Managing harvest and habitat as integrated components

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Abstract

In 2007, several important initiatives in the North American waterfowl management community called for an integrated approach to habitat and harvest management. The essence of the call for integration is that harvest and habitat management affect the same resources, yet exist as separate endeavours with very different regulatory contexts. A common modelling framework could help these management streams to better understand their mutual effects. Particularly, how does successful habitat management increase harvest potential? Also, how do regional habitat programmes and large-scale harvest strategies affect continental population sizes (a metric used to express habitat goals)? In the ensuing five years, several projects took on different aspects of these challenges. While all of these projects are still on-going, and are not yet sufficiently developed to produce guidance for management decisions, they have been influential in expanding the dialogue and producing some important emerging lessons. The first lesson has been that one of the more difficult aspects of integration is not the integration across decision contexts, but the integration across spatial and temporal scales. Habitat management occurs at local and regional scales. Harvest management decisions are made at a continental scale. How do these actions, taken at different scales, combine to influence waterfowl population dynamics at all scales? The second lesson has been that consideration of the interface of habitat and harvest management can generate important insights into the objectives underlying the decision context. Often the objectives are very complex and trade-off against one another. The third lesson follows from the second – if an understanding of the fundamental objectives is paramount, there is no escaping the need for a better understanding of human dimensions, specifically the desires of hunters and non-hunters and the role they play in conservation. In the end, the compelling question is how to better understand, guide and justify decisions about conservation investments in waterfowl management. Future efforts to integrate harvest and habitat management will include completion of the species-specific case-studies, initiation of policy discussions around how to integrate the decision contexts and governing institutions, and possible consideration of a new level of integration – integration of harvest and habitats management decisions across waterfowl stocks.

Key words: decision analysis, habitat management, harvest management, integration, objectives, population models, yield curve.

Waterfowl management in North America seeks the joint goals of providing hunting opportunity and conserving waterfowl populations by regulating harvest through the Migratory Bird Treaty Act of 1918 and of protecting and improving habitats through the North American Waterfowl Management Plan (NAWMP). Over time, waterfowl harvest management has evolved into one of the best applications of adaptive resource management in the world, where annual hunting regulations are set based on quantitative population models, data collected annually, and optimisation methods designed to make the best possible decision in the face of many sources of uncertainty to insure large sustainable harvests (Nichols *et al.* 1995, 2007). Habitat management is organised around a series of public-private partnerships (Joint Ventures) that endeavour to protect and improve waterfowl habitat to meet specific population goals for each of several species. While both harvest and habitat management efforts are designed for the same populations, they are administered under different and independent regulatory contexts with goals that are possibly not consistent (Runge *et al.* 2006). The NAWMP population goals were developed in reference to waterfowl populations and habitat conditions of the 1970s, a decade of above-average habitat conditions, and without reference to a specific harvest policy. Harvest policy does not explicitly give a population goal, but instead is designed to achieve sustained harvests over a very long timeframe, which implicitly strives for an average population size to support that harvest. Because expected population size is linked to harvest rate and habitat conditions, interpreting the population goals stated in the NAWMP is impossible without reference to specific habitat conditions and harvest policy (Runge *et al.* 2006). In other words, population goals specified under harvest and habitat management plans are not currently coherent, and recognition of this problem has catalysed several efforts to reconcile these plans.

The first effort was the formation of a Joint Task Group (JTG) sanctioned by NAWMP and the International Association of Fish and Wildlife Agencies "to explore options and recommend preferred solutions to reconciling the use of [NAWMP] population objectives for harvest and habitat management" (Anderson *et al.* 2007). NAWMP partners needed a shared context for habitat and population goals; harvest managers needed to be able to translate NAWMP accomplishments into harvest opportunity. To accomplish this, a theoretical assessment framework was formulated around a population model that included density-dependent relationships in survival and reproduction, which could then be translated into ecological concepts of carrying capacity and a sustainable yield curve (Fig. 1, Appendix 1). The JTG

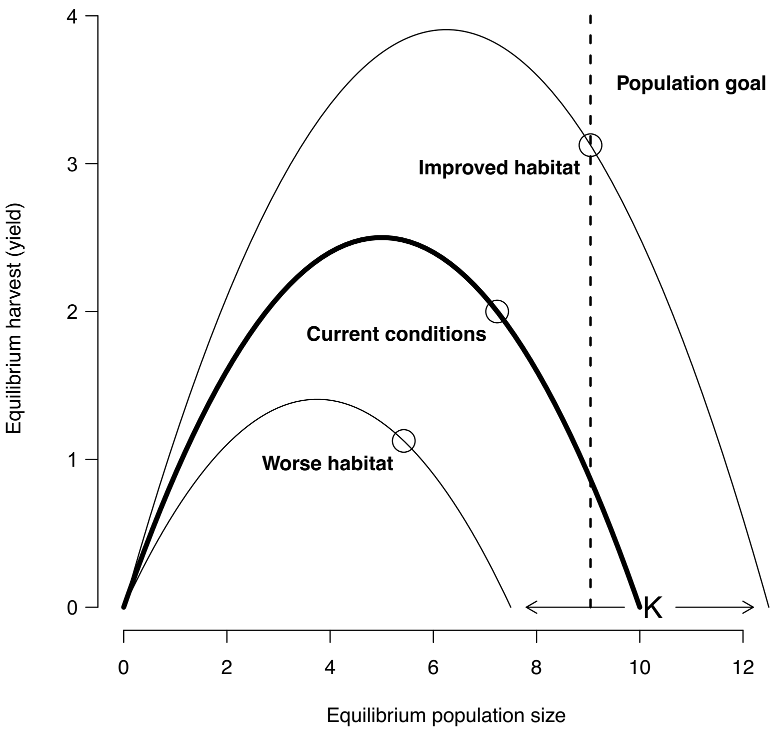

Figure 1. Using yield curves to understand the relationship between harvest and habitat management. The open circles represent a "right-shoulder strategy" – a harvest policy that maintains a yield less than the maximum sustained yield (the choice of the position on the right shoulder, here 80%, is a policy determination). Improved or worsened habitat is shown by an expanded or contracted yield curve (the curves shown are based on a 25% increase or decrease both in intrinsic growth rate, *r*, and in carrying capacity, *K*). A population goal (dashed line) is said to be "coherent" if it falls at the intersection of the desired harvest strategy and the desired habitat conditions.

explored various interpretations of NAWMP population goals in terms of sustainable harvest levels in light of the above-average habitat conditions of the 1970s. The main proposal was that population goals of the NAWMP are best interpreted as the expected population size found when a harvest strategy that seeks less than maximum sustained yield (a "shoulder strategy") is overlain with a yield curve that reflects the desired long-term average habitat conditions.

