Advances in wildlife ecology and the influence of Graeme Caughley

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Abstract. Graeme Caughley produced substantial advances in our understanding of interactions between large mammalian herbivores and the environments they occupy. The strength of his work lay in the logical approach to answering fundamental questions. While his life work contributed to our understanding of animal population dynamics, it is in the application of his research and ideas that we have greatly advanced the science of conservation biology. Two central legacies of Caughley’s lifelong work are that an understanding of basic science leads to more appropriate management, and that underlying assumptions must be explicitly stated and tested. By arguing that efficient management of ecosystems requires an understanding of the underlying mechanisms, he moved forward the application of basic research to management. Future advances in wildlife conservation must focus on three aspects: (1) the rules for stability in ecosystems, and how humans cause instability; (2) the decline in native habitats, mostly from agriculture, and how to renew and reconstruct them while expanding threatened populations; and (3) how to breed species in captivity, and then reintroduce them as a last line of defence.

Introduction

‘Special causes do not produce general effects’ (Caughley 1976c)

All problems in wildlife management, said Graeme Caughley (1976a), fall into three categories: too many (overabundance), too few (conservation), and too much (overharvesting). The quintessence of Caughley’s contribution to science lies in his logical approach to answering fundamental questions, no more clearly illustrated than the first chapter he wrote for the textbook ‘Wildlife Ecology and Management’ (Caughley and Sinclair 1994), in which he explained the nature of evidence required to decide whether goals of management are achieved.

Since his first writings in the early 1960s he has addressed a range of problems in wildlife population dynamics. The two central themes of his work were, first, that an understanding of basic science is essential for more appropriate management and, second, that underlying assumptions must be explicitly stated and tested lest they become dogma. Caughley’s innovative refinements of basic, down-and-dirty field techniques led to contributions to ecology that are now regarded as classics (Caughley 1974a; Caughley et al. 1976). We review some of his contributions to fundamental science, and then how he applied them to wildlife management and conservation, illustrating where his ideas have evolved in recent years.

Vertebrate population ecology

Herbivore–plant interactions

The underlying concepts for herbivore–plant interactions are outlined in Caughley’s (1976b) chapter in ‘Theoretical Ecology’ (May 1976). His main interest lay with reciprocal responses from both trophic levels because his early studies of that (Hemitragus jemlahicus) in New Zealand (Caughley 1970) and sheep and kangaroos in Australia (Caughley 1987) involved growing plants that responded to grazing. He showed from these studies that herbivore populations would fluctuate, producing either a stable cycle or one that dampened over time, if the environment was stable. He suggested that elephants (Loxodonta africana) in Zambia could be exhibiting such a stable cycle due to the time delays in interactions with their slow-growing food supply, the baobab (Adansonia digitata) (Caughley 1976c). In Zambia, the environment is seasonal but relatively predictable. However, in Australia the environment is far from stable, causing plant food resources to fluctuate widely. The consequence is that herbivore numbers also fluctuated as a response to food supplies, as seen for western grey kangaroos (Macropus fuliginosus) that feed on grasslands in western New South Wales (Bayliss 1987). The causal mechanism is implied by the relationship of the instantaneous rate of increase of the herbivore to the food supply: at high food density the herbivore increased at its intrinsic rate, at very low density the herbivore declined, and from these one could identify the food level where the population was potentially stationary. Holling (1965) produced a quite different numerical response in which predator numbers were zero with no food, increased with more food, but then reached an asymptote with high food supplies; in effect, r was zero at high food levels, the converse of Caughley’s result. Predator numbers reached an asymptote because of other factors, such as lack of space and intraspecific interference that limit the population. For example, vertebrate predators tend to be territorial and territories limit the eventual size of the predator population. In fact, Caughley’s and Holling’s numerical responses are part of a family of curves that are
essentially isoclines (Sinclair and Krebs 2002). Although some herbivore species are territorial and would exhibit the Holling type of response (solitary antelopes, most deer species, squirrels) many others are not (herding antelopes, most macropods); the latter can tolerate high levels of crowding and would exhibit the Caughley type of numerical response.

