Strengthening biological theory in wildlife research and management: a case study for Botswana

Nathaniel T. Wheelwright*, J. Mark Dangerfield, Michael Flyman and Moremi Tjibae

In Africa, governmental wildlife agencies have traditionally shouldered most of the responsibility for developing and implementing management programmes to address conservation issues such as declining abundance of desirable species, superabundance of pest species, impoverishment of biological diversity, loss of genetic variation, shrinkage of wilderness areas, and degradation of habitats.[1,2] Effective wildlife management programmes rely on a foundation of relevant, quantitative, detailed, and reliable research.[3] But when agency resources are stretched thin, the key problem is how to prioritize research needs. At the very least, we need to assess accurately the current status of wildlife populations and the quality of their habitats. We would also like to know something about their genetic structure and predict their future status under natural conditions or in response to disturbances or experimental manipulations.

In this article we argue that research programmes in support of wildlife management in some countries in Africa can be made more effective by building their theoretical base and putting a greater effort into understanding processes rather than simply documenting patterns or reacting to specific crises.[4,5] Where general biological principles have been used to design research programmes and recommend management solutions, the principles are sometimes outdated or inapplicable, and they focus disproportionately on describing the current abundance and distribution of populations, with insufficient attention to elucidating the factors that influence populations.[6] Using as a case study the 'Strategic Plan for Wildlife Research in Botswana', prepared by the Research Division of Botswana's Department of Wildlife and National Parks (DWNP),[7] we illustrate some of the ways that theory can be incorporated to help in the design of management-orientated research. To put Botswana's Strategic Plan in context, we first briefly characterize the country's physical and biological environment, review its specific conservation problems, and describe the organization and operation of the DWNP.

The environment of Botswana

Botswana occupies slightly more than 500 000 km^2 of flat or gently undulating terrain, more than 80% of which lies on deep, wind-transported Kalahari sands with wide plains and seasonal pans. With no major mountain ranges, rivers or lakes to act as barriers, dispersal of plants and animals is relatively unconstrained, with obvious implications for local adaptation of populations, extent of gene flow between populations, and degree of endemicity. The climate is semi-arid to arid, with a gradient in annual rainfall from 250 mm in the extreme south-west to 650 mm in the north. The pattern of rainfall is strongly seasonal and highly variable between years and sites, which results in considerable heterogeneity in plant productivity and the intermittent occurrence of various species of annual plants. Due to the sparse and unpredictable rainfall, shortage of major watersheds, and high soil infiltration rates, surface water is scarce over most of the country, especially during the dry winter months.[8]

The vegetation of Botswana is mostly open woodland or bush savanna interspersed with pans, where salt-tolerant grasses persist. There are few major changes in vegetation type over very wide areas, and landscape-level heterogeneity is low. Considering the country's size and latitude, Botswana's plant species richness is poor, with 2 700 species listed, only 17 of which are endemic. There are no known endemics among the country's 565 bird species. About 160 mammal species have been recorded in the country[9] and although none is endemic, several geographically isolated populations of antelopes are distinctive in aspects of their behavior and possibly physiology [such as wildebeest (*Connochaetes taurinus*), hartebeest (*Alcelaphus buselaphus*)]. Historically, population sizes of many ungulate species in Botswana were large but population densities were low; presently, substantial concentrations of large mammals occur only near permanent water such as the Linyanti, Chobe and Okavango rivers.[8]

National parks and game reserves cover more than 17% of Botswana. Wildlife management areas (WMAs) make up an additional 21% of the country and in many cases play the important role of providing buffer zones and corridors between reserves and help in the conservation of species by safeguarding additional habitat.[8] Safari and subsistence hunting is permitted on a quota system within WMAs, but not in national parks and game reserves, where there is little or no active management by DWNP. Unfortunately, Botswana's system of parks, reserves and WMAs may be insufficient to provide adequate protection for many birds (especially birds of prey) and large mammals that migrate in response to erratic rainfall or other factors unless they can survive in surrounding, heavily grazed areas. The national policy is to encourage mainly low-density, high-cost tourism in protected areas.[13]

Current conservation problems in Botswana

Perhaps Botswana's greatest conservation concern is the recent decline in several mammal populations.[10,11] Wildebeest, whose population size in south-western Botswana alone was estimated at 263 000 just 15 years ago, are thought to number only 15 000 today, a 94% decline. The current estimate of hartebeest numbers in the south-west of the country is 46 000, or just 17% of the 1979 count, while eland (*Taurotragus oryx*) are thought to have declined by 50%. Similar declines may well have occurred in various reptile and amphibian populations, particularly in response to tsetse fly control operations, but there are no reliable estimates of population changes for those taxa. Hardwood timber exploitation has been extensive and loosely regulated in some northern forest reserves, while over-grazing by cattle and goats, damage by elephants (*Loxodonta africana*), repeated fires, and fuel wood collection have altered local plant communities elsewhere.[11]