A sustainable yield curve (Fig. 1, Appendix 1) provides the conceptual framework needed to integrate harvest and habitat management (Runge *et al.* 2006; Anderson *et al.* 2007). A sustainable yield curve shows all the equilibrium points of a deterministic density-dependent population model, such as the familiar logistic growth model (Fig. 1). This model posits that birth rate declines and/or death rate increases with population density, for which there is good evidence in waterfowl (Vickery & Nudds 1984; Cooch *et al.* 1989; Sedinger *et al.* 1995; Johnson *et al.* 1997; Sedinger *et al.* 2001; Conroy *et al.* 2002; Runge & Boomer 2005; Viljugrein *et al.* 2005). If this is the case and both environmental conditions and harvest rate remain constant, then the population size and structure approaches a stable equilibrium, where birth and death rates are equal. In the absence of harvest, the population moves toward carrying capacity, the maximum equilibrium population size determined by the density-dependent effects. With harvest, the population will reach a stable equilibrium less than carrying capacity, and the yield curve describes this equilibrium population size for all harvests (Fig. 1). Of course the environment and harvest rates are not constant and populations do not behave deterministically. The environment can fluctuate on short time scales (annual variation in precipitation) or shift to new long-term average conditions (multi-year changes in agriculture policy, climate change, or permanent habitat loss or improvements). Short-term fluctuations in the environment or population size are not reflected in the yield curve; instead, the yield curve can be viewed as an average over these fluctuations for a large population. If long-term shifts change demographic rates, perhaps through changes in the strength of density-dependence, then the yield curve itself will expand or contract, so that a new equilibrium population size is realised for the same harvest rate, or a new harvest rate is required to realise the same population size (Fig. 1, Appendix 1). This is the crux of integrating habitat and harvest management – we can now ask to what extent demographic rates need to shift due to habitat management in order to obtain a desired population size and harvest rate. Conversely, we can ask what combination of harvest rate and population size (a harvest policy) we want to achieve under current habitat conditions.

The realisation among the waterfowl management community that population goals of the NAWMP only make sense in light of a particular harvest strategy has brought the human component of management to the forefront. Hunter satisfaction underlies both NAWMP goals and harvest policy but little is known about their relative importance to hunter satisfaction, which harvest managers need to know to set a desirable harvest and habitat policy. If we are below a population goal because of a shrinking habitat base, do we reduce harvest to maintain the population at goal? Or do we maintain harvest (by increasing the *per capita* harvest rate), thus driving the population even lower, in order to satisfy harvest desires of hunters? As long as populations remain large, relative to demographic and environmental stochasticity, so that extinction is not likely or ecological services are not jeopardised, these seem like fair policy alternatives. Yet we know little about how hunters and other stakeholders value population sizes and harvests. The JTG recognised this and called for an in-depth study of human dimensions underlying waterfowl management.

While the JTG was demonstrating conceptual and empirical approaches for providing a formal integration of harvest and habitat management objectives, a parallel process was underway to evaluate, for the first time, the NAWMP's effectiveness in achieving its biological goals (Assessment Steering Committee 2007). This assessment unearthed the many strengths and weaknesses inherent in planning and delivering large-scale conservation programmes, and produced wide-ranging recommendations related to NAWMP planning, adaptive processes, implementation strategies, institutional issues, integration among bird groups and funding. Most relevant here are recommendations that focused on developing improved ways of linking demographic and population responses to habitat management at scales ranging from Joint Ventures (JVs) to the continent, determining the impact of net landscape changes on waterfowl demography, and enhancing the ability to target financial investment in different regions of North America to advance NAWPM objectives. A comprehensive review of population and habitat objectives was also advocated. Addressing these recommendations alone creates significant challenges, both conceptually and operationally. For instance, habitat management typically occurs locally, with investments intended to return long-term benefits. On the other hand, harvest management decisions are made in short time steps, usually annually, with broad-scale impacts on birds. Thus, a central problem was to provide mechanisms allowing the integration of harvest and habitat objectives in ways that could reveal how management decisions could influence demographic rates within JVs or ecologically-related regions, and in turn scale up to affect continental population dynamics. Importantly, such an approach would provide new insights into optimal allocation of limited conservation resources to where they would have potential for greatest impacts.

In 2012 the NAWMP community reached consensus that a third goal, addressing the benefits of waterfowl populations and habitats to people, should be included explicitly in the NAWMP (NAWMP 2012a), and agreed that efforts to define objectives for hunters, conservation supporters and the general public should be continued. The conceptual and technical advances required to integrate these linked NAWMP goals (*i.e.* for habitat, harvest and people) have been explored in case studies focused on Black Duck *Anas rubripies*, Northern Pintail *Anas acuta* and scaup (*Aythia marila* and *A. affinis*) populations. These initiatives were expected to reveal new knowledge about relationships between population processes and management decisions, and also trade-offs at multiple scales. Furthermore, all three species are of high conservation concern due to their population status, trends in numbers, and their importance to hunters in North American flyways. Each initiative has pursued a different analytical approach in addressing unique problems encountered in integrating harvest and habitat management. Importantly, each initiative has also engaged the waterfowl community in consultation processes, to gain critical insights from managers and scientists alike on the provision of guidance about biological models that link demographic rates to regional habitat planning and harvest, which were used to inform JV management decisions. Future implementation of the NAWMP will be shaped in part by results of these case studies. Indeed, because there has been no clear route paving the way to successful integration of different components of the plan, there is high expectation that pilot projects will help to unveil how integration may be achieved (NAWMP 2012b).