The effect of food supply on the rate of increase of herbivore populations is better illustrated if food per capita is considered rather than simple food abundance, as seen in the wildebeest (Connochaetes taurinus) of Serengeti (Fig. 1). Per capita food supply includes the density-dependent effects of population size, which eventually regulates numbers. Caughley did not use the terms ‘density dependent’ and ‘regulation’ explicitly (although he used his own equivalent ‘centrapetality’) but he recognised these processes when considering carrying capacity and harvesting rates (Caughley 1987).

Multiple states and predation
Communities can exist in different combinations of predator and prey abundances under the same environmental conditions. These multiple states within an ecosystem are detected when a perturbation radically alters the abundance of many species in the community, which then do not return to their original abundance when the perturbation is removed (Holling 1973; Beisner et al. 2003; Sinclair and Byrom 2006). Changes in state are characterised by non-linear dynamics of predation, with initial slow change followed by fast, catastrophic change (May 1977; Scheffer et al. 2001).

Predator responses to increasing prey numbers not only involve numerical changes discussed above, but also changes in the behaviour of individual predators, the functional response. Differences in the way predators search for and catch their prey ultimately affect the population rate of increase. The two basic behaviour patterns are identified as the Type II and Type III functional responses (Holling 1965). Under special circumstances of Type III functional responses, predators can theoretically hold prey populations at two levels under the same environmental conditions, a low prey level where predators regulate prey and a high level where predators do not regulate but merely eat those suffering from malnutrition or disease. These are the conditions for ‘multiple states’. Prey numbers can, therefore, jump from low to high density or collapse from high to low without returning to the original state; and such changes in the presence of the predator provide circumstantial evidence for multiple states (Scheffer et al. 2001).

Evidence for multiple states in nature is sparse, suggesting that the right conditions are rare. In an example where plants are the prey, elephants maintained two different densities of Acacia trees in Serengeti. Once mature trees had been destroyed by fire, elephants maintained a grassland state by feeding on and regulating juvenile trees. When elephants were removed by human hunting (in both the 1880s and 1980s), trees escaped herbivory and formed a mature Acacia savannah. After both removal periods elephant numbers increased, they fed on the mature trees but did not return the savannah to a grassland (Sinclair and Krebs 2002). White-tailed deer (Odocoileus virginianus) in North America maintain different plant communities by feeding on young trees. Two tree densities can be found depending on whether young trees can escape this herbivory or not (Schmitz and Sinclair 1997).

Examples of multiple states where herbivores are prey are also rare. In the Kruger National Park, initial high numbers of wildebeest were reduced by culling. When culling ceased wildebeest numbers continued to decline through lion predation (Smuts 1978), a result that suggests two states. Outbreaks of house mice and European rabbits in Australia may be interpreted as changes from a predator-regulated to a food-regulated state (Sinclair et al. 1990; Pech et al. 1992).

Eruptions and irruptions
Caughley (1981a) distinguished between the dynamics of population eruptions and irruptions. Eruptions are relatively sudden increases in population, not necessarily accompanied by an increase in range. Examples are the increases of elk (Cervus elephas) in Yellowstone (Singer and Norland 1994), elephant in many parks of Africa (Whyte et al. 2003) or African buffalo (Syncerus caffer) in Serengeti (Sinclair 1977). Irruptions refer to expansions of ranges, as crossbills (Loxia curvirostra) or snowy owls (Bubo scandiacus) exhibit when spreading south through the boreal forests of Canada. This expansion does not imply an increase in population although such increase may occur.

