1993).

2 THE BIOLOGICAL SUSTAINABILITY OF HUNTING

In this section I discuss the effects of hunting on wildlife populations. In section 2.1, I describe the simple models that have been used to predict the sustainability of hunting a single species. These models can answer questions such as what hunting rate would be sustainable for a particular species, or how many individuals can be removed from a population each year without causing the population to decline from its current size. Next I show how this simple model can be extended to include hunting effort. This allows us to predict what yield would be expected for a given level of effort. I discuss the use of statistics on the amount of yield produced for a given level of effort as indicators of sustainability, and show how these can be misleading. Finally, I discuss the complexities that mean that the very simple model is usually inadequate for making detailed predictions about the sustainability of hunting in real-life situations; these include the fact that populations are often structured, by age or in their spatial distribution, and the fact that species do not exist, and are rarely hunted, in isolation.

In section 2.2, I discuss the methods commonly in use for assessing the sustainability of bushmeat hunting. The main method was developed by Robinson & Redford (1991). I place these methods in the context of the theoretical models discussed in the previous section. Finally, in section 2.3, I combine the analyses to make suggestions about methods that could be used to assess sustainability in the future. I discuss which data need to be collected in order to make an accurate assessment of sustainability, and how these data could be collected in the field.

2.1 Theory of sustainability

2.1.1 Simple single-species biological models

The key assumption behind all sustainable hunting models is that populations of organisms grow and replace themselves - that is, they are **renewable resources**. Otherwise, it would be impossible to hunt them sustainably. Another assumption that is usually made is that populations of organisms do not continue to grow indefinitely; instead they reach an equilibrium population size (the **carrying capacity**), which occurs when the number of individuals matches the resources available to the population. The population then remains stable at carrying capacity. Given that populations increase to a limit, a function that describes the way in which they grow is needed. The function will be bounded, because populations do not grow at the two extremes - when there are no individuals there to reproduce, and when there is an equilibrium number of individuals, so all the resources are in use. One of the most convenient assumptions to make about the growth rate between these two limits is that population growth is sigmoidal (Fig. 1a). This is the assumption made in the **logistic equation** of population growth. At first the population grows fast, but the growth rate slows gradually as time goes on, until equilibrium is reached with a growth rate of zero. Figure 1b shows how the population growth rate (in numbers of individuals) varies with population size. The equation for Figure 1b is:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (1)$$

where:

dN/dt = change in population size,

r = intrinsic rate of population increase,

N = population size,

K = carrying capacity.

At very low population sizes, the value of $\frac{N}{K}$ is small, so the population growth rate is approximately equal to rN , meaning that the population is growing nearly exponentially at a rate r . Despite this, the population growth rate is low, usually because although each individual in the population is reproducing at a high rate, there are few reproducing individuals present. When the population is very large, then the value of $\frac{N}{K}$ approaches 1, so the population growth rate is again very low, either because each individual is hardly reproducing at all, or mortality rates are high. Between these two extremes, there is a balance between enough individuals being present and them having a high enough per capita growth rate. The population growth rate is at a maximum when $N = \frac{K}{2}$.

Part of the appeal of the logistic equation is that it describes population growth using very few parameters. Yet the measurement of these parameters is not necessarily simple. The two key parameters in the model are carrying capacity and the intrinsic rate of population increase. Carrying capacity is a concept that is simple in theory but slippery in application. Population sizes generally fluctuate over time, and K is then taken as the average size of the population at equilibrium. It is unlikely that it will have an exact value for many populations, and is more realistically thought of as the bounds within which a population fluctuates. Even if populations fluctuate greatly in size, they will have some upper size limit beyond which they

cannot increase further. Carrying capacity is most likely to be a meaningful concept for species with low intrinsic rates of population increase, which tend to have more stable dynamics. In these species, the population variance is normally significantly lower than the mean population size. The mean is therefore an adequate approximation to the equilibrium population size. Carrying capacity is defined as the equilibrium, unexploited, density of a particular population in a particular area. It is not intrinsic to a particular species, although the likely range of carrying capacities is. For example, the carrying capacity of elephants in a National Park in the savannah areas of East Africa might be $2/\text{km}^2$, while the carrying capacity of the same species of elephant might be less than $0.5/\text{km}^2$ in a West African forest - the habits of the species dictate that carrying capacity is never high, but it varies four-fold with habitat type (Burrill & Douglas-Hamilton 1987).

Whilst K is problematic in its interpretation and varies between populations of the same species, at least its biological meaning is relatively easily to comprehend. This cannot be said of the intrinsic rate of population increase, r . Yet r is often cited as the key parameter that needs to be known if a population is to be exploited sustainably. The intrinsic rate of population increase is best comprehended as the rate at which the population grows (the difference between births and deaths) when the population is very small and growing exponentially, as in Equation 1 when $N=1$. Mortality from factors other than resource constraints (such as predators or climate) is ignored, although in reality these factors might be very important. In practice, primary data on the value of r are rarely obtainable. In particular, it will be hard to obtain a value for r for populations already stable at intermediate or high population sizes. Usually r has to be inferred, either by fitting a population model to data with all the other relevant parameter values known, or by using fecundity data from zoo populations together with assumptions about natural mortality rates (Robinson and Redford 1991, Caughley 1977, see section 2.2).

The logistic is a simplistic model. Other functional forms for population growth have been used, particularly in fisheries (Getz & Haight 1989). I will use the logistic for the sake of simplicity and in order to make use of previous theoretical results. Most of the results I present are relatively easily generalised to these other functional forms. Whatever functional form is used, it will generally involve negative feedback; that is, the growth rate of the population in the next time-period depends on its current size (**density dependence**). Density dependence is a population-level amalgamation of processes occurring between individuals, when there is competition for scarce resources among members of a species. These scarce resources are usually assumed to be food, but another common one is space. Increases in competition for these scarce resources lead to increases in the mortality or decreases in the fecundity of individuals. The functional form of density dependence depends on these individual-level processes.

2.1.2 *The effects of exploitation*

The simplest way to model hunting is to modify the logistic equation so that a certain number of individuals is continuously removed:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - H \quad (2)$$

If the number of individuals removed (H) is constant, then the population is at equilibrium when the number of individuals removed is equal to the population growth rate (Fig 2a). If a proportion of the population is removed, then $H = aN$, and the equilibrium situation is as

shown in Figure 2b. The equilibrium population size under a particular hunting rate can be found as follows: From equation 2, the population is stable when it is not growing i.e. when $\frac{dN}{dt} = 0$. This happens when the population growth rate is the same as the hunting rate; $rN\left(1 - \frac{N}{K}\right) = H$. In Figure 2a, the hunting rate H_1 leads to two possible equilibrium points; a low population size N_a and a high one N_b . However, H_2 leads to only one equilibrium point, N_{MSY} , which is the population size that produces the maximum growth rate (half the carrying capacity with logistic growth). The offtake level H_2 is called the **maximum sustainable yield (MSY)**, because it is the largest yield that can be taken from a population at equilibrium - if H was higher than H_2 then offtake would exceed the population's capacity to replace itself at any population size (H_3). In Figure 2b, there is only one equilibrium population size for a given slope of H . If H is too steep to cross the growth rate curve (H_3) there is no equilibrium population size, as the hunting rate is higher than the population growth rate at all values of N . This rate of hunting is not sustainable.

Analysis of the stability of these equilibria in the face of environmental fluctuations gives an insight into their usefulness as targets for a hunting manager. Inspecting the equilibrium point producing population size N_b in Figure 2a, assume a perturbation increases the population size slightly, perhaps due to an especially good breeding year. This leads to the hunting rate slightly exceeding the population growth rate, because density dependence makes the population growth rate decline (thus the line for H_1 is above the dashed population growth rate line). This means that more individuals are being removed than are being added to the population, and the population size moves back to N_b . Similarly, if the population size were reduced below N_b , density dependence would lead to the growth rate increasing, and the population would return to equilibrium. So the equilibrium point H_1, N_b is stable, because the population returns to it after a perturbation. Figure 3 shows the outcome of this analysis for each equilibrium point. It can be seen that, for a constant H with two equilibria, the higher population size equilibrium point is stable and the lower unstable (because any perturbation leads to the population size moving away from the equilibrium). The MSY equilibrium is semi-stable - a small increase in population size is compensated for, a small decrease leads to extinction if H is not decreased. Hunting at MSY is dangerous, because it is on a knife-edge - any small population decline leads to positive feedback, with the population declining rapidly to extinction if the number exploited stays the same. If H varies linearly with N (Fig 3b), then all the equilibrium points are stable. The MSY hunting rate produces the same kind of equilibrium as all the other rates.

Even this very simple analysis leads to some useful observations. The first two are quite general, the other two apply specifically to the logistic model.

- Starting to hunt a previously unexploited population will always lead to a decrease in the population size. It is impossible for a exploited population to remain at carrying capacity. The exploited population will either stabilise at a new lower equilibrium size or, if the hunt rate is too high, decline to zero. The model does not specify how long it will take for the population to stabilise at its new equilibrium - this depends on the values of r and H . Thus a decreasing population size does not in itself indicate that a population is being unsustainably exploited, rather that it is not at equilibrium. This point is ignored in most of the literature on sustainable use.

- The reason why populations can be sustainably exploited is that they exhibit a density dependent response. This means that at any population size below K , the population is producing a **surplus yield** that is available for hunt without reducing population size. Density dependence is the regulatory process that allows the population to return to equilibrium after a perturbation. The logistic equation assumes that density-dependence takes the form of smooth negative feedback. If this is not the case, small changes in hunting rate can lead to sudden large changes in population size, which could be dangerous for the population. The form of density dependence assumed is a key component of model predictions about the effects of hunting on population size.

- If hunting involves removing a constant number of individuals (Fig 3a), then hunting at a level greater than the MSY leads to a rapid population decline to extinction. Hunting below the MSY level leads to a stable equilibrium population if the starting population is above the unstable equilibrium population size. The further below the MSY level the hunt is the safer it is, because the two equilibrium population sizes are further apart. This reasoning lies behind a common suggestion that hunting should not exceed half the MSY level. If a population is over-exploited, the hunt rate needs to be reduced below the current population growth rate to allow the population to recover. The fastest recovery occurs when $H=0$.

- If hunting rate is proportional to population size, a single stable equilibrium population size results (so long as the hunting rate is low enough to cross the population growth curve at some point). A slight increase in hunting rate leads to a slight decrease in population size - there is a smooth and gradual relationship between the two, with no rapid changes. Thus, in the logistic model, a strategy involving hunting a certain percentage of the population each year is safer than hunting a fixed number of individuals each year, so long as the hunting rate is not too high (the proportion taken must be less than r). There is no need for wide safety margins to guard against unstable equilibria. IUCN recently suggested that sustainable use projects should hunt at a maximum rate of $\frac{r}{2}$ (Prescott-Allen & Prescott-Allen, 1996), which is equivalent to MSY (H_2 in Fig. 1.3b). This is not a safe suggestion because hunting at MSY is dangerous, although taking a constant proportion of the population that is equivalent to MSY is safer than taking a constant number of individuals at MSY.

2.1.3 A bio-economic model of hunting

The simplest model that includes the economic parameters determining hunting level assumes that hunting rate is proportional to population size and is also determined by hunting effort. This allows us to predict the effect of hunting on population size in situations when resource managers do not intervene to set the hunting level. It is assumed that the hunting level H can be expressed as:

$$H = qEN \tag{3}$$

Here, qE has replaced the percentage of the population killed, a , that was used in section 2.1.2. E , the **hunting effort**, is treated as a variable. Hunting effort can be measured in various ways, such as the number of days spent hunting or the number of each type of gun or snare used. Data on effort need to be collected in appropriate units for the situation being analysed. The constant q is the **catchability coefficient**, which is a measure of the ease of catching an individual of a particular species. For example, if a single snare is set in a previously unexploited area, q is the probability that an individual of a particular species is caught in it. The units of q depend on the measure of effort chosen. Equation 3 says that if

either effort expended by hunters or population size increase, the number of individuals killed will increase.

By substituting $\frac{H}{qE}$ for N into equation 2, and assuming that the population is at equilibrium ($\frac{dN}{dt} = 0$), we obtain an expression for yield (H) as a function of effort:

$$H = qKE \left(1 - \frac{qE}{r} \right) \quad (4)$$

This produces a parabolic curve (Fig 4). As effort increases, yield increases to a maximum and then declines to zero. At $E=0$, the population size is at its maximum, K . As effort increases, population size decreases and more and more effort is needed to catch the remaining individuals, until at maximum effort, the population size reaches zero. The yield-effort curve is effectively a mirror image of the population growth rate-population size curve (Fig 1b). This is a very useful result because yield and effort are parameters that are easily measured and come directly from hunting data. Population size is, by contrast, very hard to measure directly; forest-living mammals being obvious examples of cases where individuals are difficult to count. If this model were to hold, simply measuring yield and effort should be enough to discover the underlying stock-production relationship, without the difficulty and expense of population monitoring.

One much-used concept in the literature on resource use is **catch per unit effort** (CPUE), the ratio of yield to the effort expended. For example, if it was known that the number of hunters in an area had remained constant over time, and nothing else was assumed to have changed, then trends in the number of animals sold in the local market could be interpreted as a trend in CPUE. Trends in CPUE are an indication of trends in population size, because Equation 3 can

be rearranged as $\frac{H}{E} \propto N$. So if the yield from a population is declining while the hunting

effort remains unchanged, the population size can be assumed to be declining as well. This relationship could be a very useful indirect measure of population trends. A non-declining CPUE has been promoted as a good indicator of sustainable hunting. However, it is important to remember the assumption that has been made to get to this useful relationship - that yield is directly proportional to effort and population size. In the early stages of hunting, a declining CPUE does not necessarily mean hunting is unsustainable, because the population may just be declining to an equilibrium size. Conversely, a stable CPUE could be due to undetected increases in technological efficiency, giving a false picture of stability as the population declines. The effects of **aggregative behaviour** on hunting costs can also lead to misleading trends in CPUE. If a population aggregates into large groups even at low population sizes, or if its location is always predictable, then the costs of hunting are not related linearly to population size. The CPUE does not decline as population size declines, because small populations are not much harder to hunt than larger ones. The population declines dramatically without any reduction in hunting effort, and without warning signs, because catches continue to appear healthy. These conditions are common in fisheries, and may affect social forest species, such as primates.

2.1.4 Adding ecological realism to the single species model

2.1.4.1 Non-linear density dependence

The simple bio-economic model is linear in most parameters. Introducing non-linearities can give insights into the dynamics of real populations. One non-linearity which is especially emphasised in the natural resource management literature (e.g. Clark 1990) is **depensation**, also known as the Allee effect. In the standard logistic model, the proportional growth rate is a decreasing function of population size, so that the smaller a population is, the faster it grows. However, if depensation occurs, the population growth rate increases with population size, so that smaller populations grow slower than larger ones. Depensation is usually assumed to happen only when the population is small, and reasons might include difficulties in finding a mate or reductions in foraging efficiency as group sizes become too small. One species for which the circumstantial evidence seems to point to depensation playing a role is the passenger pigeon. This species declined to extinction very rapidly from quite large numbers. The original cause of the decline was probably habitat destruction, but it seems likely that a critical population size was required in order for the species to find masting trees reliably. Mast is a patchy and unpredictable food source, and once below the critical size, the population could not find food reliably enough to recover (Bucher 1992).

Depensation has serious consequences for the safety of the strategy of hunting a proportion of the population each year. The effect is to make the outcome similar to that of hunting a constant number of individuals, with two equilibria; one stable, the other unstable (Fig 5). If a population is hunted to a low enough level to reach the unstable equilibrium, it may recover much more slowly from hunting, or not at all. To assess the importance of depensation in the real world, we need to know how common it is, and at how large a population size it is likely to express itself. Myers et al (1995) carried out statistical analyses of 128 fish stocks for which 15 years or more of data were available, and found only 3 that showed statistically significant evidence for depensation. There were 2 other stocks for which depensation could not be entirely ruled out, which had also not recovered from very low population sizes. It seems that depensation is only found in commercial fish species at very low population sizes. This is the only large-scale study of the prevalence of depensation that has been carried out to date, and it seems to show that, at least in fish, depensation is not a widespread problem.

Although depensation is probably uncommon, it is worth taking seriously because it could compromise the ability of particular species to recover from low numbers. However, social disruption caused by hunting is not confined to small populations. Complex behavioural effects of hunting, particularly those associated with distorted sex ratios, are better not lumped into the simple population-level factor of depensation, but included more explicitly into hunting models.

Another complexity is non-linearities in the **stock-production** relationship. These mean that the population size at which populations are most productive (the MSY population size) is not 50% of carrying capacity, as in the simple logistic model. This issue has been explored by Fowler (1981, 1984), who shows that the degree of non-linearity can be linked to a species' life-history strategy. Large-bodied, slow-growing species are likely to have their highest production at populations nearer to carrying capacity than predicted by the logistic equation. Other species, particularly insects, have their highest productivity below $0.5K$, which may be linked to population dynamics that are limited more by predators than resources.

If an exploited species has a significantly non-linear stock-production relationship, then it is important to take this into account. It has implications for the optimal population size under

hunting as well as for the population's reaction to hunting. The optimal population size for a hunter is related to the degree of non-linearity; species with their MSY well below 0.5K will be harvested to a lower level than those with their MSY well above 0.5K. Elephants have their MSY well above 0.5K, and are unusual in that tusks continue to grow exponentially with age. Basson et al (1991) showed that the optimal strategy for an elephant manager was therefore to keep the population at carrying capacity and collect ivory from animals that had died from natural mortality.

2.1.4.2 Hunting structured populations

Biological populations are structured, with individuals varying in their age, stage, sex or spatial position. In some species, this structure can have a major effect on the outcome of hunting (Getz & Haight 1989). **Age structure** has a strong effect on the outcome of hunting when fecundity and mortality rates vary with age, particularly if there is a time lag between birth and sexual maturity. Hunting lowers the mean age of a population, because the additional mortality lowers the life expectancy of all individuals. If the lag between birth and sexual maturity is sufficiently long and the hunting mortality sufficiently high, mean age can be lowered to a point at which there is a danger of recruitment failure because all remaining individuals are immature. If older individuals are selected for by hunters (perhaps because they are larger) the reduction in mean age with hunting pressure is even more pronounced. For example, the North Sea cod is a long-lived species which reaches sexual maturity around the age of 4 years. It has been so heavily exploited that some one-year-olds are now exploited, and two-year-olds are fully exploited by the fishery. Only 4% of one-year-olds now survive to age 4 (Cook et al, 1997).

Sex structure is not included in population models as a matter of course, despite often being the most obvious division between individuals in a population. This is because, at least in the case of mammals, males are assumed not to be limiting on population growth rates. However it is often crucial to include sex structure for exploited species in which hunters select by sex, particularly if they select males. This selection might be explicit, for trophies that only adult males bear (such as saiga antelope horns), or implicit for the largest individuals that provide the most meat. If a species is polygynous, so that one male mates with many females, then at moderate levels of hunting pressure, targeting males relieves the pressure on females. Because females provide the recruits to the population, the population growth rate at a given population size is higher if males are targeted than if both sexes are hunted. So hunting a high proportion of males is both less damaging to the population than hunting females, and more profitable. This is true for many hunted ungulate species, although great care needs to be taken that these "surplus" males really are surplus, and that the proportion of males in the population doesn't drop so low that it limits fecundity (Ginsberg & Milner-Gulland 1993). If the reproductive system is not polygynous, selection for males might be as damaging to population fecundity as selection for females.