Insights gained to date

In 2006, Runge *et al.* (2006) raised significant questions about the disconnected nature of waterfowl harvest and habitat management, suggesting the two programmes needed to be more coherent. The "coherence paper" (Runge *et al.* 2006) was received with scepticism by some who asked what the concern was about. The JV system is a highly successful model of collaborative landscape conservation, delivering waterfowl habitat management at a local and regional scale (Williams *et al.* 1999; Assessment Steering Committee 2007). Adaptive Harvest Management (AHM) has provided a stable and transparent way of setting harvest regulations (Nichols *et al.* 2007). Both habitat and harvest management appeared to be working well, so why make things more complicated? Was integration technically feasible? And even if it was, would it matter to the decisions being made? To some extent, we cannot yet fully answer these questions, as the various efforts to integrate habitat and harvest management are still works-in-progress, but the work of the last five years has changed much of the thinking about waterfowl management in North America. These advances include learning about potential consequences of habitat and harvest management decisions given inherent system dynamics (*i.e.* partial controllability), identifying critical information gaps (*i.e.* factors that seem most important for population dynamics but for which new information is required) and demonstrating that integration is entirely feasible and potentially useful. Thus, the case studies presented below give compelling reasons for integration, especially by providing a better understanding of population dynamics and in justifying decisions about investing scarce conservation resources in order to achieve the desired outcomes. Several important lessons about integration are emerging, as described below.

Integrating models

The first lesson concerns the efforts to build integrated models that can represent the effects of both harvest and habitat management, thus making underlying assumptions of habitat and harvest management explicit. One of the most difficult aspects of this task is not the integration of habitat and harvest in a theoretical sense (see Appendix 1), but the integration across spatial scales and the estimation of relevant parameters. The key question is this: how do habitat actions at the local scale translate into population responses at the continental scale? Habitat management occurs at a local scale where land managers work to bring about long-term habitat change in a region, such as in a JV. Bird populations that are the target of habitat management are moving among habitats within a region and across regions. These movements act to average or dampen the effects of any one habitat effect, be it local or regional, and also make it very difficult to demonstrate empirically an effect of habitat improvements on population demographic rates. Harvest management, on the other hand, occurs at the continental scale, where season length and bag limit are set annually on the basis of population goals and an underlying model of the extent to which density-dependence influences population dynamics. Integration therefore requires linking dynamics across the local, regional and continental scales. In the Integrated Waterbird Management & Monitoring (IWMM) example given below, this integration requires an understanding of the spatial structure of the landscape that links local habitat conditions with the birds' migratory behaviour, and an estimation of the parameters (sometimes difficult to establish) that describe that process. In the pintail case study, for example, the challenge of parameter estimation includes drawing inference about intermediate-scale processes that have not been observed directly in the field.

Building mathematical models is a means to make assumptions explicit and to understand the consequences of actions. Once hypotheses have been explicitly stated, they should be rigorously tested when possible if the claim of science-based management is to have any merit. There is almost 20 years of doing just this under adaptive harvest management for waterfowl (Cooch *et al.* 2014) but a similar process for habitat management is less developed. Stating and testing assumptions about habitat management is an important recommendation of the NAWMP assessment efforts (Assessment Steering Committee 2007), and the efforts toward integration have made major advances in building models that represent assumptions about how habitat is linked to demographic rates. For example, the hypothesis that winter survival is driven by energy limitation underlies many decisions about habitat management, yet demonstrating a causal link between energy limitation and survival in wintering waterfowl has been elusive. Given that some studies show relatively high survival after the hunting season (*e.g.* Dugger *et al.* 1994; Fleskes *et al.* 2007) and that energy surpluses are evoked to explain increasing goose populations (Ankney 1996), testing this assumption and considering alternatives seems reasonable, including refinements to existing energy hypotheses and other mechanisms. Efforts of integration, discussed below, provide a framework to do just this.

Integrating objectives

The second lesson follows from the first. Habitat management is done at local or regional scales to meet local and regional objectives for populations, habitat and harvest, but ultimately habitat management is meant to scale up to affect continental population objectives. Because the entire initiative to integrate habitat management with harvest management has been framed as a decision, this has led the waterfowl management community to explore and articulate these objectives, to discover new objectives, and eventually realise that trade-offs between objectives will be necessary. Thus, the work to integrate habitat and harvest management has led the waterfowl management community to focus on and articulate objectives more clearly and to use a more structured approach (NAWMP 2012a), which in itself is a major accomplishment.

More complex objectives and trade-offs emerge as we consider the entire range of scales from local to continental. At the continental scale, the simplest of these trade-offs is that one cannot have higher average harvest rate without a subsequent decrease in expected population size if harvest mortality is not fully compensated by reduced natural mortality (Anderson & Burnham 1976; Cooch *et al.* 2014; Appendix 1). This has led to an examination and re-interpretation of the population objectives in the original NAWMP (NAWMP 2012a). At the regional and local scales, issues of population distribution and equity of hunter and non-hunter access arise. This can then lead to conflicts between objectives: should conservation resources be allocated to a region if it can be shown that habitat improvement in the region has little value for improving continental populations? Simply asking this question in the context of the decision reveals that other objectives, perhaps not yet fully articulated, exist.

Integrating human desires and governance

The third lesson follows directly from considering objectives in a decision context. When we realise that decisions are ultimately grounded in the objectives, we have to ask where those objectives come from. What are our hopes for waterfowl habitat and populations, and why? What do hunters want, and how does their conservation role affect the achievement of the other objectives? How do we structure governing institutions to best meet these objectives? This leads to focusing on human dimensions of waterfowl management and on the structure of governing institutions because the human component of waterfowl management is important, perhaps most important, for understanding objectives, making optimal decisions and designing institutions that can facilitate optimal decision making. This is especially the case when trade-offs between objectives or scales become necessary. The waterfowl management community must know how objectives rank in importance across stakeholder groups and this can only come from focused research on these groups to determine their values. For example, much of traditional waterfowl management and current harvest regulation is based on the assumption that hunter satisfaction increases with larger harvests. This may be true, but how is hunter satisfaction related to continental population size? If larger harvests are valued, how do hunters value season length and bag limit combinations that might lead to the same harvest? These questions can be extended to a broader set of stakeholders. For instance, how does non-hunter (or even anti-hunting) satisfaction depend on continental population size? How does it depend on local hunting activity? The waterfowl management community knows very little about the desires of hunters, and probably even less about the desires of non-hunters. If the general assumption is that hunter satisfaction increases with harvest and population size, is it reasonable to assume that non-hunting stakeholders' satisfaction is neutral to these metrics? Do these management choices affect the political and economic support hunters or non-hunters give to waterfowl and wetlands conservation? Finally, waterfowl hunters have historically had a strong tie to conservation of wetlands and waterfowl, but hunter numbers are declining to the extent that continued participation in waterfowl hunting is itself a major concern (Vrtiska *et al.* 2013). If decisions about harvest and habitat management affect hunter satisfaction can these decisions also be used to increase waterfowl hunter numbers through recruitment of new hunters and retention of current hunters? This is currently unknown, but by focusing on the decision context, human dimensions have moved to the forefront of the integration of habitat management and harvest. These issues are especially clear in the scaup example, given below, where the hunter population was included in the scaup population model, just as in models of classic predator-prey systems. However, all the integrated models in the world won't get us anywhere if different agencies, authorities, administrations or nations are not willing to integrate and coordinate policy and programmes that affect conservation and management at the continental level.

