COMMENTARY

Managing wildlife for ecological, socioeconomic, and evolutionary sustainability

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Predicting the Consequences of Selective Harvesting

Selective harvesting of animals is widespread throughout the marine, freshwater, and terrestrial environments and affects a diverse list of species, including fish, mammals, birds, and reptiles (1). Such harvesting can cause changes in the distribution of phenotypic traits within target populations, often with undesirable biological and economic consequences. For example, selective harvesting has been linked to declines in the size of trophy horns in two antelope species in Zimbabwe (2) and of antlers in red deer (*Cervus elaphus*) in Europe (3, 4), as well as to earlier maturation in some fish species (5). However, the extent to which these changes are the result of ecological or evolutionary mechanisms has been much debated (1). In PNAS, Traill et al. (6) approach this question from a novel angle by developing stochastic two-sex integral projection models (IPMs) capable of differentiating between the ecological and evolutionary effects of selective harvest. Their finding that evolutionary mechanisms contribute relatively little to observed changes in the body mass of bighorn sheep (*Ovis canadensis*) is an intriguing contribution to the debate over the evolutionary consequences of selective offtake, contradicting earlier studies (7). In addition, Traill et al. (6) suggest that their method could be adopted more widely to allow wildlife managers and conservation practitioners to incorporate the potential evolutionary effects of selective harvesting into their management planning. Here, we explore this suggestion by discussing key challenges that would need to be addressed to translate the approach by Traill et al. (6) from a purely biological model to an effective management model, focusing particularly on issues of data availability and the incorporation of different forms of uncertainty.

Long-Term Individual-Based Data

The first challenge, if IPMs are to achieve widespread use in the management of harvested species, is their dependence on long-term individual-based data. The model by Traill et al. (6) is parameterized for a species, the bighorn sheep, which has been the subject of extensive study (7). However, the combination of long-term, individual trait-based data and detailed records of harvesting offtake is likely to be rare for (*i*) the species of most conservation concern and (*ii*) species of social, cultural, and economic importance (e.g., those targeted by fisheries, recreational, and subsistence hunting). For example, one of the longest published datasets for trophy hunted species of conservation concern suggests that declines in lion (*Panthera leo*) and leopard (*Panthera pardus*) populations are linked to trophy hunting (8), yet even here it is not clear whether the individual-level trait data needed to construct an IPM are also available. In the absence of such data, Traill et al. (6) suggest that allometric relationships could be used to parameterize IPMs, but acknowledge that further work would be needed to determine how reliable this approach would be. In principle, technologies such as global positioning system (GPS) collars and satellite imagery might allow long-term data to be collected for other species in the future (9). However, the tradeoffs arising from any large-scale investment in long-term monitoring should always be considered (10). In particular, managers should seek to determine whether the benefits gained from understanding long-term evolutionary effects outweigh those that could be achieved if resources were invested to reduce uncertainties in other components of the harvesting system (e.g., the behavior of resource users, see below).

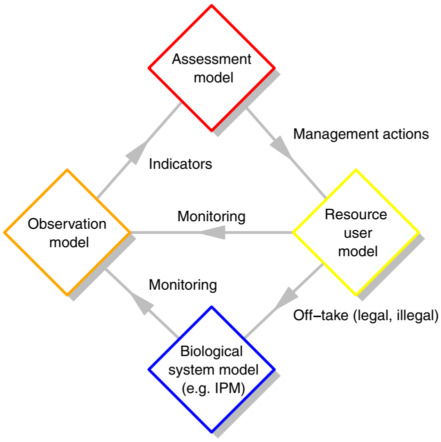

Fig. 1. Management strategy evaluation framework for the sustainable harvest management of wildlife. The framework includes a biological system model that simulates the dynamics of a wildlife species or system, an observation model that monitors the wildlife and the people involved, the assessment model that is used to make decisions based on the indicators from the observation model, and the resource user model that represents the cultural, social, and economic incentives driving people's decisions and therefore offtake.