Spatial structure in the exploited population can have major consequences for the population's dynamics, particularly in sedentary species in which interaction with neighbours is much more important to an individual than interaction with distant individuals. Plants and corals are obvious examples. Spatial trends in hunting costs introduce a non-linearity into the relationship between costs and population size, and lead to patterns of resource depletion in which the lower cost areas are exploited first. The optimum population size for a hunter could be higher in a spatially structured population than in a population with constant hunting costs, so that individuals may survive in remote areas that are very expensive to hunt (Clayton et al 1997). If resources are patchily distributed, it may become worthwhile for hunters to forage in

groups, so as to increase their efficiency in searching for prey (Clark & Mangel, 1986). Spatial structure in variables such as population growth rate could lead to different hunting rates being optimal in different sub-populations, and so to different optimum population sizes in each sub-population. Movement of animals between areas complicates the picture considerably - if an area is being heavily exploited without significant movement taking place, that area becomes depleted but surrounding areas are unaffected. If, however, individuals move into the depleted area (because the population is well below carrying capacity and so resource levels in the area are high), then the hunting depletes the surrounding areas as well. Baskin (1998) discusses how the Lapland Reserve was set up to reestablish the reindeer population in north-west Russia. The population recovered quickly, so hunting started in the area around the reserve. Six years later, it transpired that almost the whole population had been killed, because most of the reindeer had migrated out of the reserve into the surrounding area, where they were vulnerable to hunting.

Because individuals are **genetically** different, any preferential hunting for or against a genetically determined trait is evolutionarily selective for particular genotypes. The genetic effects of hunting, through selection for individuals with particular characteristics, could well have important long-term consequences for populations, that are not immediately apparent from population-level analysis. Heavy hunting pressure can cause strong selection on a population, and thus rapid evolution. Heavily exploited salmon populations may have evolved a smaller mean adult body size as a response to the selective hunting of larger individuals, while reproductive maturity has been observed at younger ages in exploited cod populations than in unexploited populations (Law 1991). It is difficult to ascertain from observations such as this whether the response to hunting is ecological or evolutionary. Individuals (particularly males) can reach sexual maturity earlier if there are few adults present, showing phenotypic plasticity rather than evolution. However, if it is suspected that hunting could be exerting a selective pressure on a population, then a genetic model might well be needed to examine the long-term consequences of hunting.

2.1.4.3 Hunting variable populations

Climatic variability is the most commonly included stochastic variable in hunting models, because it can cause significant variation in population parameters however large the population size is. Population characteristics such as a short generation time and discrete breeding seasons make a species more sensitive to climatic variability. The hunting rate also affects population variability. Variation in the population size is important for conservation and sustainable use, because the more variable the population size, the more variable the sustainable exploitation rate is, and the greater the chance of population extinction. In general, the higher the hunting effort on a highly variable population, the higher the variance in the population size (see Milner-Gulland, 1994, for an example using saiga antelopes). This is true if the variability is externally generated (such as by the climate); if variability is internally generated (e.g. population cycles) then hunting will tend to stabilise the population. Another consideration with long-lived species is that hunting, by lowering the mean age of the population, increases the relative reproductive contribution of the younger age-classes. If a population has stochastic recruitment, this increases the relative variation in recruitment by reducing the averaging-out effect of having several fertile age-classes. The more fertile age-classes there are, the lower the unexploited variation in recruitment, but the more that variation is increased by hunting (Reed 1983).

2.1.5 Interactions between species

It is not ideal to consider a single species in isolation when analysing the sustainability of hunting. This is what is usually done, however, and it is testament to the explanatory powers of simple models that they bear any relation at all to the real-world dynamics of exploited species. A single-species model is an adequate simplification for a population in which there is strong intra-specific competition for certain resources (producing density-dependence), but there are only weak interactions with other species, whether they be competitors, prey, predators or pathogens. From the economic side, the model is an adequate simplification if the population is exploited in isolation from other populations, of the same or other species. Some exploited populations fulfil these criteria, others do not, and require further analysis. In this section, I give a brief overview of some of the likely effects of hunting on systems of two or more species.

2.1.5.1 Species that interact by being exploited together

The simplest situations to model are those in which the biological interactions between two species are weak or non-existent, but they are exploited together. In this case, they can be treated as two independent populations, but with a combined hunting effort. This means that the costs of hunting are also combined, so that the costs relate to the combined population size of the two species. If one species is much more common than another, then the costs of hunting are not related in any significant way to the size of the rarer population. Thus, the simple bio-economic model considered in section 3.1.4 can predict the extinction of one of the species at the long-term “sustainable” open-access equilibrium. In the single-species model, extinction cannot happen at the open-access equilibrium unless hunting costs are zero or non-linearities are introduced into the model. Writing the model equations out as in section 3.1.4, we have:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - q_1 E N_1 \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - q_2 E N_2 \\ \Pi &= p_1 q_1 E N_1 + p_2 q_2 E N_2 - cE\end{aligned}\tag{5}$$

where

Π = profits from hunting,

p_i = price per individual of species i ,

c = cost per unit of effort (e.g. per day’s hunting),

and the other variables are as in Equations 2 & 3.

There are two conditions that must be met for hunting to lead to the extinction of one of the two populations in this model. Firstly, one of the populations (population 1 in this case) must be slower-growing and/or easier to catch than the other:

$$\frac{r_1}{q_1} < \frac{r_2}{q_2}\tag{6}$$

Secondly, the cost-price ratio of population 2 must be sufficiently low for hunting to be worthwhile when population 1 has been exterminated:

$$\frac{c}{p_2 q_2} < \bar{N}_2 \quad (7)$$

where \bar{N}_2 is the size of population 2 at the hunting effort which exterminates population 1.

This result generalises to more than two species, with the relative values of $\frac{r_i}{q_i}$ determining

the order of extermination of the species. The carrying capacities K_i do not affect the equilibrium population sizes, but affect the speed of the transition - if, as often happens, the slower-growing species is also found at lower densities, it will be exterminated more quickly. Note that the economic value of the exterminated species is not relevant to the outcome - it could be much more or less valuable than the surviving species. The cost-price ratio of the surviving population is the key economic variable - if it is too high, then hunting becomes uneconomic before population 1 is exterminated.

This simple model has been used to explain the pressures causing overhunting of various species, including blue whales (on the back of the fin whale fishery, Clark 1990) and rhinos. The Luangwa Valley saw its rhino population decline rapidly to near-extinction in the early 1980's, coinciding with heavy elephant poaching in the area. Rhino horns were much more valuable than elephant tusks (1.7x as valuable per kill), but modelling showed that the rhino population was small enough for it not to be worthwhile for organised gangs to poach specifically for rhinos. On the other hand, it was highly profitable to hunt the more numerous elephants. Hunting both species together was only slightly more profitable than hunting elephants alone. Thus the poaching gangs captured in the area were large, because hunting specifically for elephants requires carriers for the bulky tusks. As predicted by the model, the poaching gangs were caught with tusks and the occasional rhino horn. In neighbouring Zimbabwe, on the other hand, small gangs went poaching specifically for rhino horn because the rhinos were still numerous. Small gang sizes are preferable for poachers because they are less visible to guards and wildlife, and can be used for rhino horn hunting because the horns are easier to carry than tusks. So the economic analysis showed that the rapid decline in rhinos in the Luangwa Valley was not caused by poaching specifically for rhinos, but by opportunistic killing of rhinos by gangs out hunting for elephants. It was the lucrative ivory trade that was driving the rhino decline, not the (apparently more lucrative) rhino horn trade (Milner-Gulland & Leader-Williams, 1992).

If a species is already rare, a low level of opportunistic incidental offtake can have a serious impact on its population size. If the two populations are separated in any way, there is the chance of a refuge from hunting pressure for the more sensitive species. For example, Sulawesi wild pigs and babirusas are two species that are hunted together in Sulawesi (Clayton et al 1997). Because Sulawesi wild pigs are common in both primary and secondary forest, it is possible to dramatically reduce hunting pressure on the endangered babirusa (found only in primary forest) without stopping hunting altogether, simply by hunting only in secondary forest. This could be a way to make hunting more sustainable that might be acceptable to hunters. Fin and blue whale stocks are geographically separated because fin whales tend to feed in more northerly waters than the blue whales, so hunting could be confined to northerly areas (Clark, 1990). Other species might be separated in time, perhaps by coming into an area at different times of year, so that a closed season would be similarly helpful.

2.1.5.2 Hunting species that interact biologically

Models of hunting interacting species (competitors or predators and prey) have concentrated on interactions involving just two or three species. Increasing the number of species leads to complex models, that may not reveal any more general principles than the simpler models. It is hard to make generalisations about the likely outcome of interactions between populations, because depending on the model's assumptions, any type of dynamical behaviour can be generated in the system (White et al. 1996). Simple models of hunting competing species show that the effects of competition can be particularly difficult to predict (Clark 1990). A fishery can collapse due to a shift in competitive dominance before it has even reached MSY. Because the exploited species is dominant, it is the abundant species before the fishery starts, and the competitor is rare, and so easily over-looked. The apparently healthy fishery can collapse before the existence of a competitor is even noticed. Not every exploited species is going to have this kind of problem (otherwise there would have been many more observed collapses of exploited populations with subsequent take-overs of their niches by another species). The difficulty lies in identifying in advance which exploited species are vulnerable to collapse through competitive exclusion.

The results of exploitation depend on whether the hunter is taking a species that is low in the food chain, and is a resource for many other species, or whether the exploited species is a predator or competitor for other species. The competitors of an exploited species benefit from the increased availability of resources as the population size of the exploited species declines, and their populations will probably increase. The prey of an exploited species may or may not increase in population size depending on whether there are other predators present that can increase to compensate for the removal of their competitor. Removing more than one species from an ecosystem will have effects that are even more complex and hard to predict. Fisheries modellers are starting to address the effects of hunting several species from multi-species predator-prey systems, using techniques such as multi-species virtual population analysis, but there are still many uncertainties (Magnusson 1995).

Hunting does not just affect non-target organisms through their population-level interactions with the exploited population. It can also affect the physical processes and structure of the ecosystem. Ecosystem-level effects of hunting can have long-term impacts on all the component organisms of the ecosystem. Two categories of effect that are particularly important are the effects of hunting on nutrient flow and on community structure. Humans can have large indirect effects on ecosystem structure by hunting a **keystone** species. Keystone species have a disproportionate effect on their ecosystem, due to their size or their activities. Any changes in their population size have correspondingly large effects on the ecosystem. Examples of keystone species are beavers, which change water flow substantially by building dams, and elephants which can alter ecosystems by destroying trees.

2.2 Methods used for assessing bushmeat hunting sustainability

In this section, I discuss the methods that are currently used for assessing the biological sustainability of bushmeat hunting, highlighting their strengths and weaknesses. I suggest other possible methods that could be used.

2.2.1 *The Robinson and Redford method*

This is the most widely-used method for assessing hunting sustainability. Examples of recent studies that have used it include Fa et al (1995), Fitzgibbon et al (1995), Muchaal & Ngangjui (1999), Alvard et al (1997). The method is appealing to users because it is relatively simple,

uses parameter values that are on the whole obtainable, and gives a useful threshold value against which sustainability can be judged. As it has become the standard method, it is especially important that its assumptions are fully analysed and the effects of using it are well understood. The method is fully described in Robinson & Redford (1991); I summarise and critique it here.

Robinson & Redford (1991) state that the requirements for sustainable harvesting are:

- 1) that it should achieve maximum production from the wildlife population.
- 2) that the population should not be reduced to levels at which the species is vulnerable to local extinction or the ecosystem functioning is affected.

If either of these conditions are not met, the species can be considered depleted.

This definition of sustainable harvesting is ambiguous, but maximum physical yield from a population is obtainable at MSY (see section 2.1.2) while maximum economic yield is obtainable at a point dependent on the discount rate of the owner, but generally at a higher population size than the MSY level (see section 3.1.4). Assuming maximum physical yield, requirement 1 states that the population should be held at the MSY level. Requirement 2 could be interpreted as meaning that the population should be kept on the right-hand, descending portion of the logistic curve (Fig. 1), because on the left-hand, ascending portion, it may be vulnerable to unstable equilibria (if a constant number is being removed each year) or to factors such as depensation. Thus the Robinson & Redford definition could be stated as that the population is depleted if it is below the MSY level.

They then discuss the parameter values that are required for their model. These are:

- 1) Density at carrying capacity (D). They suggest obtaining this from actual data (taken as the average of estimates from unexploited and lightly hunted areas), or from a simple relationship between density, diet and body size which they have derived from a number of forest species.
- 2) The arithmetic intrinsic rate of increase of the population (λ). They suggest estimating λ from r , the geometric intrinsic rate of increase, which is related to λ as $\lambda = e^r$. They suggest that r in turn can be estimated Cole's equation, which requires data on the age at first and last reproduction and the annual birth rate of female offspring. The equation assumes no mortality in the population, which can be a problem in some species. However, Cole's equation is not ideal, because the data required are not often obtainable for the species under study, introducing estimation error, and because of the assumptions made about mortality. Instead, it might be better to estimate r for a given species using an empirically-derived relationship between known r 's for other species and characteristics such as body mass. As mentioned above (section 2.1.1) r is an extremely difficult parameter, both conceptually and practically. It is best described as the maximum rate of increase that a population can achieve under natural conditions but without any significant intra-specific competition. Thus it is best measured as the rate of increase of a very small population (assuming no depensation occurs) under the best conditions available in the habitat type under study. It is clearly unfeasible to measure r in this way in most cases. λ is the same quantity, but it relates population sizes to each other in discrete time. Thus, in the absence of density-dependence:

$$\frac{dN}{dt} = rN \quad \text{and} \quad N_{t+1} = \lambda N_t \quad (8)$$

There is huge confusion in the literature about the meanings of λ and r , including among the users of Robinson & Redford's method. Generally, people assume that λ and r are the actual growth rates of the population, which decrease as population size increases, rather than that they are constants. For this reason, it can be helpful to refer to λ and r as λ_{max} and r_{max} to clarify their meaning; I will do this from now on.

3) Density at which maximum production occurs, and the maximum production (P_{max}).

Robinson & Redford define production as the additions to the population (through births and immigration) in a given time period (e.g. a year), whether these animals survive, emigrate or die, and maximum production as the MSY. They state that production $P = N_{t+1} - N_t$, but with the caveat that no mortality has been included (i.e. actual estimates of N_{t+1} would not be useful in estimating production). They then define the population size at which P_{max} would be produced as:

$$N_{t+1} = \lambda_{max} N_t \quad (9)$$

There is clearly confusion here; as explained in section 2.1.1, when the population is growing at λ_{max} the per capita growth rate is highest, but the actual number of individuals produced is small, because the population size is small. The maximum production (in the sense of MSY; the maximum number of individuals available for harvest) occurs at intermediate densities ($K/2$ in the case of the logistic), when the population is growing at an intermediate rate per capita, but because there are more individuals in the population, the actual number of new individuals produced is highest. This is the point which Robinson and Redford are aiming for.

They also suggest that 2 empirical formulae could be used for calculating production. One (based on Banse and Mosher 1980) relates production to population density and body mass, and was derived from a comparative analysis of 7 mammal species. Robinson and Redford use the unexploited population density in this formula; as production is positively related to density in the equation, this will have the effect of maximising the production estimate obtained, as required. The second empirical relationship simply relates birth rates to body mass, again in a regression of data from a number of mammal species. However, the use of these empirical relationships is perhaps not ideal, because the point of the exercise here is to relate productivity to changes in population density; neither of the comparative relationships were designed to quantify the effects of density dependence on yields, as we are aiming to do here. If they were both derived for unexploited populations (at K) then the estimates of productivity obtained will be too low. This is because productivity (as defined by Robinson & Redford) in a density-dependent species is likely to be low at K , assuming that fecundity rates are density-dependent.

Robinson & Redford make the following assumptions in the calculation of P_{max} :

1) Predicted densities are more reliable than observed densities, in general. This is fine, and will depend on the data quality in a given case. The predicted density D is equal to K . This assumption is also uncontentious.

2) Maximum production (P_{max}) occurs at $0.6K$. The logistic equation assumes $0.5K$, but as discussed in section 2.1.4.1, the actual point at which maximum production occurs depends

on the life-history strategy of the species. According to Fowler's (1981) data, $0.6K$ would be about right for bighorn sheep, so may fit forest ungulates relatively well. However, for faster- or slower-growing species, there may be significant error in this approximation.

They then calculate maximum production as:

$$P_{max} = 0.6D (\lambda_{max} - 1) \quad (10)$$

Assuming that MSY is indeed at $0.6K$, then the main problem with this equation is that it will substantially over-estimate P_{max} , because of the use of λ_{max} in the place of the actual population growth rate at $0.6K$, which will be much lower due to density dependence. If MSY actually occurs at less than $0.6K$, then P_{max} will be further over-estimated, because in Equation 10 the estimated maximum productivity is positively related to the proportion of K at which MSY is assumed to occur. Thus in this case the logistic equation would be a more precautionary assumption than the one used here.

They then multiply P_{max} by a factor to account for natural mortality, because their definition of productivity is the population increase before natural mortality takes place. This factor varies with the longevity of the species, on the assumption that if a species has a high natural mortality rate the proportion of the harvest that would have died anyway if it had not been harvested is high, and thus hunting can afford to take a higher proportion of the population than if natural mortality rates are low. The factors suggested range from 20% of P_{max} if the species is long-lived (>10 years) to 60% if the species is short-lived (<5 years).

This assumption has the effect of moderating the over-estimation of P_{max} in Equation 10. It has the greatest effect for the more sensitive, longer-lived species which is good, but the original over-estimation may be more severe for the shorter-lived species. However, it is rather a fudge factor, because the methods used for estimating λ_{max} are actually estimating production net of natural mortality, so the inclusion of this factor is conceptually unnecessary. Only if the model were more complicated, based on birth rates rather than overall rate of population growth, would it be necessary. Perhaps the requirement for this factor is linked to the use of Cole's equation to estimate r_{max} , but it would be better to make this explicit.

In assessing sustainability, they compare the estimate of P_{max} to the production of the area (i.e. the number of individuals harvested from the area over the appropriate time period). They clarify that this should only be a crude comparison, and that any estimate of productivity close to P_{max} should be treated as worrying. This is true. However, the main concern about this assumption is that it seriously overestimates the sustainable production level if the population is already depleted. Referring to Figure 2 and section 2.1.2, if a constant number of individuals is being hunted each year, then there is a stable and an unstable equilibrium at each hunting level, from zero to just below MSY (there is one, semi-stable, equilibrium at MSY). A sustainable hunting level would best be represented by the population being at a stable equilibrium on the right-hand, descending part of the curve. If the population is already below MSY, then any hunting level above the curve is unsustainable, and leads to rapid descent to extinction. The more depleted the population, the more the Robinson and Redford method over-estimates the sustainable hunting level by calculating the MSY.

If instead, the population is being hunted at a constant rate (Fig 2b), then there is a stable equilibrium at any population size. However, if we were being precautionary, we would want to be on the right-hand side of the curve. In this case, the "sustainable" hunting rate would

need to be lower than the MSY hunting rate; the more precautionary we wish to be, the lower a proportion of MSY we should set the sustainable hunting rate at.

A brief exploration of the outcome of using Robinson & Redford's method on a model population following simple logistic growth suggests that the use of this method overestimates the sustainable yield most severely when the population is large, the intrinsic rate of increase is high, and the natural mortality factor is large (Fig. 6). Thus any estimates of sustainable yield that have been derived for short-lived, fast-growing species using this method should be viewed as suspect. Also, as explained above, if the population is depleted (below $0.5K$) then there is a danger of rapid population decline, and a precautionary sustainable hunting rate should be set at zero - any estimates of sustainable yield derived using this method for a population that is below $0.5K$ or for which population density is unknown should also be viewed with suspicion. However, for lightly-exploited populations of large, slow-growing species, although the method is conceptually deeply flawed, its use may not be disastrous because the degree of error is low. These preliminary results were obtained using a model of simple deterministic logistic population growth, and should be substantiated by further analysis under stochastic conditions and with more complex population dynamics (particularly age structure).