Several genetically distinct populations are threatened because of specialized habitat requirements (e.g. puku, *Kobus verdoni*), local degradation of habitats (e.g. Chobe bushbuck, *Tragelaphus scriptus ornatus*), or disruption of historical migration routes through the construction of roads and fences (e.g. wildebeest, hartebeest[10]). Global extinctions of species are unlikely, mostly because Botswana has so few endemics, but a few species in the country are threatened throughout their range [e.g. Cape vulture (*Gyps coprotheres*), slaty egret (*Egretta vinaceigula*), wattled crane (*Grus carunculata*), short-clawed lark (*Mirafra chuana*)]. Range degradation, fire, and elephant overabundance have reduced diversity on a local scale. The elephant population in northern Botswana is now estimated to be about 80 000 individuals, and a large proportion of them congregate at permanent water during the dry season, where they alter riverine and swamp-front plant communities. The wet season range of elephants is also expanding, increasing conflicts with human settlements on the edges of protected areas.[11] Several other species, especially large predators such as lions (*Panthera leo*), are considered pests outside reserves, and eradication is currently the main control method when they stray across unfenced boundaries into rangeland.[7]

A major threat to the integrity of many wildlife areas is the expansion of the cattle industry.[11] Livestock are almost entirely dependent on natural rangelands, which have had to absorb a tripling of the cattle population (currently 3 500 000 head) since 1966. High densities of cattle have reduced forage for native mammals and altered plant species composition. Rather than improving livestock management and controlling herd sizes, new grazing areas have been opened by drilling boreholes, with encroachment on reserves such as Makgadikgadi Game Reserve becoming an increasing problem. A network of cordon fences, erected as veterinary control measures to meet European beef import regulations, has severely restricted the migration of native mammals.[11]

Luckily, industrial and urban pollution are not yet important in Botswana. The soil's high infiltration rates and the country's flat topography mean that substantial topsoil loss occurs only locally.

The Strategic Plan for Wildlife Research in Botswana

The Department of Wildlife and National Parks, an agency of the Ministry of Commerce and Industry, is responsible for management of wildlife within Botswana's national parks, game reserves, and WMAs. Empowered by comprehensive conservation legislation,[12] DWNP also regulates subsistence and trophy hunting through a quota system, controls problem animals throughout the country, and implements international treaties such as the Convention on the International Trade in Endangered Species (CITES). DWNP is structured around three major divisions, Management and Utilization, National Parks, and Research, each with a number of support units.

The Strategic Plan for Wildlife Research in Botswana was prepared in 1993 by the DWNP's Research Division after a lengthy process involving consultation with interested parties from the public and private sectors.[7] The Plan's main guidelines were dictated by Botswana's National Development Plan No. 7 (NDP7), which obligates DWNP to administer and develop the areas under its influence, increase its 'capability for effective conservation of the wildlife resource', and encourage 'its full utilization by the private sector'.[13] NDP7 went on to define the wildlife research agenda's five goals as (1) developing an inventory of current wildlife populations and habitats, and a programme to monitor future changes; (2) conducting research into specific wildlife problems, such as the problem of elephant overabundance and control of livestock predators; (3) investigating the ecology of particular species and communities, mainly by encouraging and helping to coordinate private studies; (4) examining factors that affect wildlife utilization, such as game fencing and trophy animal offtake; and (5) studying wildlife diseases.[13] The Strategic Plan assigns Goal 1 to DWNP's Monitoring Programme, Goals 2–4 to the Applied Research Programme, and Goal 5 to the Veterinary Services Programme. Operational plans corresponding to each Program were written to meet the objectives of the Strategic Plan.[14]

As it stands, the Plan takes a population perspective rather than a community- or ecosystem-level perspective,[15] with a particular emphasis on counting large mammals. It focuses on a relatively small number of economically important species and pays little attention to the protection of non-game species or biodiversity generally. There is no mention of the use of experimental manipulations or modeling to reveal the causes of population trends, nor is there an explicit commitment to long-term studies or process-level understanding.[16,17,20]

We suggest that the goals of DWNP, like those of other agencies responsible for managing wildlife, can be more effectively met by (1) recognizing the uncertainties of wildlife monitoring protocols and the desirability of quantifying population structure, (2) allocating a portion of research programmes to determining the most suitable indicator species and monitoring those species, regardless of their economic importance, (3) making use of other species concepts, such as umbrella species or species that are phylogenetically or ecologically unique, (4) studying not just population trends but also the behaviour and basic biology of animals of concern, (5) emphasizing an understanding of processes, particularly species interactions and ecosystem-level dynamics such as nutrient cycling and energy flow, disturbance, and resilience, and (6) incorporating an evolutionary perspective where appropriate. If applied prudently, such considerations are more than academic exercises, and they need not excessively burden limited budgets, as we discuss below.