Since the early 1900s there have expanded their range in the southern alps of New Zealand (Caughley 1970). The population alternated between eruptions within a particular range, followed by a density-dependent dispersal to new areas. The low density in the new area then allowed a new increase in numbers. The result was a series of expanding waves of increasing and declining density. Since then similar phenomena have been observed with indigenous populations expanding into their original range, for example wood bison (Bison bison) in northern Canada, muskox (Ovibos moschatus) in the Arctic, and elk in Yellowstone (Larter et al. 2000).
Age structure of populations

Caughley paid particular attention to the use of life-tables to assess population trends. A cohort life-table, derived from following the fate of a single birth group through time, can give information on the rate of increase of a population. However, the time it takes to follow this cohort, especially in long-lived mammals, prohibits the practical use of this approach for tracking population change. A random sample of the population at a point of time provides a time-specific life-table. This is a cross-section of the many cohorts making up the population. If conditions that affect birth and death rates remain similar for long periods then this type of life table can approximate the rate of increase of the population. In practice this proviso applies only when the population is stationary. In addition, adequate samples of age frequencies in the live population are rarely available. Thus, it was tempting to use samples of dead animals to calculate an age frequency of deaths and from that obtain the age-frequency of the live population, as in red deer (Cervus elaphus) of Scotland (Lowe 1969) and Serengeti wildebeest (Watson 1969).

Conveniently, the calculated \( r \) from these age-at-death frequencies was close to zero, conforming to the assumption for a time-specific cohort. Caughley (1977) pointed out that the calculations transforming age-at-death frequencies to age-frequency of live animals required the assumption of \( r = 0 \). Hence the eventual calculation of \( r = 0 \) was circular. To obtain the true age-frequency \( l_i \) must be multiplied by \( e^r \). Thus, \( r \) must be known first. Therefore life-tables derived from cross-sections of the population cannot be used to obtain a rate of increase and are best used for understanding patterns of mortality (Caughley and Birch 1971).

A far more established tradition was the use of age-ratios to estimate the rate of increase of a population, in particular the ratios of calves and yearlings to adult females. The assumption was that high ratios of calves or yearlings to females meant that the population was increasing, and hence able to tolerate a high harvest rate. Ratios, of course, are determined by the numerator, denominator or both, so that a high calf to female ratio could result from an increase in the birth rate, or an increase in the mortality of adult females. The population could be either increasing or decreasing, and so the ratio of juvenile/female by itself provides no unambiguous information on trends in the population (Caughley 1974b).

The arrival of desktop computers in the 1990s has facilitated the use of Leslie matrices to compute rates of increase (Caswell 2001). These are particularly useful for populations well below their equilibrium, characteristic of those threatened with extirpation. Such populations are difficult to census, let alone to monitor for trends. Leslie matrices are invaluable in estimating whether a threatened population is continuing to decline or responding to conservation remedies. They can also be used to measure rates of increase as indices of management and population control (Smith and Trout 1994). Essentially, only four pieces of information are needed, of which any three must be measured to compute the fourth. These four are the birth rate, juvenile survival, adult survival (the stages) and the rate of increase.

For example, a population of African buffalo in northern Serengeti, Tanzania was known from censuses to be declining at a rapid rate over 1979–92. The cause of this decline, however, was in dispute: disease, especially rinderpest, was one hypothesis while illegal hunting by poachers was another (Sinclair et al. 2007). The birth rate and juvenile survival were also both known (Sinclair 1977). Leslie matrix computations using POPTOOLS software developed by G. Hood (www.cse.csiro.au/poptools) was used to calculate adult survival, which was estimated to be 80% per year; in other words there was a 20% adult mortality producing this declining population. In contrast, a stationary population would have required a 1% annual mortality. Since rinderpest affects only calves (once adults become immune, which in this case they were) while poachers attack adults these calculations point to poaching as the cause of the decline. This result led managers to investigate more closely and confirm the flourishing bushmeat trade. This example shows how the Leslie life-table approach can illuminate critical demographic factors for conservation such as which life stage was under threat.