2.2.2 Other methods

2.2.2.1 The Bodmer method

A similar method to Robinson and Redford's was proposed by Bodmer, and is described in Robinson & Bodmer (1999). The formulation below is a modified version of his equation, with different interpretations placed on the parameters used in order to clarify the procedure. The number of individuals produced by a population is calculated as:

$$P = D_f F s \quad (11)$$

where:

P = number of new individuals produced.

D_f = population density (females only). They suggest calculating this as $D_f = 0.5D_{tot}$ on the assumption of a 1:1 sex ratio, where D_{tot} is the overall population density.

F = female fecundity. They suggest calculating this as gY , where Y = Number of young recorded per female (e.g. number of embryos found in harvested females, or number of young at foot) and g = average number of gestations per year.

s = female survival from birth to average age at reproduction. This is a value ranging from 0.6 for short-lived species to 0.2 for long-lived species (i.e. the same as the Robinson and Redford mortality factor).

The actual harvest is compared to this estimated value P , in order to assess sustainability.

The method is useful in that it is simple, uses readily obtainable data and there is no assumption made about intrinsic rates of increase. Instead, birth and survival rates are used explicitly, albeit with the survival rate being a relatively crude approximation. Other assumptions need to be noted, for example the 1:1 sex ratio, which is violated in many systems where harvesters can select (e.g. for larger individuals, which may be adult males). However, if the sex ratio is female-biased, as would be the most usual scenario for mammals

subject to sex-based selectivity, assuming a 1:1 sex ratio is generally precautionary. Also, there may be a big difference between the number of embryos counted and the number of young counted at foot, because peri-natal mortality can be significant; this may be taken into account in the value used for the survival rate s . These problems are relatively minor, however, in a purposefully simple method such as this.

The main drawback of the method is related to its main strength. This is that no assumptions are made about density dependence, and there is no attempt to calculate maximum production; the use of current birth rates, measured in the population under study, means that sustainable production is assessed for the current population size only. As population size changes under hunting pressure, it would be expected that birth rates (and mortality rates) will also change. Thus the method is useful as a way of getting a quick snapshot of the current situation, not of measuring long-term sustainability. It should also be noted that in order for the method to be valid it is important that birth rates are actually estimated for the population in question at the same time as the harvest rates are assessed.

2.2.2.2 An analogue of the Robinson & Redford method

If a method was desired that had the same conceptual underpinning as Robinson and Redford's, then one simple approach would be to use the discrete-time logistic equation:

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^\beta} - H \quad (12)$$

where:

λ = arithmetic intrinsic rate of population increase

a = A constant related to carrying capacity: $a = \frac{\lambda - 1}{K}$

β = the degree of over-compensation (non-linearity) in the population growth rate.

H = the offtake. This could be a simple number of individuals killed, or a more complicated function, such as the number killed as a proportion of the population size (see sections 2.1.2 and 2.1.3).

We will assume that $\beta=1$ for simplicity, hence Equation 12 represents simple logistic growth, as shown in Figure 1. By using the discrete-time version of the equation, we make data collection and parameter interpretation much simpler; we can name a time period (such as a year) and calculate population growth rates and harvests for that time period.

If offtake is at a sustainable equilibrium then the population is stable. If we set $N_{t+1} = N_t$ and rearrange Equation 12, then a sustainable harvest rate can be obtained at any population size:

$$H = N_t \left(\frac{\lambda}{(1 + aN_t)} - 1 \right) \quad (13)$$

However, if we wished to assess sustainability, we would want to compare the actual harvest rate to a putative sustainable harvest rate. Assuming that a sustainable harvest rate is one that

maintains a population at a given proportion, p , of K , then by substituting $a = \frac{\lambda - 1}{K}$ and $N_t = pK$ and then rearranging, we obtain:

$$H = pK \left(\frac{\lambda}{1 + p(\lambda - 1)} - 1 \right) \quad (14)$$

Following Robinson and Redford, we may wish to set $p = 0.6$, although there are several options; for example it has been suggested that a more precautionary approach would set $p=0.75$ (Roughgarden & Smith, 1996), while a common fisheries definition of a depleted population is one that is below $0.35K$ (Mangel, in press).

In order to ensure sustainability, we next need to check that the population is currently on the right-hand, descending portion of the logistic curve, otherwise with a constant number harvested there is the danger of H representing the unstable rather than the stable equilibrium (Fig 2). The higher the value we set for p , the easier it is to be sure about this, because the inevitable sampling error in estimating population density is less likely to lead to confidence intervals that include values below $0.5K$. Clearly if the threshold value below which a population is considered depleted is below the MSY level (such as $0.35K$), then there is a conflict between these two steps in the process.

Although I feel that this procedure would be just as simple to use as Robinson and Redford's method, but without the conceptual flaws, it is still not ideal. There is still no easy way to estimate λ for the poorly-known species of forest mammal that it would be used for (let alone for well-studied species!), and the underlying model is overly simplistic (see sections 2.1.4 and 2.1.5). However, it might be useful for a first stab at assessing sustainability. Similarly simple models, such as that shown in section 2.1.5.1 for two species experiencing joint effort, could also be used to assess the sustainability of hunting in a similar way.

2.2.2.3 Lessons from fisheries management.

Many of the problems encountered in assessing the sustainability of harvesting of forest mammals are also encountered in fisheries. These include the poor quality of population size estimates and the predominance of offtake data as the main information from which sustainability must be assessed. Thus it is worthwhile looking at the fisheries literature to see how they have tackled these problems. Standard texts such as Gulland (1983) and Hilborn and Walters (1992) include descriptions of the methods used in fisheries. Here, I shall comment briefly on some of the basic issues that they tackle.

As we have seen in the discussions of the Robinson & Redford and Bodmer methods, natural mortality is a difficult quantity to assess. In the fisheries literature too, the natural mortality rate is generally assumed rather than being measured, and this leads to serious problems in the accuracy of sustainability assessments. Methods do exist for assessing natural mortality rates (Gulland 1983). These include relating natural mortality rates to fish growth rates and deriving an empirical relationship similar to those that can be derived for quantities such as r_{max} and body size. Ideally, tagging experiments should be carried out, so that natural mortality rates can be estimated more directly. But these are likely to be impractical for the majority of fish species, and more so for the majority of bushmeat species.

For many years, one of the planks of fishery stock assessment has been the relationship between yield, effort and population size given in Equation 3. After normalisation to account for changes in effort levels (number of fishing days, number of boats of different sizes), the yield should be directly related to the population size. The simplest assumption, shown in Equation 3, is that there is a linear relationship - a decline in yield per unit effort (usually called catch per unit effort, CPUE) denotes a corresponding decline in population size. If CPUE continues to decline, rather than stabilising at an equilibrium level, then the offtake can be inferred to be unsustainable.

Changes in CPUE are relatively easy to calculate, given a time-series of yield and effort. These data are usually available for managed fisheries, but are rarely available for bushmeat harvesting. However, given that the data can be used in this simple way, it may seem worthwhile investing in collecting them so that the time series can be used in future assessments of sustainability. Alternatively, it might be worth collecting yield and effort data in a number of locations, so that spatial variability in offtake can be linked to spatial variability in sustainability. This has been done for bushmeat, for example by Muchaal & Ngangjui (1999). However, the interpretation of trends in CPUE is fraught with difficulties, so much so that the usefulness of CPUE in fisheries assessment is being seriously questioned (Jim - a ref?). Some of the many problems with using CPUE are mentioned in section 2.1.3, others include undetected changes in hunting efficiency confounding trends, and changes in the behaviour of targeted species, which may become more reclusive or move into or out of the area as hunting pressure changes.

2.2.2.4 Population density and structure

In an excellent review of sustainability indices for bushmeat harvesting, Robinson & Redford (1994) discuss some of the issues related to CPUE mentioned above, and also discuss the problems and possibilities in using direct measures of population density and structure to assess the sustainability of hunting.

Point estimates of population density are only useful if they can be compared to estimates of population density in similar, but otherwise un hunted areas (i.e. estimates of carrying capacity). Often the reason why an area is un hunted is that it is inaccessible; this may be because it is of a different habitat type (wet or mountainous) or it may be a protected area, in which densities of hunted species may be unnaturally high. In these cases, estimates of carrying capacity will be unreliable because they are not representative of carrying capacity in the area under study. Given a reliable estimate, the fact that hunted populations have lower densities is in itself not surprising; a relationship between (long-term) hunting effort and population density is expected. If there are several point estimates from different areas, with data on CPUE attached, the shape of the relationship between population density and CPUE may be informative about the dynamics of the population and its reaction to hunting. If the point estimate shows that a population is depleted (e.g. with a density less than $0.5K$), then this may be useful as a way of highlighting that this population is of concern. However, point estimates are not useful as predictive tools, because they say nothing about the dynamics of the system; for example whether a population is stable or declining.

A trend in population estimates can give evidence that a population is declining (assuming that survey methods are comparable over time; Milner-Gulland & Lhagvasuren 1998). This may be a cause for concern, but it must be borne in mind that even ultimately sustainable harvesting causes a population decline when it begins, as the population size moves towards equilibrium. However, if there are data on factors which may be causing the decline (changes

in hunting rates over time, changes in habitat availability), it may be possible to use a model to tease out which factors are likely to have been the main causes of the population decline. Using a simple population model to link data on population decline rates and offtake rates makes it possible to suggest whether hunting has been sustainable in the past, and the size at which the population will stabilise given that hunting rates continue. Thus, trends in population size in themselves are only suggestive that the population is of concern; with the addition of data on offtake rates and a population model they can be used to assess sustainability.

Robinson & Redford (1994) also discuss the possibility of using data on age structure, either of the population itself or of the offtake, to assess hunting sustainability. Again, these data can often be highly ambiguous. If age structures in both exploited populations and unexploited populations can be obtained, then it would be expected that the higher the hunting mortality, the more skewed the age distribution will be towards younger animals. This is because as hunting mortality increases, life expectancy decreases; as the mean age of death decreases, so does the mean age in the population. In a similar way to data on population size, data on age structures tells us only that a population is being hunted, not whether the hunting is sustainable. But age structure data is even less useful because there is no clear threshold that can be set below which a population can be considered depleted and therefore of concern. However, there is one situation in which the examination of age distributions can highlight populations of concern. This is in species where it is known that reproductive maturity is at a relatively old age, but where animals that have not reached reproductive maturity are hunted. In this case, it is possible that hunting can reduce the mean age of the population low enough that reproductive failure can occur because there are not enough mature individuals in the population. North Sea cod is a good example of this; they breed at age 4, but they have been so heavily exploited that only 4% of one-year-olds survive to this age (Cook et al 1997). However, many species are able to respond to this pressure with individuals becoming reproductively active at a younger age; thus the problem may not be too serious in most cases. Another problem is that it is impossible to tell whether the population is declining or increasing from an age distribution. As the population declines, it would be expected that the population would get younger. However, as a population recovers a high proportion of juveniles is also likely to be found, due to higher birth rates.

Age structure data in the offtake may be easier to come by, but it is even less informative than age structure data from the population. This is because the distribution of ages in the offtake is the result of two confounding processes; changes in age structure in the population itself and selectivity by hunters. It is possible to disentangle these two processes in a model, and infer the most likely combination of hunting mortality and selectivity that would have caused these patterns (Milner-Gulland & Mace, 1991, did this for the ivory trade). Alternatively if there is evidence that the hunting methods used are unselective, then age structures in the offtake can be assumed to be equivalent to those in the population. However, a simple examination of age distributions in the offtake can be very misleading if there is strong selectivity operating. Milner-Gulland & Mace (1998) show several tusk weight distributions from the ivory trade and discuss the various interpretations that can be drawn from them.

Many of these problems also apply to other forms of data about the structure of the population, such as sex ratio data. Overall, the effect of hunting on population structure depends on the demographic characteristics of an individual species; inferences can be made through the use of age-structured population models, but is it certainly not a quick and easy method to use.

2.3 Assessing biological sustainability

In section 2.2, I discussed the various sorts of data that can be collected in order to assess sustainability, and their relative usefulness. From this a priority list can be drawn up for data collection:

1. Data on **population density** in the hunted area. This tells us little without comparative data, but is nonetheless the building block without which no further inferences can be made.
2. It is also necessary to obtain data on **unexploited population density** in similar habitat. By comparing the two densities, it is possible to discern whether a population is depleted, but not to infer whether hunting is to blame or whether current hunting levels are sustainable.

Data on unexploited population density may be difficult to obtain, but the data must be independently estimated in order to serve as a valid comparative datapoint. This can be done by various means, but the common practice of obtaining data from **lightly exploited** populations is not satisfactory. This is because some species' population densities may be dramatically affected by light hunting pressure. Large mammals are particularly vulnerable, both because of the functional form of the density dependence they often exhibit (in which much of the change happens near carrying capacity), and because they are often strongly selected for by hunters in the early stages of hunting.

3. Data on **number of animals killed**. This can be used to derive the hunting mortality that the population is experiencing. However, the number of animals killed must be expressed per time period and from a given area. It is important that the **size of the area** from which the offtake is obtained is estimated, otherwise it is impossible to assess sustainability. This is not always easy to estimate if the offtake is calculated by counting animals on sale in a market, for example, when all that is known is that they are local in origin.

4. With these three pieces of data, it is possible to use simple models of the types described above to assess crudely the sustainability of hunting. However, in order to do this, some estimate of the **population growth rate** is needed, so that this growth rate can be compared to the hunting rate. This is usually the most difficult parameter of all to obtain. Generally, the best approach if a predictive model is required (so that the long-term sustainability of the hunting rate can be assessed) is to estimate the **intrinsic growth rate** and make an assumption about the functional form of density dependence. If the current snap-shot position is all that is required, then estimating the **current population growth rate** will do. This is less demanding in terms of assumptions made, but also gives less information.

As we have seen, feasible approaches to estimating intrinsic growth rates include: i) using empirical relationships derived from comparative analyses to relate intrinsic population growth rates to measurable variables such as body size and trophic level; ii) using data from zoo animals, which has the problem of the artificial conditions under which the animals are kept; iii) using Cole's equation (which is not ideal); iv) observing growth rates over time of populations in similar habitat which have no density dependent constraints, usually because they are very small (which is unlikely to be possible in all but a tiny minority of species).

Measuring current population growth rates (i.e. the number of new individuals added to the population which will become available for hunting rather than the change in population size

over time) can be done by measuring female fecundity and making an assumption about natural mortality rates.

Alternative approaches to modelling include constructing models that explicitly model birth rates and survival, with density-dependence placed on one or both of these vital rates. If the population is very depleted, density dependence may be minimal and so ignorable. These birth-death models are easily extended to age-structured models, which can be useful for long-lived species. The advantages of these types of model is that they are more representative of reality than a simpler model where births and deaths are collapsed into the single parameter λ or r , and their assumptions are more transparent. The disadvantage is that they are not so tractable to analytical solution, so a simple formula like Equation 14 can't be used.

From a **time series** of data on population sizes and hunting rates, information can be gleaned on whether the system is at equilibrium or not; i.e. whether the population is still declining, whether the hunting rate is increasing or decreasing, and whether hunters are taking a constant number of individuals or a constant proportion of the population (which has implications for the stability of any equilibrium that will be reached). **Spatially extended** data sets, in which data from sites with several levels of hunting mortality and associated population densities are collected, can also be useful in the assessment of hunting sustainability. This kind of data can give information on how the species reacts to different levels of hunting mortality, and thus on what functional form is appropriate for the population model. In multi-species harvesting systems, assessments should be carried out for all the species individually, bearing in mind how a given amount of hunting effort is apportioned between the different species (see section 2.1.5.1).

The collection of data on **hunting effort** is useful, however it is not advisable to use it in assessments of CPUE. This is too fraught with difficulties. Instead, hunting effort data is useful for the assessment of the economics of hunting, and thus for assessing sustainability from the economic side. This is covered in section 3.

3 THE ECONOMICS OF HUNTING

In this section, I move on to the issue of how the number of individuals that hunters wish to kill is determined. In section 3.1, I describe simple economic models of supply and demand and relate them to the market for bushmeat. I discuss the factors which determine the quantity of a good that is supplied or demanded, including the price of the good, consumer incomes and the prices of substitute goods. I then develop the models introduced in section 2 to predict the equilibrium size of a hunted population, depending on whether there is a sole owner or whether there is open access to all who wish to hunt. In section 3.2, I discuss the models that have been used to describe the behaviour of individual hunters. These include models that answer questions about how hunters choose which species to target, where to hunt and how long for. I also show how the economic models of hunting developed in section 3.1 can be extended to model a hunter's decision-making when hunting is illegal and there is a risk of being captured and receiving a penalty. In section 3.3, I review previous studies that have looked at the economics of bushmeat hunting, and relate them to the theoretical models, while in section 3.4, I make suggestions about how the economic modelling of bushmeat hunting could be carried out in the future. I discuss the types of data that are needed to model the economics of the bushmeat trade and how these can be collected.

3.1 Supply and demand for bushmeat

3.1.1 The market model of supply and demand

People will only produce a particular good in response to a demand for that good. This is as true for the hunter who uses time and effort as inputs in order to supply dinner for the family as it is for a firm manufacturing burgers. But unlike ordinary economic goods, the size of a exploited population is affected (through hunting effort) by the amount of the good that hunters wish to supply. Two functions need to be estimated in order to estimate the amount of a good supplied to a market. One is how the costs of supply vary with the amount produced. The other is how the quantity demanded varies with the price of the good. Together, these functions determine the equilibrium price of the good. The shapes of these functions have implications for how the market responds to regulations that aim to reduce the supply of the good, such as hunting quotas. Thus the shapes of an exploited good's supply and demand functions have important implications for policies that aim to promote its conservation and sustainable use.

The market model of supply and demand describes the relationship between costs and prices and the quantity of the good supplied and demanded. It can be used to derive the equilibrium price and quantity of the good supplied. It is a static equilibrium analysis, like the previous simple bio-economic model, meaning that the long-term equilibrium is being described, not the dynamics of getting there. The basic model is shown in Figure 7. Demand is assumed to slope downwards with the quantity consumed. If a good is very hard to get hold of, consumers are prepared to pay a very high price per unit of it; if the market is swamped with a good, all the consumers have enough and are not prepared to pay much for the good. Conversely, the supply curve usually slopes upwards because the higher the price, the more of the good the supplier wishes to sell. The equilibrium is reached in this way: If the price is too high, the suppliers produce more of the good than is wanted. In order to clear excess stock, they cut their prices, which has the dual effect of increasing the amount of the good that consumers demand and decreasing the amount that they wish to supply. Similarly, if the prices are too low, there is excess demand that is unsatisfied. Suppliers increase the price, which both cuts the amount of the good the consumers want and increases the amount suppliers want to supply, and equilibrium is reached. In a competitive market, the equilibrium is reached automatically through individuals pursuing their own best interests. In a non-competitive market, the equilibrium is not reached automatically. A sole supplier of a good has the power to set the price of the good. If the sole supplier is a private monopolist, the price is set at whichever level maximises the firm's private profits. This is not usually at the socially optimal level where the supply and demand curves cross, but at a higher price, leaving demand unsatisfied.

Because bushmeat is a perishable good, prices may vary through the day as meat quality declines; near the end of the day the supplier may have to sell at a low price in order to clear stock that would be unsaleable the next day. Some solutions to this problem include smoking the meat or carrying it on ice, as a way of extending its saleable life.