The problem of monitoring wildlife

Species across a wide range of taxa are becoming rare in Botswana – at least, that is the conclusion drawn by comparing the results of a relatively small number of population censuses carried out at different times under different conditions, often using different methods.[10] Any indication of sudden population declines deserves attention, of course, even if it is preliminary or uncertain. Nonetheless, it is worthwhile to recognize how the frequency of wildlife counts as well as their coverage can affect their reliability.

The first systematic wildlife surveys in Botswana were carried out in 1978, primarily in the northern part of the country. Since 1989, the entire country has been surveyed just three times by plane, although there have been more intensive surveys of local areas and several short-term studies of individual species.[14] Familiar shortcomings of aerial surveys are that there is seldom adequate verification or 'ground-truthing' of the methods, the resolution is often inadequate to answer questions about microhabitat preferences or diet, and the accuracy of the technique varies widely between species. However, we wish to draw attention to a less obvious but potentially more serious problem. Computer simulations of population estimation yield the unsettling result that estimates of population trends are notoriously inaccurate when based on few censuses, short time intervals between censuses, low sampling efficiency, or extrapolations based on censuses of only a small proportion of the population[18] – in other words, estimates based on the sampling methodology that DWNP and many regional wildlife management agencies are forced to rely on when they face budget limitations and a shortage of trained personnel. Not only does such a sampling protocol do a poor job of making quantitative projections of population size, but it can lead to the conclusion that populations are decreasing when in fact they are increasing, and vice versa.[18]

The point here is not to criticize DWNP for making use of the limited data available, but rather to stress that wildlife research requires that monitoring programmes be as frequent and comprehensive as possible. The accuracy of aerial counts should be verified by periodic ground-truthing. Unfortunately, such changes may be difficult to implement because of their costs, but other changes – establishing consistent methods, estimating variance in population size, calculating probabilities of misreading population trends – can be implemented at little or no cost. A relatively inexpensive solution in certain situations would be to establish fixed plots to be studied over the long term. Ideally, such plots should cover substantial areas and support a diversity of research projects, much like the Long-term Ecological Research Sites in North America.

For species of special concern, an effort should be made to understand population structure and life history traits. To reconstruct the reasons for past population trends or to forecast future trends using demographic models, wildlife managers need information about such factors as population sex ratio, operational sex ratio, population age structure, and age-specific fecundity and mortality schedules.[20,21] Where feasible, population genetic structure (e.g. level of heterozygosity, frequency and consequences of inbreeding, genetic uniqueness of population) and gene flow between populations should be determined.[22] Counting the number of individuals present in a population at a particular time from an airplane cannot provide sufficiently detailed demographic data to identify critical life history stages and the causes of variation in population growth rate, predict population trends or responses to perturbations accurately, or enable effective management.[19,23]

Choosing the right indicator species to monitor environmental change

When it proves too difficult or costly to study a particular species or group of species of concern, it may be possible to monitor another species that is more easily censused or environmentally sensitive. If carefully chosen, such indicator species can allow rapid assessment of habitats and provide early warning of declines in other species, or in environmental quality.[24,25] However, not all species can be used effectively as indicators. Take large mammals, which play an important role in the economy of Botswana and elsewhere in Africa because of their appeal to ecotourists. Their big size makes them easy to spot and count under certain conditions, and they are one of the few animal taxa that can be reliably censused from the air. Consequently, Botswana's Strategic Plan concentrates on the study of large mammals.

Unfortunately, except for their size, virtually everything else about the biology of most large mammals makes them a poor choice as indicator species to monitor the status of the ecosystem and environmental change. Many species are crepuscular or nocturnal, vocalize infrequently, aggregate in clumped spatial distributions, and migrate or wander seasonally. Such features add a large amount of noise to estimates of their population sizes. Their life-history characteristics (delayed reproductive maturity, small litter sizes), adaptable physiology, and complex behaviour make them relatively insensitive indicators of short-term environmental change.