Allometry, rate of increase and environmental adaptation

Caughley’s contribution to allometry was in relating rate of increase to metabolic rates. Life-history strategies, as outlined by Pianka (1970), collate a group of demographic, morphological and physiological characters that trade-off high survival, long generation times and low reproductive rates against the converse high reproductive rates and low survival. Consequently, species with the former suite of traits (\( K \)-types) have low rates of increase (\( r \)), the latter (\( r \)-types) have high rates of increase. For any species the result of the trade-off depends on metabolic rates. Caughley showed that in mammals there is a negative relationship between \( r \) and \( \ln(\text{body mass}) \), as predicted by metabolic rates (Caughley and Krebs 1983). This relationship applies to all eutherian mammals groups (Fig. 2). Metatherian (marsupial)
mammals also show a similar negative slope, but with a lower $y$-intercept due to lower reproductive rates compared with eutherians of the same body size (Sinclair 1997a).

Mammals with large body mass and low $r$ tolerate adverse environmental conditions (droughts, cold winters) using physiological adaptations (food stores, water saving, reduced reproduction). Small mammals die during periods of stress but their populations rebound later through high reproduction. Since over evolutionary time all groups tend towards larger size there may be some overall advantage to surviving stress rather than rebounding from it and so stress-tolerance could be the selection pressure for this trend towards larger size; but the disadvantage is that when conditions change beyond the tolerance to the conditions to which large species are adapted, they die out. Why high survival (from large body size) and lower metabolism (in metatherians) may be more advantageous is not clear.

Science and management

Management as experiment

Caughley stressed that information from wildlife management operations could be used as experiments to test hypotheses on management problems (Caughley 1977; Macnab 1983). Hypotheses are tested by obtaining specific observations that are critical to the predictions. The experiment tests predictions by altering a component of the system, say population density, in one area and compares the outcome with a control area where no manipulation is carried out. All other components of the system are held constant to the best of our ability. This approach may lead to less ambiguous results, but on the scale of wildlife ecosystems it is often viewed as impractical: controlled and replicated experiments can only be carried out on a small scale (usually a few hectares) and, therefore, may not be particularly relevant to large-scale wildlife systems.

However, the manipulations of wildlife management are often at the appropriate large scale (Macnab 1983; Sinclair 1991) – predator control, herbivore reductions, or prescribed burning are examples. These manipulations can be used as good experiments if care is taken to (1) obtain scientific information before, during, and after they occur, and (2) compare the results with a similar unmanipulated area that forms the control. This means that entire systems must not be manipulated; some parts must be left as controls. The elephant, buffalo and hippopotamus populations of Kruger National Park were known to be increasing in the early 1960s (Pienaar et al. 1966). It was estimated that if elephant populations continued to increase at the same rate they would increase to over 20,000 animals, overpopulate the park, and irreversibly damage the habitats unless management implemented culling to hold the populations in check (Pienaar et al. 1966). Culling (and later live capture) was duly imposed in 1965 and continued for some 35 years (Whyte et al. 2003). Underlying this management practice were assumptions that there were no negative feedbacks on the herbivores, or at best feedbacks were so weak that they would not regulate the populations. In short, the hypothesis was that the populations were not regulated. This hypothesis was tested for at least 25 years and so became dogma. The proper experimental test was to cull in some areas and leave other areas unmanipulated to test the prediction that in unmanipulated areas populations would continue to increase exponentially. A more enlightened policy has developed since the mid 1990s (du Toit et al. 2003), culling has been much reduced and the population has effectively stabilised (Whyte et al. 2003). The variation in annual culls can be treated as a set of experimental reductions: they show that the elephant’s rate of increase subsequent to the cull is negatively related to population size and this is evidence of a negative feedback (Fig. 3). Such reductions exemplify management actions as experimental manipulation of the sort proposed by Caughley writing under the penname Macnab (1983).