3.1.2 Demand

The demand for a good is not just determined by its price, despite the emphasis on price in the market model. Price is highlighted in this model because it both determines the quantity supplied and is determined by the quantity demanded, while the other variables are externally determined in the wider economy. In the model, changes in these external variables shift the supply and demand curves to the left or right, thus affecting the equilibrium price and quantity.

The major external variables affecting demand are the **price of related goods, consumer income, and consumer tastes**. Related goods can be substitutes or complements - for example the prices of rhino horn, water buffalo horn and saiga antelope horn on the traditional Chinese medicine market are probably linked because saiga antelope horn and water buffalo horn are being promoted as possible substitutes for rhino horn. However, saiga antelope horn is generally used in traditional medicines as a complement to rhino horn. Consumer income can be a major influence on demand for a good - in fact it seems that in Japan, consumer income was the only significant determinant of demand for ivory over the period 1950-85, while the price of ivory had no discernible effect (Milner-Gulland 1993). This information is important not only for those planning ivory cartels but also in predicting possible future increases in demand for ivory as other Asian countries become richer. Changes in consumer tastes can also be important, as was demonstrated by the virtual shutting down of the markets for furs in the UK and ivory in the EU and USA. Explanations for a change in the quantity of bushmeat demanded as an isolated community integrates into the general economy might thus include a decrease in the price of substitute goods as meat from domestic livestock becomes cheaper, causing a decrease in the quantity of bushmeat demanded as its price becomes relatively higher. Changes in tastes may decrease the quantity of bushmeat demanded if other meats become more socially acceptable. The income effect is more ambiguous; as incomes increase in the community, the amount of bushmeat eaten may increase more or less than the increase in income, or even decrease. The parameter that determines the degree to which each of these competing influences affects the quantity of bushmeat demanded is the **elasticity** of the demand curve to these factors.

The price elasticity of demand measures the responsiveness of demand to changes in price. It is defined as the percentage change in the quantity of a good demanded with a 1% change in price: A 1% fall in price that leads to a 2% increase in the quantity demanded has an elasticity of -2. Elasticity is related to the slope of a curve, but unlike the slope, it is dimensionless. This allows elasticities to be compared between goods with different units, and between different-sized markets. If the demand for a good is “elastic” with respect to price, this means that the quantity demanded is strongly affected by price, and the magnitude of the elasticity is greater than 1. If demand for a good is inelastic, the quantity demanded is not greatly affected by price, and the magnitude of the elasticity is less than 1 (Fig. 8).

Elasticity is most conveniently calculated using the formula below, for small ΔP :

$$\epsilon_p \approx - \frac{|\Delta Q|/Q}{\Delta P/P} \quad (11)$$

where Δ means a change in a variable, $||$ means the magnitude of a variable (regardless of sign), P is the price, Q is the quantity demanded, and ϵ_p is the price elasticity of demand.

Similar equations can be derived for any other elasticity. For example, the cross-price elasticity of demand (how demand for a good i changes with respect to changes in the price of

another good j) is: $\epsilon_{ij} \approx \frac{|\Delta Q_i|/Q_i}{\Delta P_j/P_j}$, while the income (I) elasticity of demand is: $\epsilon_I \approx \frac{|\Delta Q|/Q}{\Delta I/I}$.

The cross-price elasticity of demand measures how strongly the demand for one good is affected by changes in the price of another good. If the goods are substitutes, such as beef and bushmeat, an increase in the price of one good should increase the quantity of the other good demanded, and ϵ_{ij} is positive. If the goods are complements, like fish hooks and fishing line, an increase in the price of one good should decrease the quantity of the other good demanded, and ϵ_{ij} is negative. The income elasticity of demand measures how a change in income affects the amount of a good demanded. The income elasticity of most goods is greater than zero, so the amount demanded increases as people's income increases. These are called "normal goods". "Luxury goods" have $\epsilon_I > 1$, so an increase in income leads to a more than proportional increase in the amount of the good demanded. Ivory and foreign travel are examples of luxury goods. If a good is particularly associated with poverty (an "inferior good"), as some bushmeat may be, then an increase in income leads to a decrease in the amount of the good demanded ($\epsilon_I < 0$).

The own price elasticity of demand, ϵ_P , is largely determined by how easy it is to substitute another good for the good in question. If there are a lot of similar goods, demand is elastic, because a small price increase causes consumers to switch to the substitute goods. Tastes and social customs are also important. For example, if a product is regarded as frivolous, then consumers have elastic demand for it and buy much less of it if the price rises. If the product is seen as a necessity, people continue to demand it despite price rises - it has inelastic demand. Long-run demand tends to be more elastic than short-run demand, because in the long run, consumers can change their behaviour and substitutes can be found, while in the short run, continuing to use a good despite price rises might be unavoidable.

3.1.3 Supply

The **production function** defines the relationship between the amount of the good produced and the costs involved in producing it. In the simple bio-economic model discussed in section 2.1.3, the production function was assumed to be linear; the total cost of producing the good increased linearly as the amount of effort put into hunting it increased. This relationship was simplistic in that it assumed **constant marginal costs** - that the cost per unit of effort was constant however much effort was put in. This is unlikely to be true - for example, there are often economies of scale. As the scale of a hunting operation increases, it is possible to introduce cost-saving technologies like larger boats or better guns. The model also assumed no **fixed costs**. This can be unrealistic, particularly for commercial hunting, because some costs, such as the maintenance of hunting equipment or the salaries of managers, need to be paid regardless of the amount of hunting that goes on. However, small-scale subsistence hunting is unlikely to have many fixed costs. The model also assumed a **constant price** throughout. This is a fair short-term assumption for open access hunters supplying only a small quantity of a good to a large market. But if a significant proportion of the market is being described, or if prices change through time, then the assumption of fixed prices is not tenable, irrespective of whether the hunting is done in an open-access system or by a monopolist.

Like the demand curve, the supply curve is also affected by variables other than price. These variables include technology, input costs and regulations. Improvements in technology shift the supply curve to the right because they make it possible to supply more of a good at a given price. This can be crucial to the sustainability of hunting because the model predicts that technological improvements such as better, more modern weapons will increase the equilibrium quantity exploited. Finally, regulations affect the supply curve, preventing producers from adopting otherwise cheaper technologies, and thus move the supply curve to

the left, leading to higher equilibrium prices and lower quantities supplied. Regulations requiring hunters to use traditional weapons would have this effect. MacKinnon (1998) discusses programmes in Irian Jaya, Indonesia, where local hunters have collaborated with a conservation organisation to develop regulations that limit hunting to traditional weapons. This allows the locals to continue to hunt in their usual way, but makes it illegal for outsiders to come into the area and hunt game using more efficient technologies.

3.1.4 Profitability and the market

In section 2.1.3, the level of hunting effort was introduced as an important determinant of the yield obtained from hunting a population. Here we explore what determines the level of effort that hunters wish to expend. So far, effort has been treated as an externally determined parameter, but in the real world, the sustainability of natural resource use is not determined arbitrarily, but by the interplay between the biology of the exploited species and market forces. A bio-economic model is needed to capture these two sides of the coin. Analysing the economics of hunting leads to insights into the likely equilibrium size of exploited populations under a range of market conditions. This range includes the situation when a sole manager has full control of the hunting of the resource, as well as when hunting is an uncontrolled free-for-all.

The level of hunting can be predicted by adding a term for the profits made from hunting to the population model. The profits made from hunting are calculated as the revenues from hunting, which depend on the yield, minus the costs of hunting, which depend on the effort expended. Costs are defined rather differently in economics than in ordinary life, using the concept of **opportunity costs**. The opportunity cost of an action is the cost of not doing whatever you could have done instead of what you decided to do. The costs of hunting include not only the direct outlays involved, but also the costs of the hunter's time. The opportunity cost of working as a hunter is the wage the hunter would have received in the best-paying alternative employment. If the hunter's revenues are not covering this wage, then it would be better to leave hunting and move into the best-paying alternative employment instead. Thus "profits" actually means the extra money that the hunter is earning over and above that which can be earned in other feasible jobs. This definition of costs is important when one considers that individuals in economically undeveloped areas may not have much alternative employment other than hunting wildlife; thus their opportunity costs are very low. Individuals in areas with more developed economies have more employment opportunities and so higher opportunity costs. Other things being equal, over-exploitation is more likely when opportunity costs are low, because low costs lead to an equilibrium point at lower population sizes and higher hunter numbers than would be the case in an area with alternative employment available.

The integration of a hunting community into the wider economy is likely to have two important effects on costs, which work in opposite directions - increasing opportunity costs because the opportunities for wage-earning employment improve, and decreasing actual costs of hunting due to the introduction of **new technology**. Frequently the latter outweighs the former. Many fisheries follow the pattern of gradual cost reduction as their equipment improves, contributing to the over-exploitation of a once lightly exploited resource. However, Freehling and Marks (1998) describe the opposite effect. In the Luangwa Valley, Zambia, in the first half of this century, the use of muzzle-loading guns became widespread, because the guns were a symbol of prestige. However, the adoption of this new technology reduced the hunting success of local hunters, compared to using traditional weapons like snares and poisoned arrows.

A simple assumption about profits is that:

$$\Pi = pqEN - cE \quad (12)$$

where Π is the profit from hunting, p is the price per unit of offtake (usually per individual killed) and c is the cost per unit of effort expended, for example the cost of a day's hunting. The yield from hunting, H , is qEN (Equation 3). Equation 12 implies that the total costs of hunting increase as population size decreases, because more effort is required to hunt low density populations. Equations 2 and 12 can be combined to produce a complete bio-economic model of the equilibrium state of the hunting system. A bio-economic equilibrium involves two separate equilibria, biological and economic. The biological equilibrium occurs the number exploited equals the population growth rate, so the population size is constant over time. The economic equilibrium occurs when the amount of effort expended is constant over time, because the individual hunters cannot improve their profits by increasing or decreasing their effort. One common assumption is that at equilibrium, profits are zero. This is not as strange an assumption as it appears, due to opportunity costs - zero profits mean that hunters are earning the same as they would earn in the best-paying alternative profession they could go into. At equilibrium, the population growth rate is zero because the population is stable. So we can write:

$$\text{Profits are zero: } pqEN - cE = 0$$

$$\text{Population growth is zero: } rN\left(1 - \frac{N}{K}\right) - qEN = 0$$

$$\text{Rearrange and substitute: } \Rightarrow N_{\infty} = \frac{c}{pq}, \quad E_{\infty} = \frac{r}{q}\left(1 - \frac{c}{pqK}\right), \quad (13)$$

where N_{∞} is the population size at equilibrium, and E_{∞} is the equilibrium level of effort. The solution, E_{∞} , is shown in Figure 9, along with the solution obtained under the assumption that instead of being zero, profits are maximised. This is denoted by E_{Π} and occurs when the distance between the revenue curve and the cost curve (revenues minus costs) is maximised. An important observation is that the profit-maximising solution occurs at a lower effort level (and so a higher population size) than the zero-profit solution. It also occurs at a population size above the MSY level. Hunting at the MSY level was a standard management recommendation until recently. We have seen that it is an unsafe strategy biologically, due to the semi-stable nature of the equilibrium. We now see that it is not likely to be the most profitable strategy either. The inclusion of the costs of hunting, which increase as stock size decreases, means that maintaining a larger population size is a better strategy for the profit-maximising hunter than hunting at MSY. Hunting at MSY is only the profit-maximising strategy if costs are zero or unrelated to population size. Otherwise, MSY will be neither be popular with conservationists nor adopted by hunters, however convenient it might be mathematically.

The zero-profit equilibrium E_{∞} is sustainable, in as much as it is a stable equilibrium if the environment is deterministic and the stock-production relationship is smooth. However, hunting at the zero-profit level is unsatisfactory both for biological and economic reasons. The resource is biologically over-exploited if the equilibrium point is on the descending portion of the revenues curve, which happens if hunting costs are sufficiently low. The

population might be in danger of sudden collapse from stochastic events, and in any case the productivity of the resource will be very low. Also, it would be more economically efficient, both for the hunters and for society, if the profits from hunting were maximised, rather than being dissipated. When benefits from the resource are being lost, the resource is considered economically over-exploited.

The key determinant of whether hunters maximise profits or dissipate them is the **market structure** of the industry. One extreme of market structure is when a sole owner has full control of the resource and can set the hunting level - a **monopoly**. In this case, the producer can choose any price to charge, knowing that the amount of the good that consumers will buy depends on the price set. The owner could be a private individual, a community or the state. A likely aim of a sole owner is to maximise profits, and thus to hunt at the profit-maximising equilibrium E_H . We are making important assumptions here, particularly that prices are fixed at a constant value and that there is no time dimension. The other extreme is that the resource is **open access**; anyone can hunt it. This leads to the other extreme of hunting at E_∞ , because as long as there are profits to be made, new hunters enter the industry. If losses are being made, some hunters leave the industry. The equilibrium number of hunters, and so the equilibrium effort level, is when profits are exactly zero. Open access hunting is also known as hunting under conditions of “**perfect competition**”. The price in an open access market is generally lower than the price in an equivalent monopoly market.

Quite specific conditions must be fulfilled if an industry is to operate at the extremes of either monopoly or perfect competition (Begg et al 1984). In order for perfect competition to exist, individual buyers and sellers must have no influence at all on the market price for the good. Then an individual can just assume that the price of the good is given, however much of it they personally buy or sell. This happens when there are a large number of individual buyers and sellers, each selling an identical product. Many cases of small-scale hunting probably fit this scenario fairly well. Monopoly markets are found wherever there are barriers to entry into resource hunting, which may be caused by the type of resource, or by regulation or legislation. Most markets are somewhere between these two extremes of monopoly and open access, although they usually resemble one or the other more closely. In particular, a competitive market can develop even when there are only two producers present, if they are engaged in a price war which drives profits down to zero.

The bio-economic models described so far give a static result rather than a dynamic equilibrium. In other words, there is no mention of time; in particular there is no account taken of how long it might take to reach equilibrium. Time is important, because resource owners trade off present and future revenues. Another way to describe market structure is to incorporate time preference (Clark 1990). Under perfect competition, producers are effectively placing a value of zero on future revenues. If the resource is open to anyone who wishes to exploit it, then the hunters look only to short-term gains and have no interest in increasing future productivity, because individuals that one hunter leaves to replenish future stocks will simply be exploited by another. Thus the effort level is E_∞ , the open access equilibrium shown in Figure 9. Monopolists are able to profit-maximise over time, because they are sure that the increased future yields will be there for them and will not be taken by someone else. Thus a monopoly hunter should preserve a larger population size than an open access hunting system. How much larger the population size is depends on the monopolist's discount rate (the rate at which value declines over time; equivalent to an interest rate). A person with a zero discount rate would hunt at E_H . E_H is thus the most conservative effort level, which is only adopted by hunters who value the future equally with the present. With a

discount rate between zero and infinity (as is usual), the optimal population size depends on the discount rate - the higher the discount rate, the lower the optimal population size. An important point raised by Clark (1973) is that it can be in the long-term interests of the sole owner of a exploited population to hunt it to extinction. This only happens under rather special conditions, the main one being that the growth rate of the population is always below the prevailing interest rate in the economy. This could be a problem for very slow-growing resources, that potentially will never yield a competitive return on an owner's investment. The rapid depletion of the population is then an economically rational act.

3.2 Individual decision-making about hunting

An individual hunter is working within the framework of a market, and is exploiting a resource that others may also have access to; these considerations have important implications for sustainability. But the way in which individuals make decisions about their hunting behaviour may also have important consequences; for example how they decide where to hunt, how many to hunt on a given day, and how they react to regulations about hunting. In this section we discuss the foraging theory approach to predicting hunting behaviour, and how economic models can be used to predict hunters' reactions to law enforcement.

3.2.1 Foraging theory

One important type of model for individual decision-making comes from optimal foraging theory. The theory was developed in behavioural ecology, to examine how animals might be expected to behave when foraging to maximise their biological fitness (Krebs & Davies 1991). Fitness is not measured directly, but a currency assumed to approximate to fitness, such as the rate of energy intake whilst hunting, is assumed to be maximised. Most of the models that have been used only consider maximising hunting rate over the short-term. The theory has been successfully used to analyse the behaviour of foraging people. Precise predictions can be made about foraging decisions, such as which prey types a hunter should hunt and which ignore, when a forager should move on from one patch to the next (Kaplan & Hill 1992), what size groups hunters should forage in (Clark & Mangel 1986), and how the arrival of more efficient hunting technology might influence these decisions (Alvard & Kaplan 1991).

These studies have some important messages for conservation. There has been a tendency amongst some anthropologists to create an image of the "ecologically noble savage" (Redford 1990), whose resource use decisions are assumed to be based on the motive of conserving that resource. Detailed studies of hunting and gathering decisions have used the framework of foraging theory to show that this is not the case (Alvard 1993). For example, it has been observed that Amazonian hunters typically do not hunt in depleted areas, which are usually areas close to settlements. They usually move on to new areas when the vicinity is getting depleted of prey. This is consistent with conservation, but is also consistent with optimal foraging models, which predict that hunters should not spend time in less profitable areas (Hames 1987). However, if hunters are simply maximising hunting returns, they should always take prey from the depleted areas opportunistically as they pass through, which is what they have been shown to do (Alvard 1995). Further, these models, based ultimately on fitness maximisation, stress that traditional populations must be seen as groups of individuals, where each person is trying to maximise individual fitness or the fitness of very close kin. Evolutionary models do not predict that such individuals will make sacrifices for the good of the wider group. A more likely explanation for the many examples of traditional foragers hunting resources sustainably is limited technology, low population growth and distance from markets. There are also examples of traditional communities cooperating to set rules limiting

hunts in places where resource scarcity has become an issue (McCay & Acheson 1990), but this involves individual fitness maximisation as well; the members of a small closed community are likely either to be relatives or to have long-term interactions with each other. Relatives may cooperate because helping kin also increases an individual's fitness. Game theory predicts that unrelated individuals within communities will cooperate to keep hunting sustainable only under rather specific conditions. Important considerations that determine when cooperation is likely to develop and be stable are:

- When there are few people involved, so that deals can easily be struck and compliance monitored.
- When there is communication between individuals.
- When the "game" between the same individuals is iterated over time, not just played once.

Thus theory suggests that small communities that interact with each other over a long period of time are the most likely to develop rules promoting sustainable hunting. These results mirror those found by researchers working on the evolutionary stability of reciprocal altruism in animal populations (Trivers 1971). Recent initiatives in conservation promote the idea that by giving communities control over, and benefits from wildlife (in the form of schools or clinics, for example), sustainability of wildlife use can be promoted. However, Gibson and Marks (1995) used a game-theoretic framework to illustrate how important individual, rather than community-based, incentives for hunters are: Individuals will only comply with rules that benefit the community as a whole if the benefits that they obtain **as individuals** outweigh their costs (Mesterton-Gibbons & Milner-Gulland 1998).

3.2.2 *Law enforcement and the economics of hunting*

Many of the crucial questions about how to make resource use sustainable revolve around illegal exploitation. The options for a manager of a resource that is being illegally and unsustainably exploited include attempting to stop the resource use entirely; legalising the resource use and then trying to find ways to regulate it at sustainable levels; and attempting to contain illegal resource use at sustainable levels through law enforcement. The last option, though rather unsatisfactory, is the one that is usually arrived at *de facto*, when insufficient funds lead to imperfect enforcement. Game theory can be used to model the incentives for people to break the law, particularly when members of the same community are both law-breakers and law-enforcers. Mesterton-Gibbons (1993) describes a community irrigation scheme in which people take turns to guard the water supply, and members of the community have the opportunity to cheat by stealing extra water for their own crops. He uses game theory to show that whether stealing is optimal or not depends on how much extra benefit the stealers receive. If the probability of the supply failing is high enough, it is optimal to be trustworthy, even when there is no-one guarding the water supply.