Expanding the range of objectives under consideration raises questions about the governance structures that support management. Government agencies have a public trust responsibility to include input from a broad array of stakeholders, the hunting and non-hunting public alike. But the strongest "stakeholder" input for government agencies comes from their statutory mandates. For waterfowl management, U.S. federal agencies must adhere to the Migratory Bird Treaty Act, which puts a primary emphasis on migratory bird populations and their habitats, with only secondary consideration given to consumptive and non-consumptive use. Thus, other entities (*e.g.* state agencies and non-government organisations (NGOs)) may be better enabled to pursue objectives like hunter satisfaction, but the current governance of habitat and harvest through the flyway system might not yet provide an effective structure for inclusion of these broader aims. These governance issues, along with the complicated governance issues associated with habitat protection and management by a diverse array of landholders, point to the need for thoughtful consideration of the institutional relationships that underlie waterfowl harvest and habitat management.

In short, the emerging efforts to integrate harvest and habitat management, which originated from a simple suggestion that the NAWMP population objectives might need revision (Runge *et al.* 2006), have precipitated a much deeper examination of the decision structures used for habitat and harvest management and the technical tools used to support them. It has been both a significant challenge, with many technical issues yet to address, as well as a unique opportunity to push the boundaries of our current approach. Success is not assured, but we will learn much even if our aspirations are not fully realised at the operational level. The following case studies describe these efforts in more detail.

Case studies

"Integrated Waterbird Management and Monitoring Initiative" (IWMM)

The U.S. Fish and Wildlife Service (USFWS), Joint Ventures (JVs), and the Flyway Councils work to conserve migratory waterbird populations by informing and implementing habitat and other management actions. The conservation of migratory waterbird populations and their habitats is an inherently challenging proposition given the geographic and temporal scope of species' life histories. Few biological models exist to address problems at such a large scale. Furthermore, the challenge is amplified by the fact that biological processes do not align with administrative programme boundaries and successful management for these species depends on linking management decisions at multiple spatial scales. At each scale, habitat management decisions involve allocating resources efficiently, in light of financial and personnel limitations and the need for public accountability, to maximise the benefits for waterbird populations. Decision analytic techniques hold promise for addressing these challenges in a structured and transparent manner (Wilson *et al.* 2007; McDonald-Madden *et al.* 2008; Thogmartin *et al.* 2009).

The IWMM seeks to provide decision support tools at multiple scales to aid waterbird habitat managers across the Atlantic and Mississippi Flyways. IWMM represents a joint initiative of conservation partners, including the USFWS, U.S. Geological Survey, state agencies and Ducks Unlimited. To date, IWMM has provided standardised waterbird and habitat monitoring protocols and a common database with reporting tools to participants across the two flyways, and coordinated pilot data collection has been underway for more than three years. Through the application of structured decision analytic techniques (Gregory *et al.* 2012), IWMM identified pressing waterbird management decisions at multiple spatial scales. At a flyway scale, decisions must be made about habitat acquisitions and restorations within the context of budgetary constraints. At a local scale, managers annually determine how to manage habitat within a wetland or collection of wetlands to maximise long-term benefits for waterbird populations. IWMM recognises that these habitat management decisions are naturally linked across scales.

IWMM's technical team is developing models for decision support at multiple scales. To address habitat acquisition and restoration decisions at a flyway scale, the team has developed a continental scale simulation model to couple waterbird survival during the migratory period to the amount and distribution of energy (in the form of appropriate habitat) across the flyways; thus, incorporating explicit hypotheses about energy limitation as a determinant of survival during the migratory period. The model uses geospatial land cover layers and land cover-specific roosting and caloric values to represent the quality of stopover sites. Portfolios of land acquisition and restoration decisions are evaluated by altering flyway food energy content and examining the change in survival that results from these decisions. The model identifies areas along the flyway that have a large benefit for the survival of individuals within a specific guild or species relative to the cost of management or acquisition. Insight can be provided to local managers about the importance of their general areas for non-breeding survival of specific guilds or species, linking management priorities at flyway and local scales.

For the eastern U.S., the flyway scale model is in the late stages of development (Eric Lonsdorf, unpubl. data). The model represents an important advance in guiding land acquisitions by explicitly linking hypotheses about waterbird biology to alternative acquisition and restoration decisions. The model can also help local managers understand the importance of their wetlands for specific waterbird guilds or species in a larger flyway context. For example, the flyway model can be incorporated into a structured decision making process to evaluate land acquisitions by the National Wildlife Refuge system. This framework can also allow for the inclusion of alternative models in an adaptive management programme to learn about population demographic rates while guiding refuge acquisition and management.

Although the IWMM initiative was not originally designed to integrate harvest and habitat, it has provided valuable tools and insights about the process of integration. The development of the IWMM predictive models has faced a deep challenge: integrating habitat management and waterbird demography across scales. This requires identifying the mechanisms that connect local-scale influences to broad-scale outcomes, in this case, physiological energetics and behavioural adaptations to the distribution of food resources (and thus energy) across the landscape, so that individual and local habitat mechanisms give rise to patterns of migration at the flyway scale. Processes that connect the local to the continental scales are often not observed directly, and yet they are the crux of understanding how habitat management translates into demographic change. There are significant challenges in estimating the parameters of these processes, but formal methods of expert judgment and modern Bayesian hierarchical methods are bearing fruit. The important lesson, perhaps, is that we cannot shy away from understanding the complex processes that link dynamics across scales; indeed, that is one of the most important aspects of developing integrated models.

Northern Pintail

In the integration efforts focused on pintail, the central focus was to build a formal mathematical framework to link habitat and harvest management across spatial scales. The integrated pintail model is a spatial version of that currently used in pintail harvest management (USFWS 2010; Mattsson *et al.* 2012). This is a spatial matrix-projection model with an annual time step partitioned into seasonal components to reflect the annual cycle of breeding, autumn migration and winter through spring migration. Breeding areas are separated into two spatial components to reflect regional differences – Alaska and the prairie potholes and parkland, with a third "breeding" class used to represent drought years when pintail are less likely to attempt breeding and are generally less observable (Runge & Boomer 2005). Wintering areas are divided into two regions – the California Central Valley and the Gulf Coast, to reflect potential differences in non-breeding season survival and density-dependence (Mattsson *et al.* 2012). The key aspects to the model are: 1) the migratory transitions that link winter grounds to breeding grounds, and 2) the density-dependent relationships for recruitment and survival in each breeding and wintering region, respectively (Fig. 2).