A second assumption underlying management in Kruger was that the ecosystem must be kept in some sort of constant configuration, the status quo must be maintained. Long-term studies on biological trends in Kruger (Ogutu and Owen-Smith 2003) and Serengeti (Sinclair et al. 2007) indicate that ecosystems are in a continual state of flux and that resilience is maintained if change is allowed (Willis et al. 2004). Ecosystems can exhibit both slow change and sudden shifts in state from perturbations such as drought or disease, and circumstantial evidence for this comes from palaeoecological studies covering millennia in both Tsavo National Park and Kruger (Gillon and Willis 2004; Gillson and Willis 2004). Caughley (1976a) had suggested that elephant–tree interactions exhibited cycles, indicating delayed negative feedbacks. Gillson (2004) found some evidence for cycles but more for sudden phase shifts between savannah and grassland consistent with the mechanisms documented in Serengeti. Early on, Caughley questioned the wisdom of managing ecosystems to maintain particular biological states (Caughley et al. 1987) and, indeed, systems are continually changing and management should track change rather than counteract it to maintain the status quo.

Carrying capacity and overgrazing

The term ‘carrying capacity’ had its origins in Leopold’s (1943) study of deer in Wisconsin. As herbivore populations increased, habitat and food resources declined until both animal and plant
populations reached equilibrium. This concept of equilibrium was conveniently described by the logistic equation where \( K \) became the carrying capacity, as an upper limit to the population. Such an upper limit, therefore, implied the concept of overpopulation (above \( K \)) and hence overgrazing.

Overgrazing, in turn, could be identified by the seemingly aberrant configuration of the plant community, a convenient short-cut avoiding the necessity to count animals. In North America, at least, rangeland used by domestic ungulates can be described botanically along a continuum of grazing pressure. Without grazing there is a preponderance of palatable grasses and forbs. As grazing increases these species decline in abundance (labelled ‘decreasers’), while less palatable plants increase (increasers). Eventually, the sward incorporates species that are inedible (invaders), and if these are high in abundance the sward is deemed ‘overgrazed’ and ungulate numbers overabundant (Dyksterhuis 1949; Lewis 1969). This distinction between economic and ecological capacity, first highlighted by Caughley (Caughley 1976c), explains how criteria on vegetation condition developed for harvesting often lead to erroneous conclusions of overgrazing when applied to natural areas in protected parks where populations were at ecological carrying capacity; for example, buffalo were deemed to be overgrazing in Kruger, hippopotamus similarly in Queen Elizabeth Park, Uganda (Petrides and Swank 1965; Pienaar 1983) and elk in Yellowstone (Pengelly 1963). Culling programs were implemented on the evidence of inappropriate plant community indices.

The general meanings of carrying capacity and overabundance have already been discussed at length (Caughley 1976c, 1979, 1981b; Macnab 1983, 1985; Sinclair 1997a, 1997b), and we have illustrated them as a phase diagram of herbivore numbers and vegetation biomass (Fig. 4). Any definition of carrying capacity must imply a long-term stability of herbivore numbers, vegetation biomass, and community species composition; that is, biodiversity should be stable and a reasonable value for ‘long term’ would be the average longevity of the habitat in question. This avoids the need to suggest absolute values, and so one can apply the term ‘carrying capacity’ to different systems with different time scales.

In Fig. 4 the solid line represents a series of points at which a herbivore can hold vegetation biomass constant (an isocline). Some natural biological equilibria can be identified along this isocline (the solid points). One is the trivial point of maximum vegetation, \( V_{\text{max}} \), at which there are no herbivores. Another is the Ecological Carrying Capacity (ECC), determined by intraspecific competition for food under long-term natural conditions. Any other level of vegetation and herbivore between ECC and \( V_{\text{max}} \) requires that herbivores be harvested by predators or humans, the harvest rate being indicated by the broken line. The Economic Carrying Capacity is about half way along the isocline. This point is at the peak of the harvest curve (Fig. 4), indicated on the isocline as Maximum Sustainable Yield (MSY). However, MSY is not achievable in practice and some lower safe harvest level should be sought, as emphasised by Caughley in 1977.

Conservation
Causes of decline
Caughley (1994), in a landmark paper, pointed out that conservation problems fall into two categories – problems for those species that were once abundant but are now declining towards extinction versus problems for those species that currently exist in small numbers but are not declining. This distinction was critiqued by Hedrick et al. (1996) on the grounds that it was a misleading dichotomy, and that problems associated with the two groups usually co-occur. In fact, Caughley would have agreed: his distinctions were to help focus the logical analysis of problems.