A key component for understanding how different law enforcement policies work is the theory of how individual decision-makers chose whether or not to undertake an illegal activity. This has been studied in the economic theory of law (Becker 1968, Eide 1994). The theory was first developed to understand the behaviour of burglars in the USA. No empirical testing of its applicability to natural resource use has been carried out. However, the results of these studies do have direct relevance to the problems of resource management. A person's attitude to risk is an important determinant of the decisions they make. The most analytically convenient assumption to make is that people are **risk-neutral** - they calculate the monetary values of the possible outcomes of a risky decision, and weight them by the probability of occurrence to find the optimal decision. However, if people are not risk-neutral this is not a

valid approximation to their behaviour when considering whether to undertake a risky enterprise. People are generally risk-averse. Poor people who are barely surviving might be more prepared to take risky decisions, such as poaching in a Protected Area or hunting unsustainably, so as to survive. Those who are slightly better off are generally more risk-averse, tending to act conservatively. Usually only relatively well-off people are prepared to gamble, for example with new, perhaps more sustainable, methods of resource use.

A person's attitude to risk and uncertainty is a crucial determinant of the mix of activities undertaken; a risky high-return crime versus a safe, legitimate job. The amount of risk involved in the crime, and the amount of security in legitimate employment, varies with the type of crime and the social circumstances of the person involved. In general, a risk-averse person undertakes a greater proportion of legitimate activity than a risk-lover. As Cook (1977) pointed out, illegal activity also has a threshold caused by respect for the law and social opprobrium, which is not easily quantified and varies with the type of crime. In the economic theory of law, the law-breaker is seen as a rational utility maximiser in an uncertain world, i.e. as risk-neutral. There has been strong resistance to the idea that law-breakers act in a rational economic way (Eide 1994), but poachers are perhaps more likely than most to act this way, either because they are already hunting legally and are weighing up whether to take a bit extra, or because their social climate is relatively positive towards poaching, and they feel they have a right to hunt their local resources. Abbot & Mace (1999) describe how law enforcement aimed at regulating fuelwood gathering in Lake Malawi National Park came under strain for this reason. Most women have no source of fuel available to them other than firewood from the Park. Collecting wood from the Park is legal, provided an inexpensive permit is purchased from Park authorities. Due to the poverty of the women, the permits have to be extremely cheap. But the women resented any expenditure; they felt they had an historical right to collect wood in the area. As society in general agreed with the women's view, penalties for illegal wood collection were rarely imposed on transgressors. This meant that it was not economically rational for women to purchase permits, and they rarely did so. Eventually the Park scaled down enforcement of the permit scheme.

Factors likely to reduce the crime rate are an increase in the perceived probability or severity of punishment; a decrease in the profits made from the crime; or an increase in the opportunity cost of crime through improved wages elsewhere. Studies seem to show a strong deterrent effect of the probabilities of being caught and convicted, but are contradictory as to whether the severity of the sentence has a deterrent effect. It is the perceived severity of the sentence before the crime is committed that is the relevant factor affecting incentives to commit crimes. If a prison sentence is given, the person's discount rate and time horizon (the distance into the future they look) affect the sentence's perceived severity. With a positive discount rate, one year in gaol with a probability of 0.2 is a worse option than two years with a probability of 0.1 (Cook 1977), because the second year in prison is valued less highly than the first. With a short time-horizon, 10 years in prison may look exactly the same as 5 years. This discounting, together with the empirical evidence, suggests that with a limited budget, it could be better to concentrate on increasing the perceived probability of detection than to spend the same amount on housing prisoners for long periods.

Natural resource users' attitudes to law enforcement measures have been little-studied. Sutinen & Gauvin (1989) showed that the rate of violation of regulations by lobster fishermen in Massachusetts varied with the perceived probability of detection and conviction, as predicted by the theory. Freehling and Marks (1998) show how hunter behaviour in the Luangwa Valley, Zambia, has changed as law enforcement has increased. They now tend to

use less easily detected snares, rather than guns, and are more secretive in their consumption of meat. Simple bio-economic models of hunting can be altered to incorporate the risk of capture and a fine into the costs of hunting (Sutinen & Anderson, 1985). Mazany, Charles & Cross (1989) modelled the likely extent of illegal fishing in a situation where there was a legal fishing quota, with imperfect enforcement. People who fish above their quota face an expectation of a fine, expressed as the fine received multiplied by the perceived probability of receiving it. The hunter's short-term profit-maximisation (in an open-access situation) then becomes:

$$\max_E [pH - cE - \theta \mathcal{J}] \quad (11)$$

where p is the price per unit of output, H ; E is all the inputs to production, not just effort; c is the cost per unit input; and θ is the probability of receiving the fine \mathcal{J} . θ is assumed to depend on the amount of input E . \mathcal{J} can be expressed as a function of either input or output. The profit-maximising condition found by Mazany, Charles & Cross (1989) for Equation 11 was:

$$pH_E = c + H_E [\theta_H \mathcal{J} + \mathcal{J}_H \theta] \quad (12)$$

where H_E means the partial differential of H with respect to E . This is equivalent to the profit-maximising condition found for the standard model, but with the addition of a term for the marginal change in the expected fine with a change in the output H . The mathematical analysis assumes that the decision-maker is risk-neutral, because it assumes that the cost of the fine is the expected monetary value of that fine; we have already seen that reality is more complex than this. The model also assumes that the actual fine and the probability of capture have equal weight in calculating the expected fine, implying that the policy-maker can increase the expected fine in two, equally good, ways - increase the probability of capture or increase the fine. As increasing the probability of capture is expensive, the strategy of lobbying for increased penalties has been a common reaction of wildlife authorities to unsustainable poaching (Leader-Williams & Milner-Gulland 1993). But the socio-economic studies discussed above suggest that the best strategy to achieve effective law enforcement is to increase the perceived probability of detection. This whole discussion is made more complex by the involvement of several authorities, with different priorities and budgetary arrangements. Crime-reduction initiatives taken by law enforcement officials may not be supported by the judiciary in sentencing. For example, in Zambia, concern about the loss of elephants and rhinos, and about ivory and horn trafficking, led the government to introduce mandatory 5-15 year prison sentences for elephant and rhino poachers in 1982. After 1982, magistrates did tend to deliver more prison sentences to elephant and rhino offenders, but not all of them received prison sentences. Those that did receive prison sentences received only short ones, of a few months. The maximum length given over the first 3 years of the new law was 36 months. The legislation that was required to increase the penalties was slow and difficult to enact, meeting much opposition. Once in place, it has been widely ignored by the magistrates, and has failed to curb poaching. The rhino population of the Luangwa Valley declined rapidly to near-extinction over the same period as the new legislation was coming into force (Leader-Williams et al 1990).

3.3 Assessing the economics of bushmeat hunting

3.3.1 Previous studies

Much less work has been published in the conservation literature on the economics of bushmeat hunting than on the biological sustainability of hunting. This is also true in the fisheries literature; research on the behaviour of fishers and the dynamics of markets for fish has a much lower profile than that on fish stock dynamics. However, if the system is to be fully understood so that adequate assessments of sustainability can be made, then the economic and social sides of sustainability must also be considered.

Many of those studies that do exist report the quantity of bushmeat found in a market. They usually break this down by species and report quantities over time or in different markets in the area (e.g. Juste et al. 1995). On its own, such information tells us little. If quantities found in a market can be related to the offtake of hunters from a particular area, then the information can be used in an assessment of biological sustainability (see section 2). However, it is still virtually useless for assessing economic sustainability. The biological analogy would be collecting data from an area on population density alone; this is crucial data without which one cannot go any further, but by itself is not useful.

Other studies look at bushmeat demand on a household level, assessing the amount of meat that a household eats in a given period (e.g. Wilkie & Carpenter 1999, Njiforti 1996). This is another useful measure of current offtake that can be used to assess biological sustainability (as done by Njiforti 1996), but in itself says nothing about the dynamics of demand. The main case in which it is necessary to obtain estimates of household bushmeat requirements is when hunting has a subsistence component, rather than being purely for sale or exchange. Even then, it is the households of the hunters that are relevant, not the households of purchasers.

Clayton et al. (1997) calculate the long-term equilibrium population sizes of two wild pig populations under open access harvesting. Thus their model does involve both the economic and the biological sides of hunting. They identify transport costs as key determinants of the equilibrium wild pig population size and hunting level. However, they assume a constant price of wild pig meat in their calculations; although their short run market observations did suggest that this was the case (Clayton & Milner-Gulland, in press), longer run data on the market are needed to give a full picture of the supply of and demand for wild pig meat in their study system.

A number of researchers have collected data on hunter behaviour, showing how individuals choose which animals to target and how they make use of their hunting areas. These data are often suggestive of the impacts of hunting on surrounding animal populations, typically showing depletion near villages, or changes over time in the distance that hunters need to travel to catch their prey. They can also illustrate the effects of changes in technology on offtake rates. Good examples of this kind of study are Marks (1994), Alvard (1995), Collet et al (1994) and Hofer et al. (in press). These studies can be very useful in assessing hunter effort, and showing how various factors (such as law enforcement) can influence it. But these results at the individual level need to be translated up to the market and population levels before they become useful for assessing overall sustainability: how many individuals are likely to wish to go hunting at a given set of market prices and hunting costs, and how does the total number of hunters interact with the price of the good and the quantity on sale in the market? How does the behaviour of all the hunters in the area interact with the population sizes of their prey? Milner-Gulland & Leader-Williams (1992) use an analysis of the costs

and benefits of ivory hunting at the level of the individual gang to predict how many elephants and rhinos would be left in the Luangwa Valley area of Zambia at the open access equilibrium. However, their job was made easier by the fact that ivory is an internationally traded good, so that the quantity of ivory removed from one area is unlikely to affect the price; thus a fixed price could be assumed. If bushmeat hunting is for the local market, then this is unlikely to be the case.

Other studies have assessed the impacts of external factors on hunting effort, and thus have direct relevance to policy. For example, Jachmann & Billiouw (1997) and Martin (1996) looked at the effects of law enforcement spending on elephant and rhino poaching. They showed that there was a direct relationship between spending on informant networks and the number of hunter arrests (used as a proxy for the amount of poaching activity). Dublin et al (1995) looked at the effect of spending on law enforcement in general on detected poaching rates, and found that there was a positive effect. The main problem with this kind of study is that the rate of illegal hunting detected is not a suitable proxy for the actual illegal hunting rate: At low levels of law enforcement, detection rate will be low and hunting rate high, while at high levels of law enforcement, detection rate will be high but hunting rate low. Other studies looking at the impact of external changes on hunting effort include Ayres et al. (1991), who looked at the effects of a new road on hunting yields and diets, and Wilkie et al (1992) who assessed the effects of a logging concession on hunting rates.

The requirements for a full economic analysis of bushmeat harvesting are rather extensive, and I have yet to see a study that carries one out. However, even if a particular study does not aim to carry out a full analysis, it is useful to know which kind of data to collect so as to allow future researchers to carry out studies on other aspects of the system. One way to approach the issue is to divide it into two components; studies of the incentives facing individual hunters and studies of the dynamics of the market and consumer choice. Broadly these can be thought of as addressing the supply side and the demand side of the market. The way in which individual incentives translate up the the market level depends on the market structure. This also needs to be addressed.

3.3.2 Market structure

As the market structure is an overriding influence on how hunting proceeds, it is useful to assess it first. Generally, bushmeat hunting would be expected to be competitive, leading to **open access** behaviour (see section 3.1.4). It is probably a fair assumption that open access conditions prevail unless there are obvious barriers to entry into bushmeat hunting. These might include community-level controls such as the handing down of a gun through a lineage with hunters only being allowed to operate after training by the previous owner of the gun (Freehling & Marks 1998) or intimidation by other hunters (such as is practised by lobster fishermen in parts of the USA, McCay & Acheson 1990). They might also include barriers such as access to capital to buy equipment to hunt or to transport the meat to market. If barriers to entry do exist, there may be imperfect competition operating, leading to hunters being able to make supernormal profits, and to a more complex analysis being required. Otherwise the system will tend towards an open access equilibrium, with profits at zero (so that there is no incentive to enter or leave the hunting profession and hunter numbers remain stable). Assuming an open-access equilibrium is precautionary, inasmuch as it predicts lower population sizes than would be expected with imperfect competition. If an assessment of hunter profits shows that they are not making super-normal profits, and that the total number of hunters in an area has remained roughly stable over time (despite individuals entering and leaving the industry) then this suggests that open access equilibrium has been reached. If

however, as is the case for wild pig hunting in Sulawesi (Clayton & Milner-Gulland, in press), dealers are making super-normal profits and the number of dealers is expanding rapidly, this suggests that the system is in disequilibrium and hunting pressure will continue to increase in the short term.

One important consideration is the structure of the **supply chain**. It is important to identify the decision-maker; the person whose incentives affect the number of animals killed. It is at this level that the economic analysis should be carried out. In the case of wild pig hunting, this is the dealer, not the hunter. The hunter can be treated effectively as an employee. In the case of elephant and rhino hunting, two types of poacher were identified; organised gangs who were hired by a middleman and were similarly best thought of as employees, and local poachers who themselves decided when to go hunting (Milner-Gulland and Leader-Williams 1992). If the trade structure is complex, with a number of middlemen and thus a number of different markets, analysis can be difficult; this is the case for internationally traded goods like ivory and rattan. In this case, it may not be possible to attempt a full assessment of trade economics and sustainability. If hunting is by local people for local consumption, with no complex supply chain, then market structure is relatively easily analysed and a full assessment is feasible.

3.3.3 *Individual hunter incentives*

A study of individual-level hunter incentives aims to estimate the **production function** of bushmeat hunting (how a given set of inputs is combined to produce a particular level of output). The production function is estimated for a particular hunting method; this is usually assumed to be the optimal method (because the hunters have chosen to use it), but if there are several methods in use, each could be assessed for its cost-effectiveness for different types of game (e.g. Noss 1997). A study of hunters' production functions can be used to assess the effectiveness of interventions at the individual level, such as banning a particular kind of weapon, increasing law enforcement patrols or preventing logging companies from allowing their vehicles to be used by hunters. However, effects of interventions at the individual level do not always translate up simply to the market level. By including information on prices, a study such as this can predict the profit that a hunter would make at a given price level. This prediction can then be combined with information on market structure and demand to make a full economic model.

The first issue to address is hunter behaviour; this affects how a given level of **effort** (or inputs) translates to a given level of offtake. In the simplest case, one could assume that hunters lay snares in an area and that for a particular species, the more snares that are laid, or the more individuals of that species there are in the area, the greater the offtake. Equation 3 shows a linear relationship of this kind. However, hunter behaviour cannot always be assumed to be this simple. If for example they stalk their prey and are able to maximise the chances of killing a particular species, then more complex formulations for the production function will be required. It is particularly important that when a hunter targets more than one species, all the species are included in this analysis; often it is found that when hunters kill several species together, the slowest growing species can be exterminated while the hunter is still making good profits from the other species (section 2.1.5.1). Similarly, if hunters change their selectivities as different species become more scarce (by actively targetting progressively smaller-bodied species, not just taking species in the proportion that they encounter them) this needs to be modelled in the production function.

Once the function relating a given level of inputs to a given level of outputs has been specified, then the next step is to put a **cost** on the inputs. Costs may be fixed or variable. In the case of bushmeat hunting, where technology is generally simple and people are self-employed, there are few fixed costs. This means that the costs can be expressed per unit of input (e.g. per day's hunting) or, more conveniently, per unit of output (per animal killed). Costs do not necessarily need to be expressed in monetary terms. If the hunting is purely subsistence, in a non-market economy, then it is perfectly feasible to express costs in terms of a metric such as time. But if the offtake will be sold or is a substitute for meat that would otherwise have had to be bought, then money is the best metric to use. If the hunter has a number of income-generating activities as well as hunting, it can be useful to compare the inputs and outputs from each of these activities, to gain an understanding of how the hunter determines how much effort to invest in each activity (e.g. Noss 1997).

In order to calculate the costs of hunting, each component of cost must be assessed and included. For example, in the case of wild pig hunting, data were collected on the costs of one week-long trip to buy wild pigs for sale in the market (Clayton & Milner-Gulland, in press). These costs (at 1995 prices and wild pig population sizes) are made up of:

Vehicle costs: Each trip costs the dealer approximately Rp 89,428 in fuel, parts, maintenance and amortised vehicle purchase costs.

Opportunity cost of time: The average wage/week for a person in the nearest alternative employment (owner of a medium-sized shop) is approximately Rp 70,000. Each trip involves a week's full-time work, as the dealer leaves home on Monday evening and returns home at 6am on Friday. He then sells from his house for a few hours on Friday and at the market all day on Saturday.

Food on trip and table in the market: Rp 10,500/trip.

Pay for hunters: The case study dealer pays Rp11,200 per pig to the hunters. Each dealer has approximately 33 hunters on his books (as there are 12 dealers and around 400 hunters operating in North Sulawesi). The case study dealer buys an average of 24 pigs per trip, paying Rp268,800. This represents an average weekly wage to a hunter of Rp8,145, and a yearly wage of Rp423,564. The hunters work in Gorontalo district, where the average wage is Rp462,850, very similar to the wage calculated for hunters.

String: The dealer buys string to give to hunters for snares. The hunters receive the string as payment, together with the money received per pig. Each hunter receives approximately Rp100,000 worth of string a year. Assuming 33 hunters per dealer, this gives a string cost per trip of Rp63,460.

Opportunity cost of capital: The major capital that the dealer requires is a truck. The cost of a truck is Rp3,300,000. This money could have been invested elsewhere. The rate of return on capital is assumed to be 20% per annum in Minahasa (the bank interest rate). The investment in the truck thus represents an approximate opportunity cost of Rp12,690 per trip.

At the open access equilibrium, when the hunters are just making enough to keep them in the profession, a hunter's costs should add up to the amount he is paid by the dealer. The equipment needed to make a snare is just string and natural materials, so their only cost is the opportunity cost of time; the time taken to walk into the forest and walk out again carrying the week's worth of pigs for sale to the dealer, and the time taken to set and check snares. This time cost is calculated from the average wage/week for an agricultural labourer.

If there are costs of law enforcement, these can be added into the calculation of overall costs. The costs of law enforcement could include both a penalty and the confiscation of the hunter's

kill. These costs need to be multiplied by the probability of being caught (section 3.2.2) and assumptions must be made about the hunter's attitude to risk and the monetary value of the penalty incurred (if it is a prison sentence, for example).

In the case of ivory hunting in Zambia, the cost to a middleman of mounting an ivory hunting expedition was calculated (Milner-Gulland & Leader-Williams 1992). One expedition was the unit of effort, and was assumed to consist of one gang (2 hunters & 6 carriers), on a one week trip, using one automatic rifle and one other weapon. This level of effort was assumed to enable the gang to kill every elephant it encountered. A linear relationship was assumed to exist between the elephant population size and the number of elephants encountered by the gang during the expedition (i.e. Equation 3). Given these assumptions about the production function, the costs of hunting were calculated as:

Opportunity costs of time: The total wage bill that the gang would command in the nearest alternative profession. The hunters were assumed to be able to command higher wages than the carriers. It might be appropriate to include a risk premium in the wage if there is a significant chance of a hunter being killed by a game scout; this means that a rather higher wage would be needed to attract a hunter into the profession than simply the wage in the nearest alternative (safe) profession.

plus

Costs of equipment: The guns and ammunition.

plus

Costs of law enforcement: In this system it was usual for the middleman to pay the fine incurred by their hunters if caught. So the cost of enforcement was the average fine payable per person multiplied by the number of people caught (most of the gang escapes, leaving an average of one person being caught) plus the cost of losing the output of the expedition through confiscation of tusks (calculated as the average number of tusks the gang is caught carrying) multiplied by the probability of the hunters being caught. This last parameter is actually the hardest of all to estimate, as it cannot be obtained directly from law enforcement data, which only gives the number of gangs detected, not the number that operate undetected. Instead it needs to be obtained from independent sources such as village heads or the hunters themselves.