In contrast, consider a resident bird species that is diurnal, territorial and relatively uniform in spatial distribution, and conspicuous in terms of song and behaviour. Birds can be accurately censused and their population densities extrapolated with reasonable confidence over wide areas. They are also sensitive to many of the same environmental factors as mammals (e.g. patterns of precipitation, plant productivity, temperature, and pollution). Yet birds are hardly mentioned in Botswana's Strategic Plan. There is no university-level course in ornithology offered in Botswana, and avian research at DWNP is a low and apparently declining priority. The Strategic Plan pays less attention to other potentially useful indicator species, such as amphibians and reptiles. Invertebrates are ignored altogether, in spite of their sensitivity to changes in vegetation structure and productivity;[26,27] soil invertebrates, for example, have been used to assess elephant impacts on vegetation in northern Botswana.[31] Research on plant communities is scarcely mentioned.[28,29] Also overlooked are lichens, which have been used elsewhere to gauge air quality, and aquatic organisms, which can be used to reflect water conditions.[30] Using small or sessile organisms to monitor environmental change and supplement aerial surveys of more economically important species can be cost-effective if censuses are systematic, long-term, and focused on permanent plots or transects. Within budgetary and personnel constraints, at least a small portion of wildlife research should be dedicated to identifying appropriate indicator species and habitats of concern, and developing low-cost, consistent methods for studying them.

Paying attention to process

Grant[22] notes, the focus of management is the population, but the focus of understanding is the ecosystem. The implications of certain types of species interactions – predation, competition, pollination, seed dispersal – are relatively straightforward and well-studied, and there is little justification for dedicating scarce wildlife research funds to extensive additional studies. Other interactions are more subtle. For example, in the Serengeti the maintenance of savanna where acacia woodlands once occurred was believed to be caused by the feeding activities of large numbers of elephants. Unexpectedly, however, regeneration of acacias did not occur after the reduction in elephant populations in the 1970s and 1980s.[32,33] Apparently, impalas (*Aepyceros melampus*), which prospered in the open habitats created by elephants, slowed the recovery of the woodlands by browsing on seedlings and saplings. Another example from the Serengeti involves the 'grazing succession' of Grevy's zebras (*Equus grevyi*), wildebeests, and Thomson's gazelles (*Gazelle thomsoni*).[34] Migratory herds of zebras graze tall grasses, and are followed by wildebeest, which prefer less coarse grasses and new growth. Finally, Thomson's gazelles, the most specialized of the three species, can eat the fine grasses and herbs exposed by the feeding activities of the other grazers. The interaction is further complicated by the different degrees to which plants show compensatory responses to herbivory.[35] These two examples illustrate the importance of understanding indirect effects and emergent properties in species interactions. Other key concepts and processes include guild structure, seed-bank dynamics, multi-trophic level interactions, decomposition and nutrient cycling, energy flow, disturbance (especially fire and drought) and ecosystem stability.[20,36,37]

A knowledge of processes comes most readily from carefully controlled and replicated experiments, ideally on a long time frame and covering a range of spatial scales.[6,38] Manipulative studies investigating the responses of plants to fire and grazing, carried out on permanent plots ranging in size from 0.1 ha to 225 km^2, yielded insights that could not have easily been predicted from within-site analyses.[39] Understanding species interactions and the ecological processes that drive such changes can take the guesswork out of 'adaptive' management.

The relevance of animal behaviour

A given lion pride is generally dominated by one or a few related males who exclude subordinate males and are responsible for fathering most or all of the young born by females of the pride.[40] Because of their size, dominant males are prized by trophy-hunters. If the dominant male is shot, a young male typically takes over the pride and may kill unrelated offspring. With the change in succession, often the pride degenerates, fracturing into small groups which have reduced reproductive success and are less likely to survive stressful periods.[40] It was basic research in animal behaviour that revealed the complex social system of lions. Such research can provide the underpinning of effective wildlife management.[4] For example, a goal of Botswana's Strategic Plan for Wildlife Research is to increase the abundance of roan, sable, and other game species for hunting. To determine the factors that influence population dynamics, a sensible place to start is natural history, including habitat requirements, diet, social organization, mating behaviour, physiology, mortality factors, and other seemingly unrelated aspects of basic biology. One might ask whether wildlife management agencies can afford the time, personnel and resources to study natural history. Unless such information is being gathered by other groups (university researchers, NGOs), we would ask, can they afford not to?