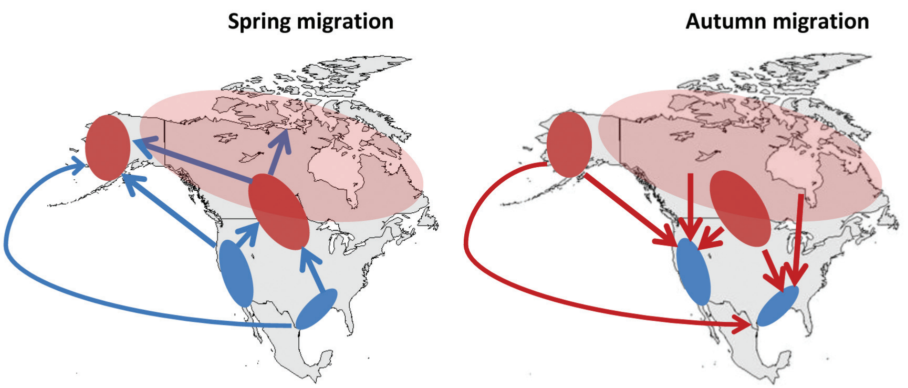

Figure 2. Pintail metapopulation model that allows analysis of the interaction of habitat and harvest management (after Mattsson *et al.* 2012). Two core breeding areas (Alaska and prairie-parklands, red) and two core wintering areas (primarily the California Central Valley of the Pacific flyway and the gulf coast of the Central and Mississippi flyways, blue) are linked through autumn (red arrows) and spring (blue arrows) migratory transitions. A third breeding season state is used to represent movements of pintail in drought years when breeding effort and observability of the population is low (large light red area). Arrows represent starting and ending locations of migration and not the geographic route of migrating pintail.

Using parameter values from published literature and expert judgment, the model can then be analysed to investigate the effects of habitat improvements on the yield curve. Efforts are now underway to use available long-term data sets on harvest, band recoveries and breeding population surveys to refine parameters for the model, including estimating the form and strength of the regional density-dependent relationships. Just as with IWMM, there are few direct data to inform intermediate processes. The ongoing approach to estimation is to use multiple data sources linked by the matrix projection model in a common hierarchical Bayesian statistical analysis, which can provide information on these hidden processes.

There have been two major accomplishments from work on the integration of pintail harvest and habitat data to date. The first is the demonstration that it is theoretically possible to link habitat and harvest across scales (Mattsson *et al.* 2012). The integrated pintail model shows how habitat improvements at the regional level might increase pintail demographic rates in that region, and hence can increase the continental yield curve. In the future, this model can be used to inform allocation of conservation resources. For example, preliminary analyses of the initial model suggests that proportional habitat-related improvements on prairie-parkland breeding areas could be more effective at increasing the yield curve than equal proportional improvements to wintering areas (Mattsson *et al.* 2012). Confirmation of this conclusion awaits formal parameter estimation and a better understanding of local processes through the development of mechanistic models, which are underway.

The second major accomplishment has been to motivate in-depth discussions about the assumptions and mechanisms of population regulation at the regional scale, as these are critical for translating local habitat management into continental demographic impacts. In several workshops, hypothesised mechanisms of density-dependence were elicited from local experts, resulting in a series of conceptual models that link changes in habitat to regional productivity or survival. In the prairie-parkland breeding region, competition for space is thought to be the leading driver of density-dependence. Annual variation in precipitation produces variation in pond numbers and distribution and this leads to variation in pintail breeding effort and distribution. However, the key element here is that, after controlling for precipitation-induced variation, pintail density has an additional effect. Thus in years of higher than average pintail numbers, more pintail nest in habitats of the prairie-parkland region where reproductive success is lower (J.H. Devries, pers. comm.). In the wintering regions, the focus is on the relationship between density and post-hunting season survival, through the effects of a limited food supply (and thus energy intake) on the birds' body mass in winter and spring. The assumption here is that habitat managers can increase pintail survival by providing more nutritious food resources; in years with higher post-hunting season population size and greater food depletion, survival is reduced compared to years with lower populations and identical habitat. These regional sub-models are intended to provide predictive tools that, when coupled with the continental demographic model, will provide an analytical framework for assessing the effects of local habitat changes on the continental yield curve.

Two insights emerge from the pintail work. First, one of the most challenging aspects of integrating habitat and harvest management is developing demographic models that integrate dynamics across spatial scales. Indeed, as with the IWMM project, the pintail project recognised that the crux of the modelling effort was the identification of intermediate-scale mechanisms of population regulation, such as the regional density-dependence relationships. The second insight arises from an ongoing challenge: these intermediate-scale mechanisms are difficult to observe directly, and so estimating the functions and parameters is likewise difficult. Fortunately, modern hierarchical statistical methods can potentially be used to make inference about such hidden processes, in this case by using observations at both the local and continental scales to gather insights about the mechanisms that link the dynamics across scales. Where possible, of course, efforts to measure demographic rates directly and to test hypotheses underlying habitat and harvest management should be encouraged, but modern inferential methods provide a promising alternative.

Scaup

Substantial declines in the continental scaup population in the 1980s and 1990s attracted concern from biologists and hunters alike. Biologists first approached the problem from the bottom up, examining long-term population and harvest data to develop hypotheses about factors that potentially were contributing to population decline (Austin *et al.* 2000; Afton & Anderson 2001; Austin *et al.* 2014). However, a model-based approach such as that used for the Northern Pintail was precluded because of broad uncertainties, particularly the absence of contemporary annual survival rates, sparse data on vital rates from breeding grounds in the boreal forest and taiga, and uncertainties about the population trends for each scaup species separately. It was clear that the research and monitoring necessary to fill these knowledge gaps, and to clarify the key factors affecting scaup, would require substantial resources, time and collaboration. At the same time, debate was growing about how adaptive harvest management affected the harvest of species other than Mallard *Anas platyrhynchus*, and was a particular concern for the scaup harvest which, like for other long-lived and slower-producing ducks, is more sensitive to the duration of the hunting season (Allen *et al.* 1999).