These costs can be varied as other factors vary, such as the chance of being caught, the number of elephants in the area, or the cost of hiring a hunter (for example through improvements in local employment prospects). They can be compared to a given price per tusk to give an overall profit that the middleman would expect to make per hunting trip. If this is more than he could make by investing in some other activity (such as drug smuggling) it is worthwhile continuing to hunt. This model of the ivory trade (and the model of wild pig hunting) can then be linked to a calculation of biological sustainability by using a population model for the number of wild pigs/elephants in the area, and seeing at which population size the profit for a unit of effort are zero - this is the size towards which the population is tending.

The calculation of **revenues** obtained from hunting is straightforward if the hunter is selling his entire catch in a local or distant market; it is simply the price per unit of offtake multiplied by the amount of offtake. However, there is usually a spectrum from entirely subsistence

hunting through selling only the surplus after the household has taken their requirements to completely market-orientated hunting. Rather than selling for cash, a hunter may also exchange his kill for other goods. In the case of a purely subsistence hunt, the demand to be satisfied is generated purely by the households of the hunters, and money is an inappropriate metric to use to assess hunter incentives. The overall dynamics of demand can still be modelled, but in this case will be driven by processes such as human population growth rather than consumer incomes and preferences. The metric used to assess hunter incentives at the individual level might be time; the hunter may act to maximise offtake per unit of time invested, for example. If, as is often the case, hunter households consume a proportion of the meat and sell the surplus, then the revenues that the hunter obtains from the portion consumed at home can be estimated from the cost of the food that would have had to be bought if the bushmeat supply was not available. Money is still the appropriate metric to use. If hunters exchange bushmeat for other commodities, and these commodities have a price, then money can also be used.

A major assumption that is made in an equilibrium analysis such as the one for ivory poachers in Zambia is that the price is constant. As mentioned above, this is an adequate assumption when the harvest in the area concerned is a very small proportion of the total quantity of the good on the market. But if this is not the case (for example, the wild pig trade is being described in full; there is no other source of wild pig meat available), then the demand side must be considered.

3.3.4 Assessing market demand

As the quantity of bushmeat in a market changes, for example because of the increasing scarcity of a particular species, or because of an increasing number of people becoming hunters, then the price that consumers will pay for it also changes. Generally, as a particular good becomes more scarce, consumers would be expected to pay more for it, while if there is a lot of it on sale, they will pay less. The degree to which the quantity of bushmeat consumers buy varies as price varies is measured by the own price elasticity of demand. Consumers are also generally prepared to pay more for goods as their income increases; this is measured by the income elasticity. Finally, as the availability of substitute goods changes, so does the amount consumers are prepared to buy of a particular meat at a given price (see section 3.1.2). In this analysis, we assume that the person who makes the decisions about hunting levels (the “hunter” above) is also the person who sells the meat in the market (the “stallholder”), so there are no supply chain complexities.

In order to assess demand for a good, the following data are needed at the absolute minimum:

1. The total **quantity** of each species of interest on sale in the market.
2. The **price** of each species of interest on sale in the market.

Price and quantity data need to be collected over as long a period as possible; one-off market surveys give very little information about market dynamics. What they can tell us is: a) how profitable hunting currently is, if combined with data on hunter costs. This might give a hint as to whether hunting pressure is likely to continue to increase. b) what the current offtake level is, which together with population estimates and a population model gives an idea of how sustainable hunting is; thus whether the population is likely to continue to decline.

We are assuming a competitive market, so that the price charged by all stall holders should be about the same. This should be checked. If the system is still in disequilibrium, the price that

they can charge is higher than their costs, but at competitive equilibrium, the price that a hunter receives is the same as his costs. This is a useful comparison to make.

Data collection is complicated in the case of perishable goods like meat, which may drop in price at the end of the day; thus market prices and quantities must be assessed first thing in the morning. They should also be assessed by an inconspicuous monitor, such as a local woman doing her shopping. Ideally, she should buy a piece of each type of bushmeat, as quoted prices are not always the same as actual prices. However, ethical issues then emerge when the species in question is endangered.

In order to carry out a full economic analysis of the trade in bushmeat, so as to be able to assess the likely effects of conservation actions and how trends in the general economy will affect hunting sustainability, more data are needed. These include:

1. **The inflation rate.** This is crucial, as prices can only be compared over time when they have been deflated (ie the inflationary trend has been removed). Inflation affects all prices in the economy at once, and so it has a neutral effect overall, hence the need to remove it so that true trends in bushmeat prices can be discerned (e.g. because of increasing scarcity of bushmeat). Inflation rates in local regions can be rather different to the national published rates, for example if the economy of a particular region is linked to a particular sector of the general economy such as agriculture or timber. National rates are easy to obtain, local ones may be obtainable from local government statistics offices, or are even calculable directly from the prices of a representative bundle of goods.

2. The price of **substitute goods.** It can be difficult to decide *a priori* which goods people would be likely to buy as substitutes for bushmeat, but being too inclusive makes for an enormous data collection task. In some cases it is clear; for example domestic pig meat is a substitute for wild pig meat in Sulawesi. Asking consumers can help to clarify their preferences. Often the various bushmeat species that are harvested together are close substitutes; it is thus important in multi-species systems that data are collected for all the species that are harvested and sold together.

3. Consumer **incomes.** In a country without a developed statistical service, this can be incredibly difficult information to get. It is also rarely useful to obtain it at the national level, because bushmeat hunting often happens in areas which are poorer than the national average, and where the benefits of economic growth may be slow to trickle down. Incomes are often estimated in one-off surveys, but these are not very useful unless they are regular enough to be relatable to the collection frequency of the other data. While extremely difficult to get, income data are important, particularly if income changes seasonally (with harvest triggering a feast, for example) or if there is a trend or step change in income levels which may affect demand (perhaps caused by an integrated conservation and development project or a logging concession). If data are collected long enough before and after a policy is implemented, its effect on demand can thus be assessed.

Other variables may be important in particular markets; for example if the good is exported, exchange rates may be important, or if it is kept as a store of wealth (like ivory) interest rates may be relevant (Milner-Gulland 1993). However, the three listed above are likely to be the key ones for bushmeat markets. These variables only need be collected if a time series of market data is being collected, as without a time series, no full analysis can be carried out. The frequency of market monitoring then becomes an issue. Generally it is impossible to

record every piece of bushmeat sold, unless the market only happens once a week and all stallholders are present at the beginning of the day. Monitoring should be tailored to capture as much of the predictable variability as possible. For example, if there is a daily market but its size varies, then monitoring should sample each day of the week in order to get a true picture of the flow of bushmeat into the market, and then perhaps concentrate on the busiest day of the week on the assumption that the relative importance of a given day does not vary. If there is seasonal variability (for example due to changes in hunter availability with crop-growing commitments, or due to inaccessibility of hunting areas in rainy seasons), then each season needs to be sampled. In our wild pig study (Clayton & Milner-Gulland, in press), we have been surveying the main market fortnightly on a Saturday for 6 years, checking other days and minor markets monthly to ensure that there is no change in their status. This time series should be long enough to ensure useful results are obtained from the analysis. The general rule is that the more data points can be collected, the more power there will be in the economic analysis. It is particularly important to capture variability, for example in consumer incomes or meat availability, because it is only when quantities available and consumer preferences vary that the dynamic behaviour of the market can be seen - if there is no variability, the information received is not much more useful than a single point estimate.

Econometric analysis of demand is data-hungry, principally because there are many different factors that affect demand, all of which need to be included in a multiple regression, usually with several lags. This means that the data need to be collected over as long a period as possible to maximise the degrees of freedom available to the regression. It is also important to collect every piece of information at each time point, so that the data sets are comparable, and preferably to collect data at the same regular interval throughout. Holes in one data set can cause all the other other data sets to be discarded for that day, and when several lags are included in a regression, losing one data point can be very expensive. Interpolation can fill blanks to some extent, but should be kept to a minimum. I will not go into econometric analysis of market data, but a good text on the subject is Maddala (1989). It is not a simple process, but is basically a multiple regression, in which changes in the quantity demanded are related to the price of a good and other factors such as incomes and prices of substitute goods. The fully specified model, containing all the variables that might be important, is simplified until its explanatory power is significantly weakened by removing any more variables; the ones that are left are the key variables driving the bushmeat market. If the equation is specified in a particular way, the coefficients of these variables are their elasticities, which can then be used to interpret how changes in policy (for example by providing a cheap alternative meat source) would affect the quantity of bushmeat demanded.

4 APPLICATION TO THE BUSHMEAT INITIATIVE

4.1 Summary of data requirements

Below is a summary of data requirements for a full study of the biological and economic sustainability of bushmeat hunting. This is based on the previous detailed discussion of the data needs for answering specific questions in sections 2 & 3.

Biological Sustainability

1. Data on population density in the hunted area. This tells us little without comparative data, but is nonetheless the building block without which no further inferences can be made.

2. Data on unexploited population density in similar habitat. By comparing the two densities, it is possible to discern whether a population is depleted, but not to infer whether hunting is to blame or whether current hunting levels are sustainable.

3. Data on number of animals killed. This can be used to derive the hunting mortality that the population is experiencing. The number of animals killed must be expressed per time period and from a given area.

4. An estimate of the population growth rate. Preferably an estimate of the intrinsic growth rate or independent estimates of birth and death rates, with an assumption about the functional form of density dependence. Alternatively an estimate of the current population growth rate / birth and death rates.

5. Added value can be obtained by collecting data as a time series or for a number of similar sites under different hunting pressures.

Market structure

1. Can hunting be considered to be open access? Are there any barriers to entry?

2. Is the market at equilibrium? Have there been changes in numbers of hunters over time and/or profits made by individual hunters?

3. Description of the supply chain. Who is the decision-maker about hunting levels?

Supply side

1. The production function. How do hunters combine inputs to produce a given level of outputs? How do changes in effort level and prey population sizes affect output levels?

2. The costs of hunting, per unit of input or output. Divided into fixed and variable costs, and including the opportunity costs of time as well as costs of equipment. May include a cost from law enforcement activity.

3. The revenues obtained per unit of output by an individual hunter. Price may be fixed or determined by the market.

4. By combining 2 & 3, the profits of hunters can be obtained. These need not be expressed in monetary terms if the economy is purely subsistence.

5. The number of hunters currently operating, their hunting methods and overall offtake levels. This links to the biological sustainability data collection.

Demand side

If the bushmeat is sold in a market:

1. The total quantity of each species of interest on sale in the market.

2. The price of each species of interest on sale in the market.

If an analysis of market demand is to be done, a time series of 1 & 2 is needed, together with an equivalent time series of:

3. The inflation rate, local if possible.
4. The price of substitute goods.
5. Consumer incomes.

If the bushmeat is not sold or exchanged:

6. An estimate of household requirements to be supplied by the hunters.

If the bushmeat is exchanged for other goods or partly consumed at home:

7. The replacement cost of the bushmeat eaten or exchanged (i.e. the price of goods that would need to be bought to replace the meat in the household's diet or the price of the goods that it is bartered for).

4.2 Policy issues

4.2.1 General considerations

Many authors have discussed the policy alternatives that are available for increasing the sustainability of bushmeat hunting (e.g. Wilkie & Carpenter 1999, Feer 1991, Bowen-Jones & Pendry 1999). In practice, this often means finding a way to reduce offtake from its current level, at least for particularly vulnerable species. In order to reduce offtake, hunters' incentives must be changed so that it is no longer worthwhile to hunt at the previous unsustainable levels. There are two approaches to doing this; imposing **regulations** to prevent people from hunting as they otherwise would, or changing people's **opportunities** so that they decide that they would do better by hunting in a sustainable manner (or by leaving hunting for another profession, which also reduces overall hunting rates). In both cases, the costs of continuing to hunt as they do currently are increased, either actually (e.g. through fines) or via opportunity costs (e.g. a better option is available). Although the former is the usual approach for controlling large-scale commercial exploitation (e.g. many fisheries) and has been the usual approach to controlling hunting in protected areas in the past, it is not currently in favour.

Regulations require enforcement, and it is increasingly clear that if people have no incentive to abide by rules other than the threat of punishment, enforcement can be very expensive or ineffective. This is particularly true of laws protecting wildlife from over-exploitation when people rely on bushmeat for their livelihoods and the areas being policed are large, remote and have poor boundary control. On the other hand, regulations can be swift to implement, unambiguous in their intent and effective immediately. For example, it is apparent that the only way to control rhino poaching for the international market is first to protect them in small, highly guarded areas, and only then to find ways for local people to benefit from their presence. In the case of wild pigs in Sulawesi, one species is protected and highly endangered by hunting and the other can sustain a reasonable level of offtake. Current conservation initiatives are concentrating on firm enforcement of the law banning hunting of the endangered babirusa, which is possible because dealers can be arrested along the single road

which all must travel along to the market (Clayton & Milner-Gulland, in press). The circumstances under which the exploitation takes place thus determine whether regulation is a feasible option.

Regulations can be on the hunters themselves, on people that are facilitating their hunting activities (such as logging companies), or on people further up the supply chain such as middlemen or consumers. The point at which they are most effective is that at which they can best be enforced; this is often a bottleneck where there are few people involved. Thus if one logging company is required to change its policy towards hunters, this will have a much larger effect than targetting the hunters themselves. Similarly, targetting stallholders in markets may be more effective than targetting hunters. Note that regulations do not just include total bans on hunting, but also systems such as offtake quotas or limitations on the equipment that hunter can use. These too need to be enforced, and are unlikely to be suitable for most bushmeat harvesting systems, as they require a high level of management intervention in order to work (Milner-Gulland & Mace, 1998, discuss various regulatory options in more detail).

Changing people's incentives is the method by which hunting can be made sustainable in the long term. Regulations only work in the long run if people are prepared to enforce and abide by them. Methods that specifically aim to change hunter behaviour or consumer preferences by providing more attractive options include promoting alternative sources of income or protein and carrying out environmental education that highlights the non-market values of natural resources. This latter can (and probably should) be carried out alongside all other types of policy. Setting up economic enterprises that provide more attractive options than bushmeat hunting or consumption can be extremely difficult, as the enterprises must:

- Be mutually incompatible with unsustainable bushmeat hunting (e.g. ranching that relies on wild populations for seed individuals).
- Be not just profitable with respect to the general economy but **more** profitable than bushmeat hunting (otherwise the opportunity costs of carrying out the new activity are too high for it to be worthwhile).
- Be attractive to the individuals who are making the decision to go bushmeat hunting, not just to the community as a whole or to non-hunting members of the community. Individual hunters may not be interested in supporting an initiative that doesn't offer advantages to them personally (Mesterton-Gibbons & Milner-Gulland 1999).
- Be financially viable in the long term, without continued external support, and be robust to likely changes in circumstances in the area (such as increases in incomes, increased linkage with the general economy and inward migration, perhaps even caused by the project's success).

These issues have been addressed by a number of authors. For example, Oates (1995) describes a conservation project that aimed to provide an alternative income for local residents; it caused large-scale immigration to the area, which led to even more environmental damage. Thus projects that involve improving people's incomes can be successful in altering incentives at the individual level, but at the market level can increase environmental damage by making the area more attractive to newcomers. Community dynamics can be extremely important to the success of these projects. For example, Solis Rivera and Edwards (1998)

discuss an iguana ranching project that generated income and had positive social effects, but was threatened by internal divisions within the village. Gibson & Marks (1995) discuss how the ADMADE scheme in Zambia was effective in bringing benefits at the community level, but did not succeed in deterring individual hunters from continuing to hunt, as they saw no benefits coming to them as individuals.

4.2.2 Summary of the effects of policies to increase hunting sustainability

In Table 1, I list some of the approaches that have been suggested to improve the sustainability of bushmeat hunting, including those suggested by Wilkie & Carpenter (1999) and Bowen-Jones & Pendry (1999). In the table I show who is targetted by the policy, where in the economic system the approach has its effect, and whether it is the type of approach that relies on regulation or persuasion. If the approach requires enforcement, I show whether this can be carried out by the local community or whether it is more easily done by external agencies such as government officials. If the local community can enforce its own regulations, this has the advantage of allowing control of resource use to be devolved; if local communities have control of the process, regulation may be better accepted by local people. Finally, I list some of the major pros and cons of each policy. As can be seen from the table, each policy does have both advantages and disadvantages, and most are not mutually exclusive. Which policies are best depends on the particular situation in which they are to be used.

5 CONCLUSIONS

In this report, I have covered the broad issue of assessing the sustainability of bushmeat harvesting. This has two facets, biological and economic. Both need to be considered if a full understanding of the dynamics of bushmeat hunting is to be obtained, and thus if conservation policies are to be effective. Too often people consider the biological side in isolation. Offtake levels are determined by the action of many individuals; hunters, dealers and consumers, whose incentives need to be understood if changes the level of offtake is to be predicted. Although a full assessment is ideal, there are a number of types of information that can still be useful in a preliminary assessment of the situation without necessarily carrying out a full analysis. In this report I have highlighted the use that each individual piece of information can be put to, and suggest which types of data are indispensable and which can be left to future studies if time and money are short.

Bushmeat hunting is a complex process. It often targets a number of species, with differing resilience to hunting. Protecting particularly threatened species without destroying the livelihoods of people who rely on bushmeat is a problem that particularly needs addressing. A number of the policies available to conservations are able to distinguish between species, and may be particularly useful in this case. On the economic side, bushmeat hunting for local markets is relatively simple to address, compared to hunting that supplies a market with a complex supply chain. In the latter case, expert analysis will be necessary.

I have devoted a lot of space to the theoretical underpinnings of the techniques that are used to assess hunting sustainability. I feel that this is important, because many conservationists do not have a background in economics or population ecology, where these theoretical issues are raised. However, without a theoretical underpinning, discussions about which policies work and why tend to rely on opinion or particular cases. The case-by-case approach, although it

can be useful, does not help to build a framework within which new information and experience can be placed.

Finally, it is important to consider the scale at which processes operate to determine hunting sustainability. These include the level of the individual hunter, the community, the market and finally the national and global economies. Although we can have a lot of influence at the smaller scales, there is little that a project to promote bushmeat hunting sustainability can do to affect events at larger scales. As the linkages between each scale get stronger, these larger scales (national, global) will have more and more influence at the local level. For example, the economic crisis in Asia in 1998 clearly influenced the behaviour of rattan collectors in the forests of North Sulawesi, causing them to turn to gold panning instead (Clayton et al., in press). This is not a reason to stop attempting to influence sustainability at the local level; rather it highlights the increasing importance of taking economics into account when considering the sustainability of bushmeat hunting.

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Table 1. A summary of policies for increasing the sustainability of bushmeat hunting and their effects.