The Importance of Uncertainties in the Management Process

In their model, Traill et al. (6) assume a simple proportional harvesting strategy and test their method for harvest pressures ranging from 1% to 85% of males in the bighorn sheep population. Similar assumptions are common in harvesting models, but fail to capture important sources of uncertainty present in real-world systems. The outcomes of harvesting arise from the interactions between management authorities, legal and illegal resource users, the exploited resource and the environment, and the effectiveness of management strategies can be strongly influenced by uncertainty arising from any one of these components (11, 12). An illustrative example concerns the effects

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of uncertainties in the observation process. The true size of a population is never known and can only be estimated with error by managers through monitoring. In some cases, this observation error (e.g., the discrepancy between the expected offtake and actual offtake) can be substantial and dramatically increase the risk of population collapse, as shown for hunted ungulate and bird species (11).

A second example concerns uncertainty in the implementation of management strategies. Managing a harvested resource successfully depends on being able to manage the behavior of resource users (12). However, there remains a tendency for harvesting models to incorporate only simplistic representations of harvester behavior (e.g., assuming a proportional offtake). Failures to properly account for economic, social, and cultural processes can lead to unintended and unexpected consequences. For example, a comparison of reported sales data with recorded catch data for the Southern Bluefin Tuna (*Thunnus maccoyi*) found that total catches were up to 50% higher than had been assumed due to a large proportion of catches going unreported. These unreported catches arose because of the difficulty involved in monitoring compliance with catch quotas for a high-value fish and contributed to the collapse of the resource (13). Another example comes from grizzly bear (*Ursus arctos horribilis*) hunting in Canada, where realized offtakes were higher than set by management plans in 19% of populations studied (14). In many cases, the incentives underlying the illegal and unreported harvest remain poorly understood because case studies have focused entirely on ecological data, despite the fact that harvesting is also a topic of considerable interest in the social sciences (15). An important and often-cited challenge for wildlife management is how to combine the diverse expertise, data, and insights available from social scientists, ecologists, and evolutionary biologists together to achieve effective outcomes.

Moving Toward Social-Ecological-Evolutionary Modeling?

One approach to integrating the multiple processes, dynamics, and sources of uncertainty associated with harvesting within a common framework is termed management strategy evaluation (MSE; Fig. 1) (16, 17). MSE was pioneered by fisheries scientists, and its strength comes from explicitly modeling harvesting as a set of interconnected subsystems: a biological resource model, simulating the dynamics of a species or natural system; an observation model, incorporating uncertainties from the monitoring process; and an assessment model reflecting the management decision-making process based on the monitoring. Recent developments have also included an additional decision-making model for the resource user based on their economic incentives (18). In most applications to date, the biology of the harvested species has generally been represented in MSE by matrix population models (19). However, if data requirements can be met, it would be straightforward for future MSE models to adopt the type of IPMs developed by Traill et al. (6) as their biological resource model, thereby allowing managers to examine ecological, evolutionary, and economic criteria together when making decisions on harvest strategies (Fig. 1).

Novel approaches, such as the IPMs outlined in Traill et al., represent another valuable step toward a broader, multidimensional understanding of harvesting systems.

Understanding and predicting how to manage harvested resources effectively and sustainably is one of the central challenges facing wildlife managers, applied ecologists, and social scientists. Models can undoubtedly play an important role in disentangling the complexity inherent in harvesting systems, but our ability to model management decisions under uncertainty for ecological, evolutionary, and socioeconomic sustainability is still in its infancy. To date, models of harvesting have predominately focused on its ecological effects; few tools exist for predicting its evolutionary consequences, and none has yet combined ecological and evolutionary considerations with realistic representations of harvester behavior. Novel approaches, such as the IPMs outlined in Traill et al. (6), represent another valuable step toward a broader, multidimensional understanding of harvesting systems.

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