The waterfowl management community also was coming to recognise the importance of understanding the human components of waterfowl management, specifically, the hunter desires and factors that affect hunter participation (Case & Sanders 2008). Waterfowl hunters were expressing strong concerns about fewer scaup and the loss of hunting opportunities associated with restrictive regulations, and waterfowl managers were concerned about declining hunter numbers because of their important influence in conservation.

Moreover, waterfowl hunters and managers voiced concern about the decline of the diving duck hunting tradition – notably the use of large decoy sets in large open water bodies, often using low-profile layout boats – a practice that has changed little over the last century and are considered by many to be among the purest of all waterfowl hunting traditions. While this concern does not directly relate to conservation *per se*, it highlights the importance of human values in waterfowl management that is reflected in the NAWMP revision (NAWMP 2012a). Hence, waterfowl biologists and managers were challenged to develop approaches to decision-making in the face of deep sources of uncertainty in scaup biology as well as in the objectives of the scaup conservation and management community. As a result, efforts were initiated to address scaup conservation planning through the principles of structured decision making (Gregory *et al.* 2012), with a focus on how best to allocate scarce conservation resources among management actions on an annual basis.

The structured decision-making approach first required a clear, explicit statement of scaup conservation and management goals and objectives. Participants in the process quickly realised that there was one over-arching goal: to conserve scaup populations at levels that satisfy societal values. Under this goal, a resulting objectives hierarchy established linkages among three fundamental objectives (Fig. 3): 1) achieve continental habitat conditions capable of supporting a target scaup population; 2) maintain or increase the sustainable scaup harvest; and 3) sustain the diving duck hunting tradition. This last objective explicitly brings people into the objectives and recognises the important contribution of hunters to waterfowl conservation, through direct financial contributions, advocacy and economic activity. Thus, sustaining the diving duck hunting tradition through maintaining the number, participation and identity of diving duck hunters becomes an explicit conservation objective. Although participants thought this was fundamental, it is not to say that maintaining hunter tradition and numbers is equally important compared to the other objectives. Determining the relative importance of each objective remains to be determined and will require input from all societal stakeholders, hunters and non-hunters included.

To predict the consequences of conservation actions on each objective, a coupled scaup-hunter model (*i.e.* predator-prey or consumer-resource type model) was developed with explicit relationships between potential management actions and key scaup demographic processes as well as diving duck hunter dynamics. Hunter recruitment and retention were modelled as a function of scaup population levels, and scaup harvest rates were driven by the number of diving duck hunters. These linked models project scaup and hunter numbers forward through time, predicting the numbers of breeding scaup, numbers of diving duck hunters and scaup harvest. Initial functional relationships relating retention and recruitment to management actions were developed based largely on expert judgement and limited knowledge from other species. Using the model,

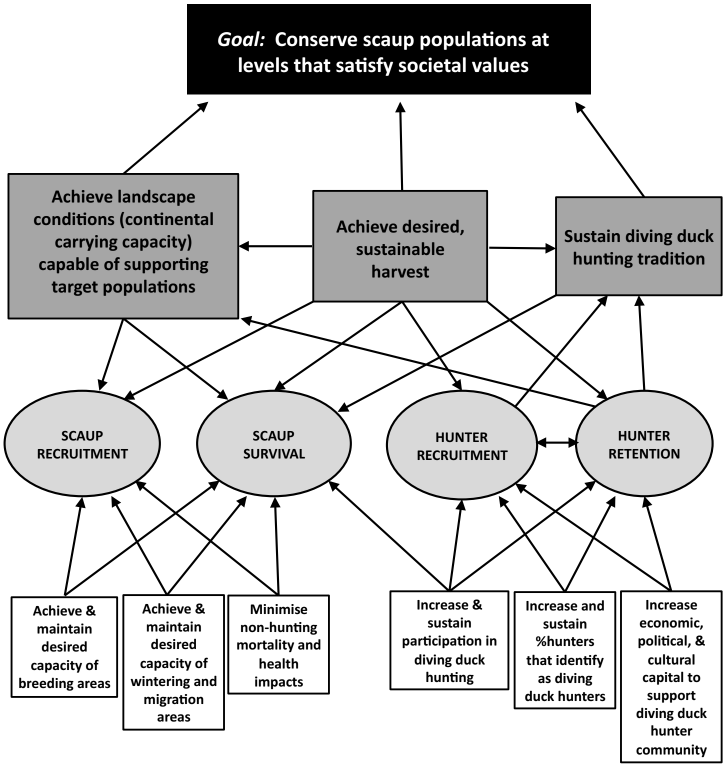

Figure 3. Objectives hierarchy for scaup conservation. After extensive discussions and revisions over three workshops, participants arrived at a set of three fundamental objectives under one overarching goal to conserve scaup populations at levels that satisfy societal values (black box). The fundamental objectives (medium grey boxes) identify issues of most concern. Each fundamental objective is linked to means objectives (white boxes) through simple functions that are hypothesised to affect survival and recruitment of scaup and hunters (light grey ovals).

waterfowl managers can ask: what affects each vital rate for both scaup and hunters? Also, what actions could be taken to alter or improve each vital rate? For each possible action, simple functional relationships were developed that linked how a management action affected a landscape variable (*e.g.* amount of nesting cover on the landscape), and how that in turn was related to a vital rate (*e.g.* probability of breeding success). Possible actions affecting hunters included harvest regulations (*e.g.* bag limit, season length), hunter access (*e.g.* alter amount of hunting habitat available through conservation or access programmes), or social networking (*e.g.* mentor programmes, web forums, community events). This modelling framework helps to identify portfolios of management actions (*e.g.* breeding or wintering habitat management) that have the greatest impact on scaup and hunter population change. Work is ongoing to finalise the modelling framework, establish a baseline parameterisation and conduct a sensitivity analysis (Austin *et al.* 2010). This will result in a robust platform to test assumptions about scaup and hunter population dynamics and to support decisions about the allocation of scarce conservation resources.

The key lessons from the work on scaup integration have been first, that there is a complex set of objectives involved when harvest and habitat management are considered together (see the "Integrating objectives" section above). Here participants thought that because encouraging and preserving hunter participation was fundamental, adding hunters explicitly into the objective was not only desirable but necessary. This ultimately took the form of a mathematical model to predict the consequence of management actions on hunter participation, a novel innovation in waterfowl management. Second, by admitting hunter objectives the question arises as to who is the decision maker and how can institutions be structured to best meet these hunter objectives (see "Integrating human desires and governance" above). These questions are largely unresolved for scaup, or for waterfowl management as a whole.