Target	Policy	Effect	Type	Local?	Pros	Cons
Logging company	Reduce access to hunters (use of company vehicles, roads)	Increase hunter costs (of transportation to market and to hunting site)	Regulation or persuasion (by govt on company)	No	Easy to implement (small number of companies involved), may have impact on large scale	Top-down approach, relatively short-term
Logging company	Reduce demand for bushmeat by employees (e.g. provide food)	Reduce hunter revenues (demand decreases, so price does)	Regulation or persuasion by govt on company	No	Mitigates impacts of immigration. Easy to implement, may have impact on large scale.	Doesn't address general wealth and/or population increases in the area due to company presence.
All	Education & awareness	Change preferences	Persuasion	Ideally	Can change situation permanently. without need for continual management. Relatively cheap	Not always effective in short term. Individual responses differ. Changing culture/imposition of other values.
Stallholders	Market inspections and arrests for illegal meats	Increase stallholder costs.	Regulation	No	Can be very effective, particularly if few markets. Message clearly sent on which meats are acceptable to sell, which not.	Trade may shift location. Regular inspections needed on continuing basis.
Consumers/Hunters	Promote alternative protein sources (e.g. smallstock rearing)	Increase opportunity costs of hunting; provide substitute good.	Persuasion	After initial phase	May be sustainable in long term, if alternative continues to be better option than hunting.	Link between conservation and livelihoods removed. May be slow to implement.
Hunters/dealers	Checkpoints on roads (confiscation, arrest or taxation)	Increase hunter costs	Regulation	No	Very effective if cannot be circumvented. Can target endangered species.	Must be continued regularly and indefinitely.
Hunters	Limit weapon types that can be used	Decrease hunting efficiency so increase hunter costs	Regulation	Can be	Protects traditional way of life. Can target endangered species.	Not long-term solution; clock can't be turned back. Imposing unnecessary inefficiencies is not best approach to the problem except for protecting endangered species.
Hunters	Restrict hunting effort (locations, seasons)	Decrease offtake	Regulation	Can be	Should have direct effect on wildlife population sizes. Can distinguish between species.	Needs continual monitoring.
Hunters	Offtake quotas	Decrease offtake	Regulation	Can be	Direct link to biological sustainability. Can distinguish between species.	Needs high level of management.

Hunters	Ownership allocation (to indivs or communities)	Change market structure	Regulation	Can be	Long-term solution.	Over-exploitation can still occur. Often impractical in forest ecosystems.
Hunters	Patrolling protected areas (arrests, snare removal)	Increase hunter costs	Regulation	Can be	Clear statement. Can protect populations directly.	May be resented by local community. Must be continued regularly & indefinitely.
Hunters	Increase bushmeat production (ranching, food supplements)	Increase offtake rates	Neither	Can be	Improves livelihoods. Direct link between production and forest conservation. Can promote community-level conservation.	May distort ecosystem dynamics for other species. May just increase profitability of hunting, so increasing hunter numbers. Ranching better as more control possible.
Hunters	No-take areas	Increase offtake rates. Buffer against overharvesting	Regulation	Can be	Buffers against uncertainty & error. Clear designation of zones aids enforcement.	Still needs enforcement. Resentment likely if imposed. Yield improvements not guaranteed.

Figure legends

Figure 1. Curves of the logistic equation. a) Sigmoidal population growth, as described by the logistic equation. b) The parabolic relationship between the population growth rate and the population size.

Figure 2. The equilibrium population sizes under various hunting rates. The solid lines represent the number of individuals removed from the population at particular values of H . The dashed line is the population growth rate at a given value of N . The equilibrium population sizes occur when the number of individuals removed by hunting is equal to the population growth rate (where the growth curve and the hunting rate curve intersect). Three hunting rates, H_1 to H_3 , are shown for each hunting strategy. a) Hunting removes a constant number of individuals. b) Hunting removes a constant proportion of the population.

Figure 3. Stability analysis for the equilibrium population sizes shown in Figure 2. a) Hunting removes a constant number of individuals. b) Hunting removes a constant proportion of the population.

Figure 4. The yield-effort curve for a population with logistic growth.

Figure 5. The effect of non-critical depensation (the Allee effect) on the parabolic relationship between the population size and the rate of population increase. a) Harvesting a proportion of the population each year produces two equilibria, N_1 and N_2 . b) The yield-effort curve for non-critical depensation. If the effort level increases above E' , yield declines rapidly and effort must be reduced to E_1 in order to allow the population to recover above the unstable equilibrium level N_1 .

Figure 6. The relationship between the sustainable yield calculated by the Robinson & Redford method and the true sustainable yield for a population with simple logistic growth in discrete time. The graphs show the degree to which the Robinson & Redford method over- or under-estimates true sustainable yield (the difference in yields as a proportion of carrying capacity) as a function of the intrinsic rate of population increase, λ . The results are displayed for 4 population densities, expressed as a proportion of carrying capacity, ranging from 10% to 100% of K . Three levels of the Robinson & Redford natural mortality factor are shown: a) Factor = 1, so that there is no correction to their calculation of maximum production to account for natural mortality. b) Factor = 0.6, the value they suggest for short-lived species. c) Factor = 0.2, the value they suggest for long-lived species. Note the different scales of the y-axis between the 3 graphs.

Figure 7. The market model of supply and demand. The supply and demand curves intersect at the market equilibrium. The equilibrium price, P_E , and quantity demanded, Q_E , are shown.

Figure 8. Inelastic and elastic demand curves. If demand is inelastic, a small change in price leads to a small change in quantity demanded, while if demand is elastic, a small change in price leads to a large change in quantity demanded.

Figure 9. Equilibria for the bio-economic model. Revenues are related parabolically to effort, while costs are linearly related to effort. Profit is the area between the two curves (Revenues - Costs). The equilibria shown are the profit-dissipating equilibrium E_∞ and the profit-maximising level E_{IT} .

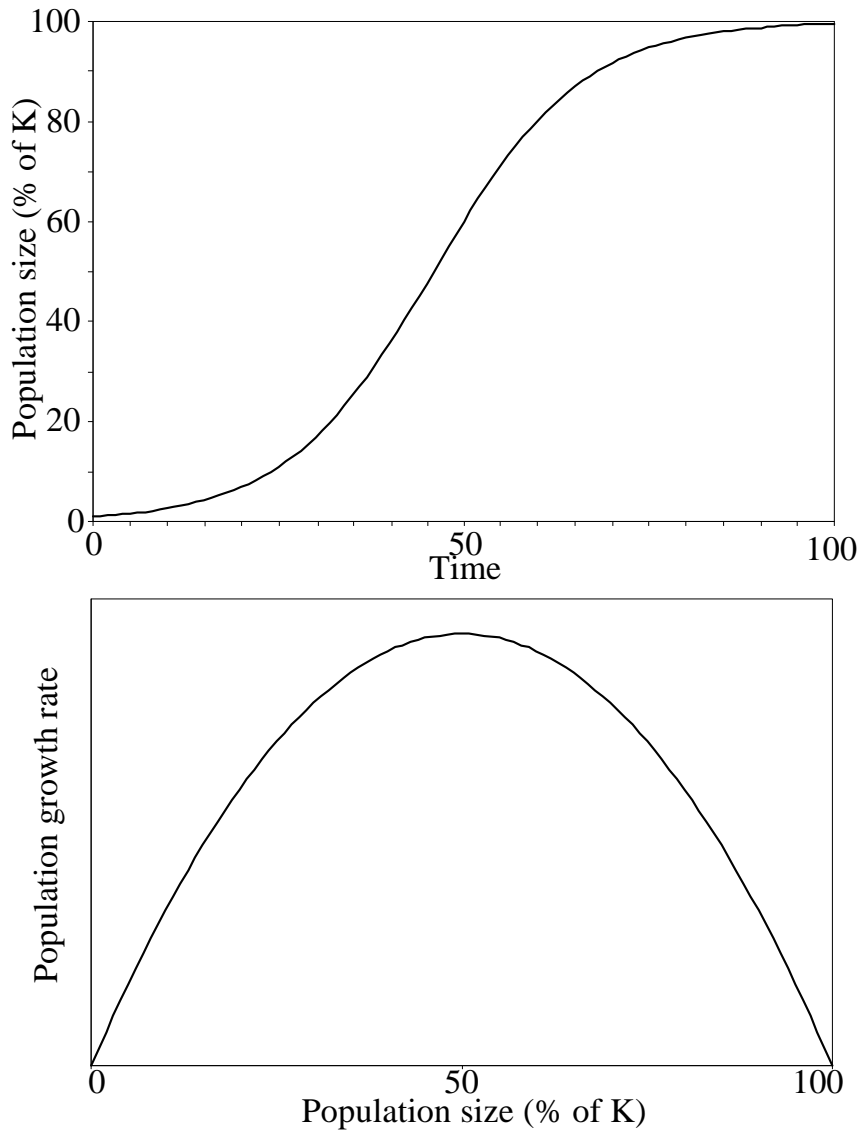


Figure 1. Curves of the logistic equation. a) Sigmoidal population growth, as described by the logistic equation. b) The parabolic relationship between the population growth rate and the population size.

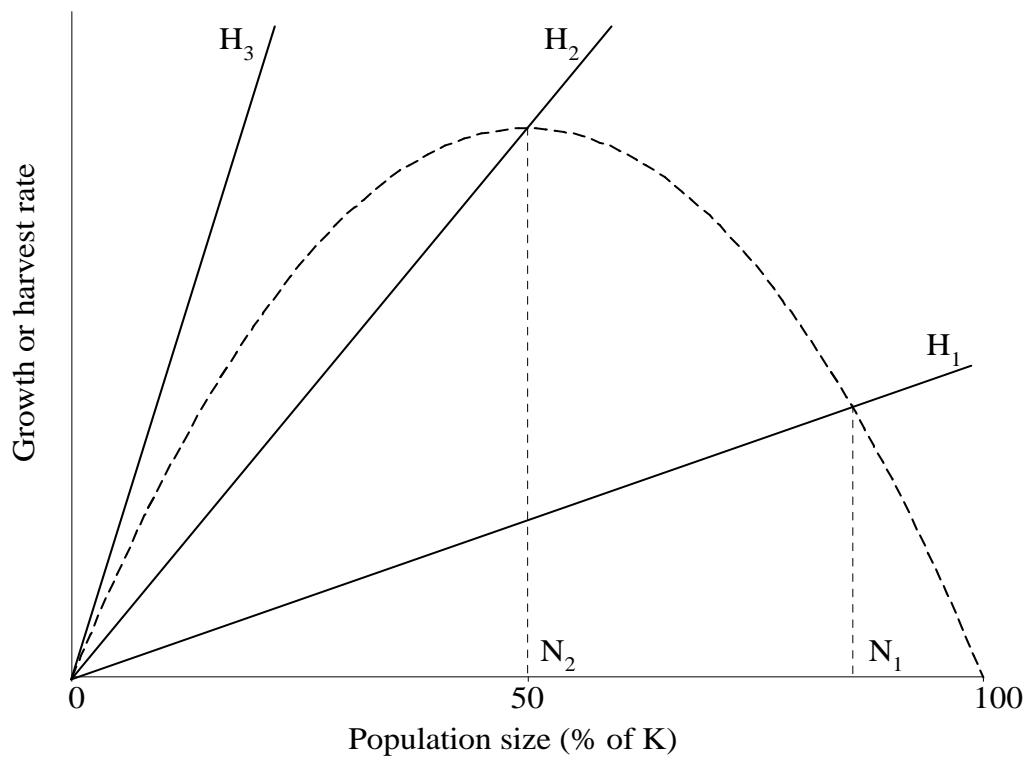
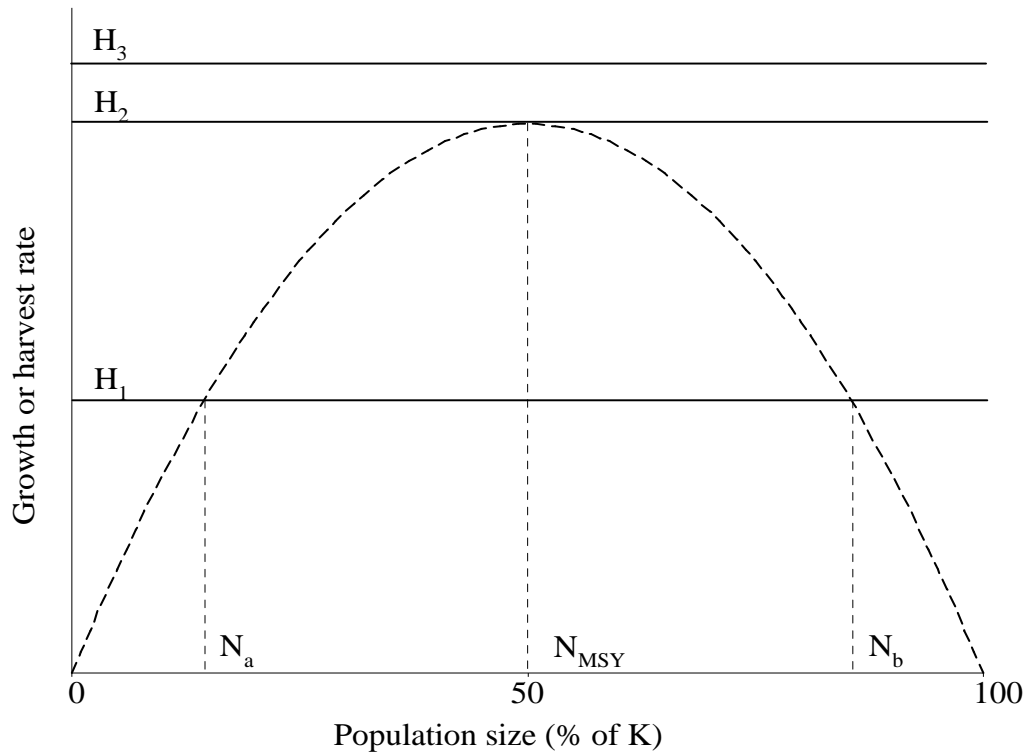


Figure 2. The equilibrium population sizes under various hunting rates. The solid lines represent the number of individuals removed from the population at particular values of H . The dashed line is the population growth rate at a given value of N . The equilibrium population sizes occur when the number of individuals removed by hunting is equal to the population growth rate (where the growth curve and the hunting rate curve intersect). Three hunting rates, H_1 to H_3 , are shown for each hunting strategy. a) Hunting removes a constant number of individuals. b) Hunting removes a constant proportion of the population.

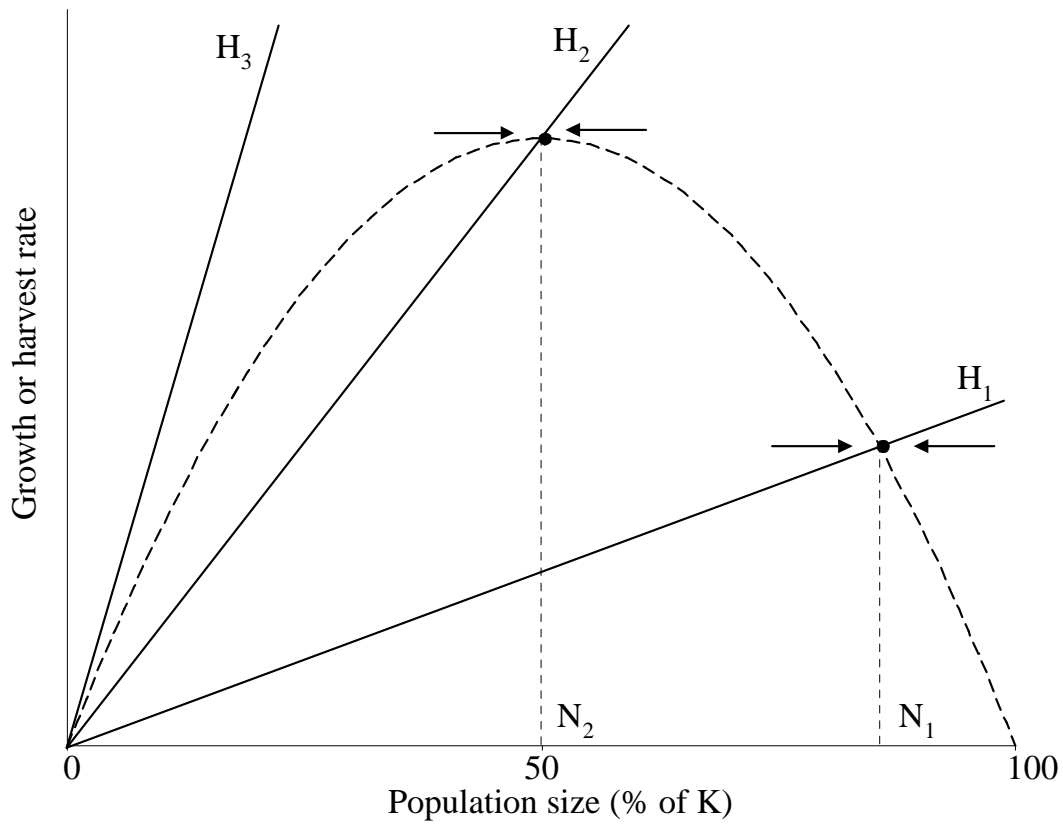
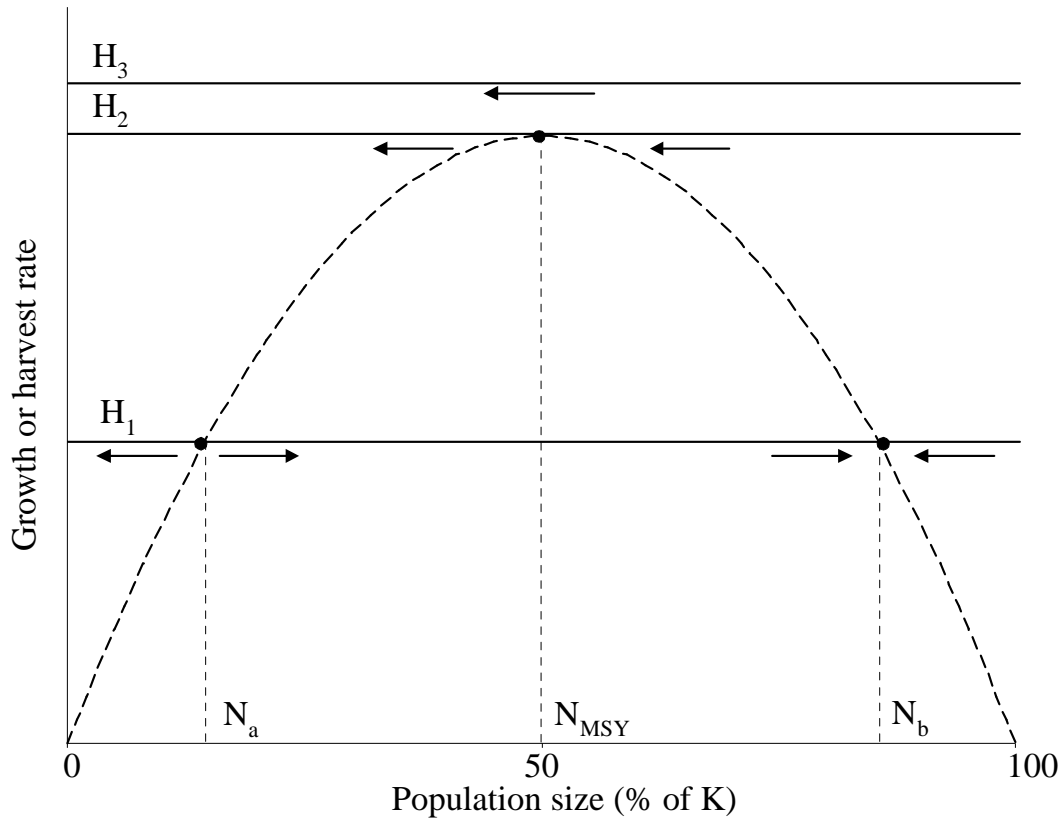


Figure 3. Stability analysis for the equilibrium population sizes shown in Figure 2. a) Hunting removes a constant number of individuals. b) Hunting removes a constant proportion of the population.