The fundamental conservation problem underlying the decline of once-widespread species is finding the cause of the decline. First, clues can be found from analysing the demography of a population. In other words, the cause of the decline may be elucidated by examining the stage in the life history of a population most at variance with a healthy stable population. Thus, if fertility, egg production or births are low, then it is unlikely that direct predation is involved (indirect effects from stress may apply, however). In contrast, malnutrition due to habitat loss or competition from exotics can affect fertility and survival of newborns. If mortality of juveniles is exceptionally high then one might suspect excessive predation – as seen in the kiwis of New Zealand where juveniles are preyed upon by stoats. If mortality of adults is abnormally high then one would look for the arrival of exotic disease or predators or over-harvesting by humans.

Second, direct evidence for the cause of decline comes from autopsies, the availability of food and habitat, and the population trends of predators. For example, the decline of populations of common bird species in Britain was attributed to the intensification of agriculture through application of herbicides and insecticides – in essence, there were no insects and seeds for the birds (Butler et al. 2007). The collapse of the vultures in India is now known to be due to ingestion of diclofenac from

![Fig. 4. The isocline where herbivore numbers are stationary as a function of vegetation biomass (solid line). At maximum herbivore numbers, the population is regulated by vegetation available, which is itself held at a low level. This point is the Ecological Carrying Capacity. At maximum vegetation there must be zero herbivores. Any other point on the isocline requires a constant harvest of herbivores, the harvest indicted by the broken line. At maximum harvest (MSY) the herbivores are held at the Economic Carrying Capacity (adapted from Caughley 1976a).](image)
carcasses of cattle: the drug is given to cattle as an anti-inflammatory drug and vultures are exceptionally sensitive to it (Green et al. 2004).

Meta-analysis on causes of threat to vertebrate species consistently shows that agriculture is the main cause of decline. This has been established in North America, China, Europe and Africa (Li and Wilcove 2005; Venter et al. 2006). There are, of course, many other factors in addition and these vary with region.

Declining small populations also suffer from the same problems as those of large populations but with less time for remedial action. There are additional threats even when the population is stationary. Demographic problems arise if, by chance, the sex or age distributions become so distorted that the birth rate falls below the mortality rate. Similarly, homozygosity of sublethal genes could spread, thus causing inbreeding depression and high mortality. These sorts of problems are far more likely to arise in recent small populations, remnants of a once-large population arrived at from habitat loss. In this context they are an outcome of the declining population scenario.

Ancient small populations, however, have solved such demographic problems, homozygous lethals having been successfully selected out, while birth and survival rates have become adapted to the constrained situation. Such populations occur on islands where they have become adapted to local conditions. For example, the flightless phasmid (Dryococelus australis) that was recently discovered on Ball’s Pyramid, a 500-m-high rock 23 km from Lord Howe Island in the Pacific, has probably been isolated since the ice age, some 20,000 years ago (Campbell and Hutching 2007). The population numbers probably less than 100 individuals and it must have always been this size because its habitat cannot have been larger than the present dozen or so manuka (Leptospermum polygalifolium hovense) bushes clinging to the rock face. In contrast, the Floreana mockingbird (Nesomimus trifasciatus), which has lived on that Galapagos island in small numbers possibly for hundreds of thousands of years, was extirpated when humans reduced its scrub habitat and introduced rats (it remains only on two satellite islands) (Grant et al. 2000). Thus, the problems for these restricted species arise, like those for abundant species, from changes in their habitats compounded by depredation and competition from exotics, both pests and weeds (Hutton et al. 2007). In addition, climate change may be increasing the frequency of hurricanes from which populations cannot rebound fast enough.