Incorporating an evolutionary perspective

Although evolution is considered the 'unifying concept in biology', wildlife researchers seldom pay it much attention.[6] Like medical and agricultural researchers who failed to anticipate the evolution of resistance to antibiotics or pesticides, wildlife researchers ignore evolutionary principles at their own hazard. The current debate within DWNP about the wisdom of drilling boreholes to provide surface water to sustain antelope populations and to spread out local concentrations of elephants is a case in point. The risk of epidemic diseases sweeping through wildlife populations aggregated around permanent water sources and causing epidemics is obvious.[10] However, the Strategic Plan does not address a separate risk, namely that relatively benign parasites can quickly become virulent pathogens under conditions where transmission rates are increased.[42]

Another advantage of taking an evolutionary perspective is that systems are seen as dynamic, encouraging the consideration of wildlife management strategies over broader time scales and the anticipation of long-term environmental problems such as global climate change. An evolutionary perspective also highlights the value of conducting baseline genetic inventories. An understanding of the genetic characteristics of populations (the frequency of unique genetic traits or adaptation to local conditions) is particularly important when contemplating reintroduction schemes such as those involving gemsbok and white rhinoceroses.

Beyond the biological species concept: 'conservation species concepts'

Botswana's Strategic Plan recommends concentrating research efforts on a small number of species selected mainly because of their importance in ecotourism, trophy hunting, or human conflicts, or because they are recognized as endangered or threatened. Conservation biologists have adopted a variety of 'conservation species concepts' in an effort to establish priorities for wildlife research and protect biodiversity most effectively. One example, indicator species, was discussed above. Cryptic species are populations that resemble named species, but they show subtle distinctions in terms of genetic characteristics, behaviour, or ecology. Siegfried and Brooke[43] estimate that there are as many as 10% additional unrecognized species of vertebrates in southern Africa. Identifying such cryptic species should become a higher priority of wildlife research. Keystone species (predators, parasites, competitors, or mutualists that play such a central role in plant or animal communities that any change in their abundances affects a much larger set of species) in different communities also need to be recognized; unless keystone species are monitored and protected, high-priority species like large mammals may be unwittingly jeopardized. The preservation of umbrella species, such as large raptors or carnivores, can be a useful strategy because it incidentally shields other species from extinction as long as the expansive ecological requirements of the umbrella species are protected. Finally, phylogenetically or ecologically distinctive species merit special attention from wildlife researchers because their survival preserves a genetic legacy or type of ecological interaction unrepresented by other taxa. Botswana's Strategic Plan would be strengthened by the explicit recognition of the importance of such conservation species concepts.

Conclusions

In this article we have recommended that strategic plans for wildlife research in Botswana can be improved by increasing the rigor and breadth of population monitoring techniques, studying in detail the natural history and behaviour of a broader diversity of animals and plants,[44] especially carefully chosen indicator species, and building an understanding of ecological and evolutionary processes. Unfortunately, the conservation problems faced by Botswana and other developing countries are as complicated and pressing as those elsewhere in the world, but the resources and trained personnel to tackle such issues are far fewer.[45,46] Is it naïve, then, to expect that small governmental research divisions with limited budgets and staff will be able to do much more than focus on problem animal control or censuses of economically important species? Not necessarily. An inexpensive first step towards creating a climate of exploratory, concept-driven research and on-the-job training would be to establish in-house seminar series, organize periodic meetings on special topics (e.g. techniques in population monitoring), and promote intellectual cross-pollination through visits by specialists from outside agencies and sabbatical leaves for staff members. Such innovations would lead to greater regional collaboration and more efficient transfer of new technologies and information.

Increasingly, wildlife research divisions must tap the skills and energy of biologists outside and inside government. This may mean streamlining regulations and shifting agency attitudes away from law enforcement towards the promotion of collaborative research with their natural allies in universities, museums, other governmental agencies, and NGOs.[47] By communicating to basic researchers the information needs of wildlife managers and by co-ordinating research endeavours and encouraging government biologists to collaborate with, for example, university students and faculty, agencies can acquire useful data at little extra expense. With a relatively small investment in additional training, park staff such as game wardens and scouts can play more active roles as researchers and parataxonomists.

Finally, strategic plans for wildlife research should have built into them a means for assessing their success. Follow-up studies should be conducted to evaluate the accuracy of population projections and assess the effects of natural disturbances or artificial manipulations, and research results should be published in peer-reviewed journals.[48] By adopting a few relatively inexpensive approaches, wildlife research and management in Botswana and other countries with limited resources can be greatly strengthened.

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The authors are in the Department of Biological Sciences, University of Botswana, PB 0022, Gaborone, Botswana. *Present address: Department of Biology, Bowdoin College, Brunswick, ME 04011, USA.
E-mail: nwheel@bowdoin.edu