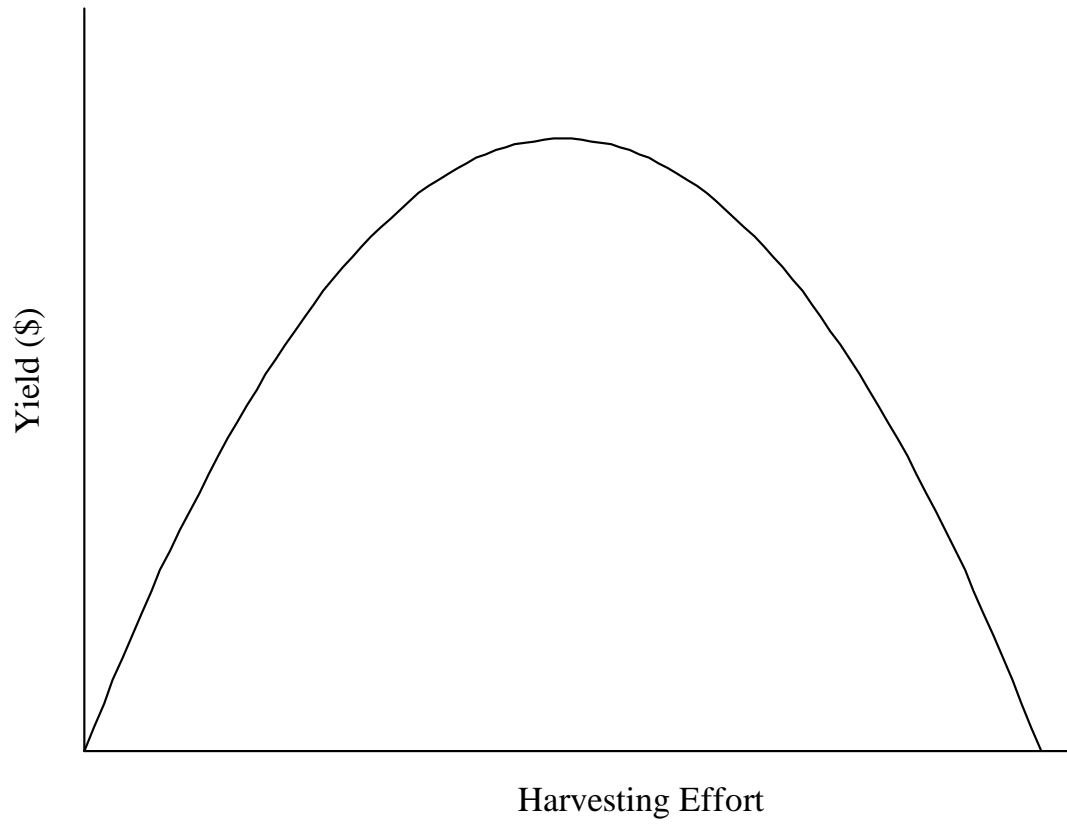


Figure 4. The yield-effort curve for a population with logistic growth.

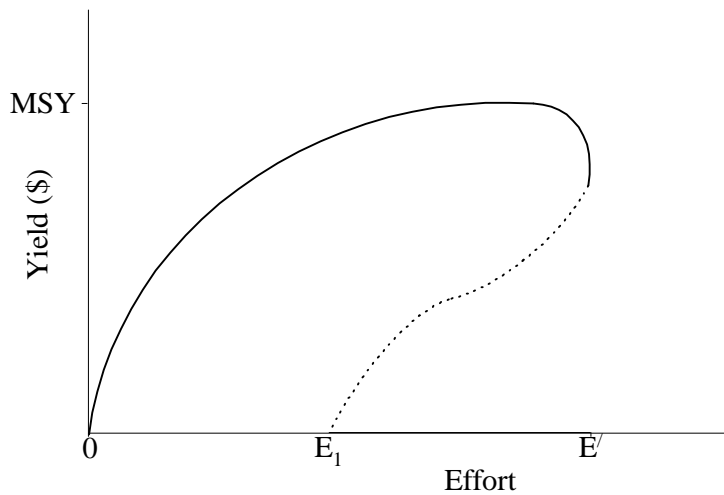
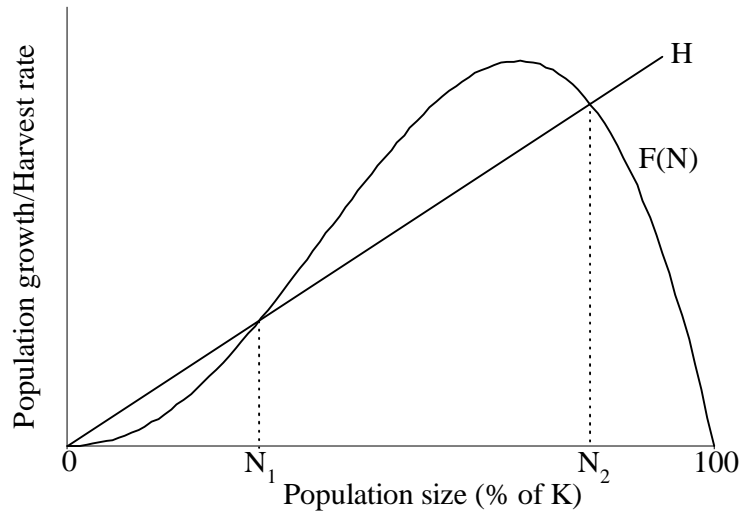


Figure 5. The effect of non-critical depensation (the Allee effect) on the parabolic relationship between the population size and the rate of population increase. a) Harvesting a proportion of the population each year produces two equilibria, N_1 and N_2 . b) The yield-effort curve for non-critical depensation. If the effort level increases above E' , yield declines rapidly and effort must be reduced to E_1 in order to allow the population to recover above the unstable equilibrium level N_1 .

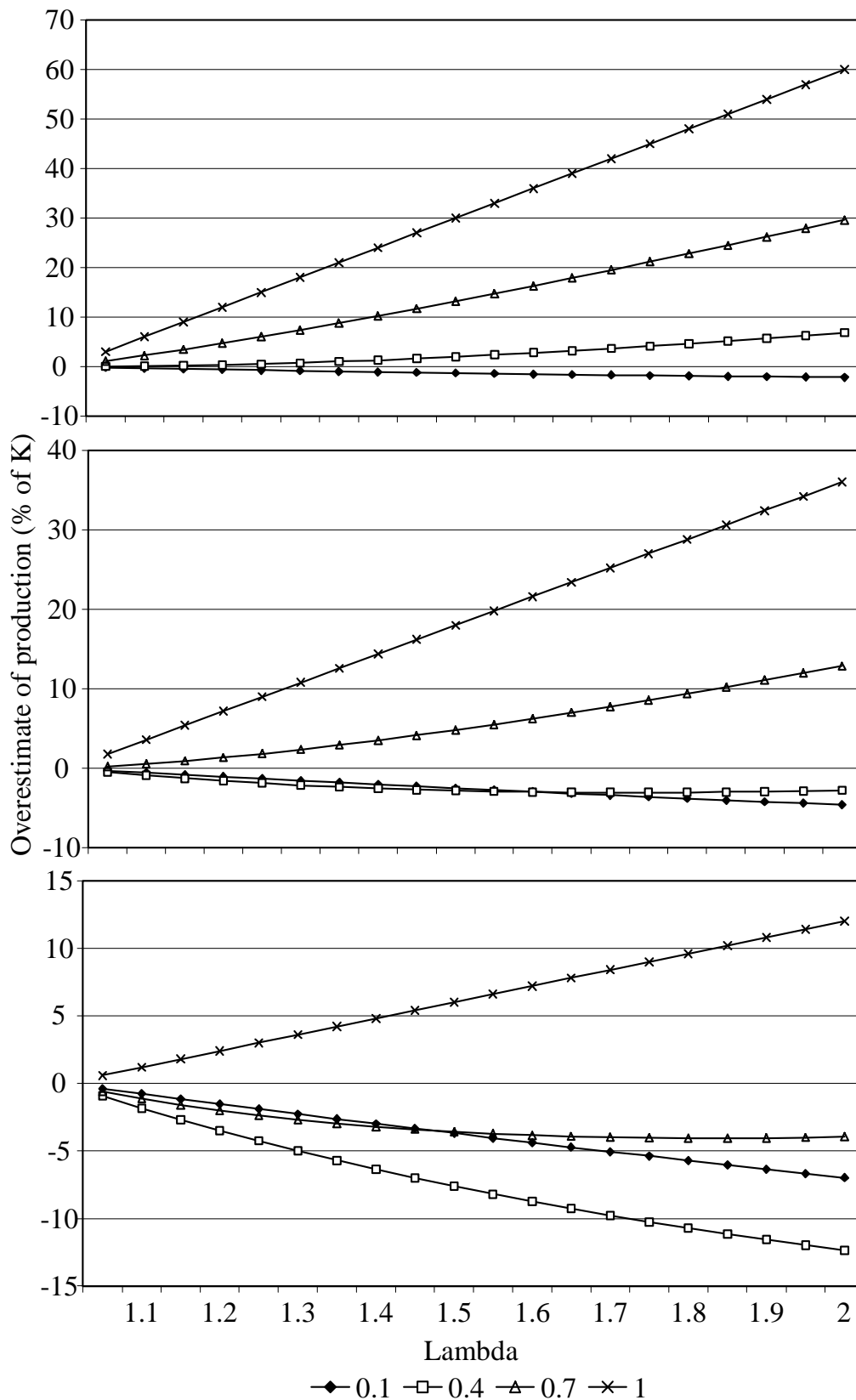


Figure 6. The relationship between the sustainable yield calculated by the Robinson & Redford method and the true sustainable yield for a population with simple logistic growth in discrete time. The graphs show the degree to which the Robinson & Redford method over- or under-estimates true sustainable yield (the difference in yields as a proportion of carrying capacity) as a function of the intrinsic rate of population increase, λ . The results are displayed for 4 population densities, expressed as a proportion of carrying capacity, ranging from 10% to 100% of K . Three levels of the Robinson & Redford natural mortality factor are shown: a) Factor = 1, so that there is no correction to their calculation of maximum production to account for natural mortality. b) Factor = 0.6, the value they suggest for short-lived species. c) Factor = 0.2, the value they suggest for long-lived species. Note the different scales of the y-axis between the 3 graphs.

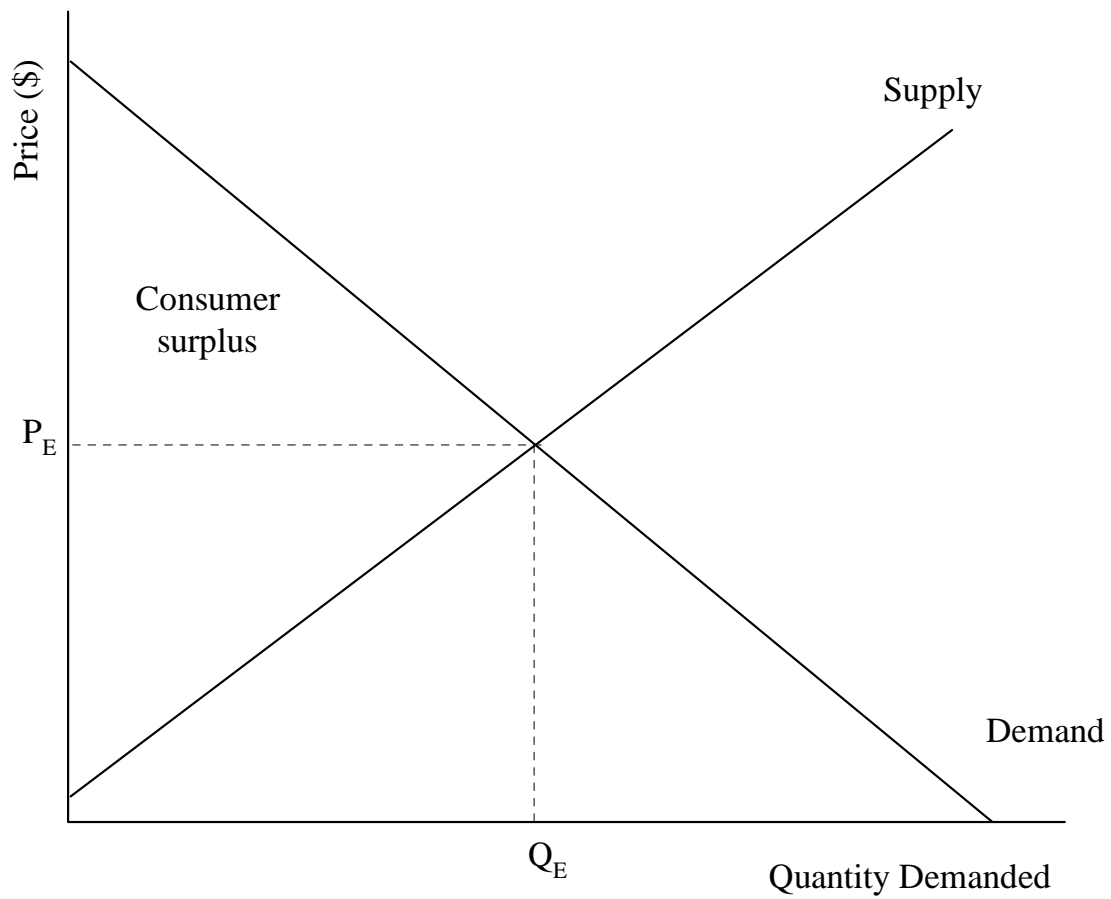


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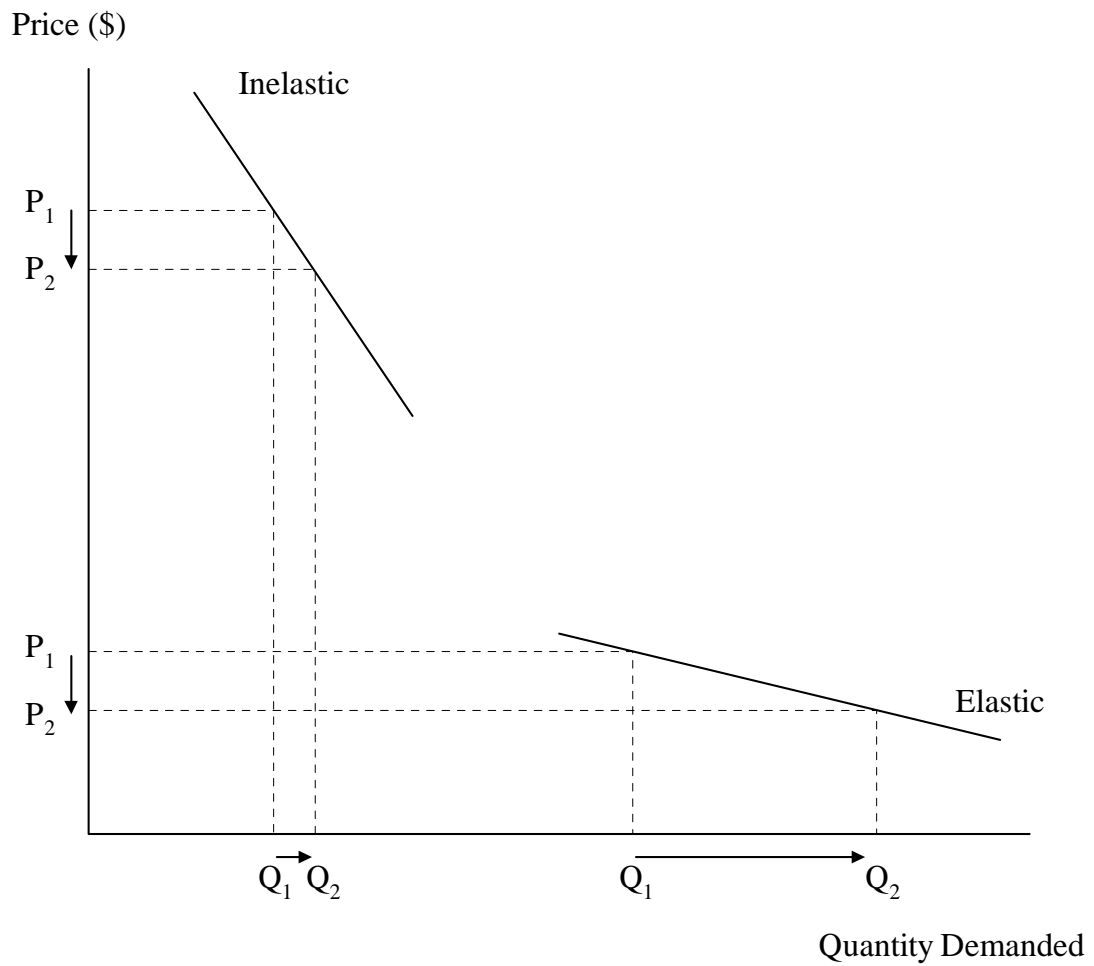


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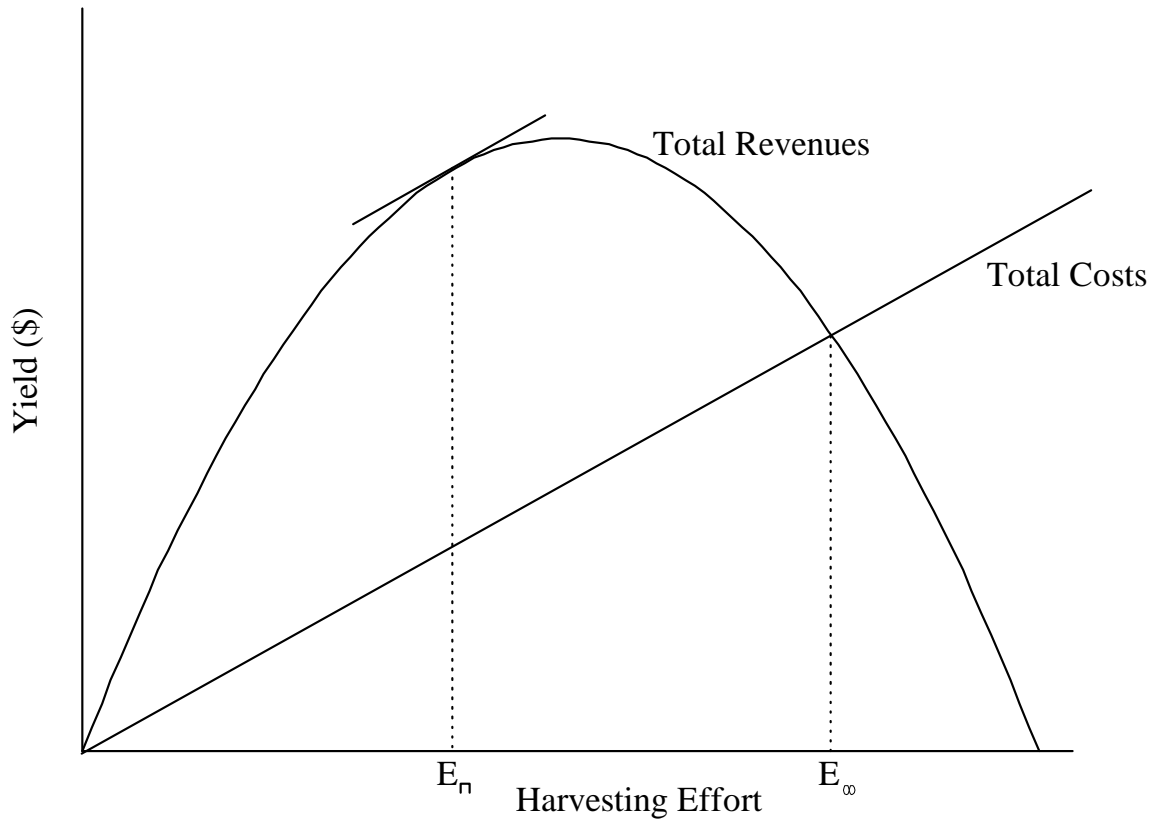


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