American Black Duck

At the time of the first NAWMP Continental Assessment (Assessment Steering Committee 2007) and release of the Joint Task Group report (Anderson *et al.* 2007), the Black Duck Joint Venture (BDJV) was finishing work on two priority issues: the development and implementation of the Eastern Waterfowl Breeding Survey and the completion of the technical framework of an international, adaptive harvest management strategy for Black Ducks (BDAHM). This confluence of events allowed the BDJV to re-evaluate priority information needs for the conservation of the Black Duck. The BDJV decided to focus greater effort on understanding Black Duck habitat ecology. The BDJV also agreed to focus on information needs required to determine where in the annual life-cycle limited financial resources should be allocated for habitat protection, restoration and enhancement to meet four fundamental objectives: 1) maintain Black Duck abundance at levels that meet legal and policy mandates; 2) maintain the relative distribution of breeding and non-breeding Black Ducks corresponding to the 1990–2012 period; 3) maintain carrying capacity to support the desired population and distribution; and 4) maintain consumptive and non-consumptive recreational opportunities commensurate with population sustainability and carrying capacity. Framing information needs in this context forced the community to address the issue of integrating habitat and harvest objectives (in "Integrating objectives" above). To address the trade-offs between objectives 1 and 4, above ("coherence", Runge *et al.* 2006), the desired NAWMP population goal was interpreted in reference to the BDAHM strategy, to harvest the population at 98% of maximum sustained yield (*i.e.* the 98% right-shoulder strategy). Therefore, objective (1) can be interpreted as achieving the NAWMP population goal for the Black Duck given a 98% right-shoulder harvest strategy. A future step is to re-evaluate, and potentially revise, the NAWMP population goal for Black Duck conditioned on the BDAHM strategy and capacity of the habitat JVs to increase continental carrying capacity.

The BDJV developed a conceptual annual life-cycle model relating Black Duck population dynamics to habitat limiting factors at the regional scale while accounting for annual harvest, much like that for Northern Pintail (Devers & Collins 2011; Mattsson *et al.* 2012). While progress on parameterising the life-cycle model and associated decision framework continues (see "Integrating models" above), several insights have emerged. The first insight concerns the decision context – "where" and "how much" habitat is needed; it became clear through this effort that there are multiple habitat decisions to be made at multiple scales. Habitat delivery on the breeding grounds of eastern Canada is independent of habitat delivery during the non-breeding season (*e.g.* the North American Wetland Conservation Canada programme *versus* the North American Wetland Conservation programme in the U.S.). In the case of each programme, no trade-off exists in terms of funds or resources between the breeding and non-breeding period; this is an important consideration as it establishes two separate decision processes. This is probably true for most waterfowl species. The decision context is also complex within countries because habitat decisions are made at the national, regional and local scales using a variety of funding mechanisms. Moreover, we cannot identify a single funding mechanism that is designed to fund projects based solely on waterfowl objectives. The vast majority of, if not all, habitat programmes are designed to achieve multiple objectives by providing habitat for threatened and endangered species, waterfowl and other species. The decentralised nature and multiple objectives of habitat conservation programmes create challenges regarding governance, not only across the waterfowl enterprise but more broadly within the wildlife conservation community. These insights about governance and sources of uncertainty have forced the BDJV community to think more broadly about the decision process, including the multi-objective nature of habitat programmes, and to consider a wide array of decision tools such as dynamic optimisation and robust decision-making (Lempert & Collins 2007).

The second insight is that, despite challenges related to integrated governance, a decision analytic approach based on an integrated population-habitat model allows the BDJV to make better decisions regarding the allocation of limited monitoring and research funds to address key uncertainties and assumptions ("Integrating models" above). For example, the Black Duck conceptual model assumes habitat restoration results in increased food availability (*i.e.* energetic carrying capacity) and post-hunting season survival. However, the BDJV lacks empirical data to parameterise this hypothetical relationship. To address this assumption, the BDJV has invested resources into a two-season banding programme to estimate post-hunting season survival and research to quantify the effect of restoration efforts on food availability. The results of these projects will be used to parameterise the life-cycle model and provide insight into the relationship between local scale habitat management and population response at the continental scale. In the long-term, the BDJV anticipates using the life-cycle model and analytical tools to guide the development of future research and monitoring projects.

The main lessons from the work on Black Duck have been, much like the scaup example, that the objectives become very complex and that governing institutions are not well-structured with respect to these complex objectives. The multi-species nature of habitat investment decisions allow for very little direct control to influence Black Duck conservation in particular. In these complex cases, the use of models becomes especially important for understanding the consequences of decisions.

Conclusions

Work on the integration of harvest and habitat management is ongoing. The species-specific initiatives must be completed, followed by a dedicated effort to implement these frameworks and use their guidance to inform management decisions. This will require commitment and buy-in by decision makers and local managers, and this can only come through continued engagement between the research and management communities, enhanced understanding of the underlying objectives of all stakeholders, and continued critical re-examination of the governance structures surrounding habitat and harvest management. Future work in this area should use the species-specific examples to build models that are capable of predicting the consequences of large-scale landscape change, such as those resulting from land use and climate changes. In addition, habitat and harvest management are not single-species endeavours. For harvest management, a common framework of hunting regulations affects many species at once, including species of significant conservation concern. In habitat management, decisions are rarely made in reference to a single species, or even just waterfowl. Thus, future efforts to integrate these management decisions must embrace a wider set of objectives, which undoubtedly will lead to more complex and difficult trade-offs.

Integration initiatives to date have shown that the management of harvest and habitat should not continue to be viewed as separate endeavours if the waterfowl management community desires to make optimal decisions with scarce resources. These two management regimes affect the same social-ecological system; thus, the question naturally arises as to whether the current governance system for waterfowl is in some sense sub-optimal (*cf.* Ostrom *et al.* 1999; Dietz *et al.* 2003; Ostrom 2009) and, if so, what parts need to change. The efforts to integrate harvest and habitat management have, if nothing else, raised this question and led to an examination of waterfowl management in a broader context that includes the waterfowl resource, habitat ecosystems and the objectives and desires of people interacting with those systems (NAWMP 2012a). Conservation decision-makers are challenged by increasingly complex decisions, fewer conservation and administrative resources, and changing social values. In addition, conservation planners are confronted with system change brought about by agricultural commodity markets in the short-term and climate in the long-term. Thus, waterfowl are only one component of a complex system, and the larger hope is that what started as a simple proposal to manage coherently hunter harvest and waterfowl habitat will lead to stronger and more adaptable technical, conceptual and institutional structures to address these larger challenges.