**Mitigating threats to endangered species**

The two main approaches to protecting species and their ecosystems are the use of protected areas where the impacts of humans are kept to a minimum, and the use of sustainable exploitation in human-dominated ecosystems, one of the main approaches to community-based conservation in Africa. Both approaches have their benefits but neither is sufficient alone for the long-term sustainability of biodiversity (Sinclair and Byrom 2006; Sinclair 2008).

Protected areas are needed to conserve those species that cannot coexist with humans, such as large carnivores, large ungulates such as elephants, those that require intact ecosystems such as interior forest species (many birds, large primates) or species that require fragile ecosystems such as wetlands (many plants, insects, amphibians), or undisturbed breeding sites. Protected areas also provide ecosystem baselines undisturbed by humans. The rationale is that in order to understand the impacts of humans on ecosystems we need ‘control’ areas where human interference is kept to a minimum. Baselines allow us to distinguish between natural or long-term disturbance and local human impacts, in order to predict the potential outcomes of current and future disturbance events. Without such baselines we can misinterpret causes of change (Willis et al. 2005).

Protected-area conservation has been challenged on philosophical grounds (Adams and Mulligan 2003), in particular that such areas have never been pristine and so cannot act as baselines. There is plenty of evidence to show that most areas of the world have changed over the past millennia. Even the densest currently uninhabited Congo forest is now known to have been inhabited by humans some 2–3 millennia ago (Willis et al. 2004). However, ‘pristineness’ is not the premise for protected areas, only that they receive lower human impact than surrounding areas (Sinclair et al. 2008).

Nevertheless, protected areas cover less than 10% of the global terrestrial surface, and it is unlikely that this value will increase much more. Thus, from standard species–area relationships less than 50% of the terrestrial biota will ever be found in protected areas. Second, many protected areas are not large enough to maintain viable populations in isolation from the surrounding matrix. Therefore, we need to conserve species in human-dominated ecosystems if we are to ensure the persistence of the other half of the biota.

However, implementation of community-based conservation around the world has led to problems and the policy has not always been successful, central government authorities often retaining the revenues while leaving local peoples without benefit (McShane and Wells 2004). Caughley (1993) showed that with slow-reproducing species such as elephants, there is an economic incentive to over-exploit the population in community areas and invest the profits because compound interest usually exceeds the intrinsic rate of increase of the animals. This derived from the seminal work of Clark (1973) of the economics of overexploitation. Elephants were seen to be overexploited throughout Africa (Caughley et al. 1990) and are continuing to decline. Additionally, Caughley, writing as a co-author under the penname Macnab (1991), stressed that one aspect of ‘community-based conservation’, namely commercial game cropping, could be disastrous for conservation efforts, in contrast to the alternative of promoting limited harvest for luxury meats and skins, adventure safaris and sport hunting on private ranches of Africa. Thus, as currently practiced, community-based conservation has some fundamental problems that limit its effectiveness.

In general, community-based conservation is essential for the long-term sustainability of the biota but we must find ways of counteracting the destabilising trends of overharvesting and loss of habitat while maintaining the full complement of species. In the end, the costs of conservation must be met by those who benefit the most, mainly those in the developed nations. These nations...
must devise adequate benefit programs for local communities (Woodroffe et al. 2005).

Conclusion

Graeme Caughley exemplified the logical analysis of scientific problems in ecology. He also challenged the assumptions of traditional wildlife management, pointing out the inherent inconsistencies in logic. It was from this that a better understanding of population dynamics has prevailed in the practice of wildlife management; for example, in the use of management as scientific experiment. In the 21st century modern computer power has advanced the techniques of demographic analysis in ways not foreseen by him.

His focus was on populations. Now the advances must come in three areas. First, we must address the questions of what are the rules for stability in ecosystems, and how do humans cause instability. Second, with the decline in available habitats, mostly from agriculture, we must focus on how to renew and restore native habitat to expand threatened populations. Third, as a last line of defence, we must learn how to breed species in captivity, and then reintroduce them. Indeed, a broader approach to reconstructing lost communities should be a priority (Hutton et al. 2007).

References


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