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Appendix 1. A technical primer on integrating habitat and harvest: derivation of a sustainable yield curve based on density- and habitat-dependent demographic rates.

Harvest management has a long tradition of explicit quantitative demographic modelling as the basis for decisions (Beverton & Holt 1957; Getz & Haight 1989; Hilborn *et al.* 1995). Habitat management is implicitly based on an underlying population model (*e.g.* Fretwell & Lucas 1969; Fretwell 1972), but it is less common for the model to be made explicit in the context of habitat management decisions. For habitat and harvest management to be integrated in a meaningful and useful way, parameters of a population model (*i.e.* the demographic rates) must ultimately be functions of habitat characteristics and harvest rates. The simplest representation of a population model where density (N, numbers per unit area of space) varies over time (t), and where *per capita* birth (b) and death (d) rates are functions of N and habitat (H), is:

$$\frac{dN}{dt} = b(N,H) - d(N,H) \qquad \text{Equation (1)}$$

The birth and death functions, $b(N,H)$ and $d(N,H)$ respectively, are also functions of time, reflecting the seasonal nature of waterfowl reproduction and mortality, but this notation has been dropped for clarity. These functions might be very complex, for example N might be a vector that refers to densities at various locations (spatial complexity), times (delay effects), or to different species (interspecific competition), and H might be a vector that refers to the area of different habitat types or the state of resources within each habitat type. In addition, $b()$ or $d()$ might be non-linear, such that the effect of a density or habitat manipulation is not constant across all N or H. This might be the case for $d()$ with respect to N if hunting mortality is compensatory to other mortality sources (see Cooch *et al.* 2014, this volume, for a discussion of density-dependence and other mechanisms of compensation). While many biologists might envision very complex hypotheses about the form of these functions, practical limitations and parsimony will limit the form to fairly simple representations. The simplest form is a linear relationship in birth and death rates

$$b(N,H) = b_0 - b_1N + b_2H + b_3NH \qquad \text{Equation (2a)}$$

$$b(N,H) = b_0 - b_1N + b_2H + b_3NH \qquad \text{Equation (2a)}$$

where h is the harvest rate and b_i and d_i are parameters relating demographic rates to density and habitat. In addition, there is the constraint that $b(N,H) \geq 0$ and $d(N,H) \geq 0$. Even if reality is much more complex, this linear model can be thought of as a first approximation to a more complex model, especially if one is interested in small perturbations from a particular point of interest (*i.e.* current conditions).

With these relationships, equation (1) can be rewritten into the familiar logistic growth form with harvest,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN \qquad \text{Equation (3)}$$

with $r = b_0 - d_0 + (b_2 + d_2)H$ and $K = r/(b_1 + d_1 - (b_3 + d_3)H)$. Equation (3) has several interesting properties from the perspective of integrating harvest and habitat management. First, the "intrinsic growth rate", r – the growth rate as density approaches zero – is a function of the birth and death rate intercepts and the habitat coefficients. Thus, the "intrinsic growth rate" can vary with changes in habitat (see figures in Anderson *et al.* 2007). When r increases with H, this effect has been called "habitat quality" (Anderson *et al.* 2007; Mattsson *et al.* 2012, and see Fretwell & Lucas 1969 or Fretwell 1972 for an original formulation of essentially the same ideas) because this effect is independent of population density.

Second, "carrying capacity" (K) is a function of the "intrinsic growth rate", the birth and death rate density coefficients (b_1 and d_1), and the habitat-by-density interaction coefficients (b_3 and d_3). Therefore, habitat-related changes in "carrying capacity" may come from "quality" effects or through the habitat-density interaction coefficients, which have been called "habitat quantity effects" (Anderson *et al.* 2007; Mattsson *et al.* 2012) because the effect of habitat depends on the population size by changing the quantity of resources available per individual. Regardless of how the coefficients are named, it is important to realise that changes in habitat can have both "intercept" and "slope" effects on demographic rates. A major empirical challenge for integrating habitat and harvest is estimating these effects and determining the habitat dimension(s) along which they occur.

This second point is also important because the term "carrying capacity" is often used imprecisely in reference to habitat management, rather than as a specific rescaling of density- and habitat-specific demographic parameters. Without explicitly stating the functional form of birth and death rates, "carrying capacity" has little meaning other than as a dynamic equilibrium in the absence of harvest, which is never actually observed in exploited systems. Only with an explicit model (functional form) for demographic rates does "carrying capacity" have any practical utility.

Third, besides the undesirable state $N = 0$ when $h \geq r$, and the dynamic equilibrium $N = K$ when $h = 0$, there is a wide range of equilibrial N for $0 < h < r$ that satisfy:

$$rN\left(1-\frac{N}{K}\right)-hN=0 \qquad \text{Equation (4)}$$

If we let $Y = hN$ be the total sustainable harvest yield, a plot of Y versus N gives a "yield curve" (Fig. 1). Because we have explicitly written r and K as functions of habitat, we can show how the yield curve changes with habitat and how this depends on specific values of the coefficients (Fig. 1).

Some points about the yield curve deserve emphasis. First, the yield curve is not directly observable. Instead it is a representation of the dynamic equilibria of a population model only reached with constant parameter values and at infinite time. It can be thought of as a long-term attractor of population size if harvest and habitat remained constant. Yearly observations of population fluctuations or demographic rates are not changes in the yield curve but are instead, stochastic realisations around an average described by the yield curve. The yield curve then serves as a summary of the consequences of equations (2a,b); and the challenge for scientists and conservation planners is to propose a functional form of equations (2a,b), estimate the relevant parameters, and then make decisions based on the consequences as summarised by the yield curve. This is not a trivial task. Second, by "habitat change" we mean long term changes such as climate, agricultural policy, or actions of conservation planners that work to shift the equilibria of the model (*i.e.* the yield curve). Most conservation planners seek to affect long-term shifts in habitat that change population equilibria, not short-term fluctuations around existing conditions. Third, under AHM the USFWS derives harvest regulations through optimization of a stochastic version of a population model related to equation (1). The yield curve developed from the deterministic version of that model is extraordinarily helpful in understanding the results of the stochastic dynamic optimisation. Thus, the yield curve serves as a tool to communicate the relationship between expected harvest and expected population size.