Conditions and limitations on learning in the adaptive management of mallard harvests

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Abstract In 1995, the United States Fish and Wildlife Service adopted a protocol for the adaptive management of waterfowl hunting regulations (AHM) to help reduce uncertainty about the magnitude of sustainable harvests. To date, the AHM process has focused principally on the midcontinent population of mallards (*Anas platyrhynchos*), whose dynamics are described by 4 alternative models. Collectively, these models express uncertainty (or disagreement) about whether harvest is an additive or a compensatory form of mortality and whether the reproductive process is weakly or strongly density-dependent. Each model is associated with a probability or "weight," which describes its relative ability to predict changes in population size. These Bayesian probabilities are updated annually using a comparison of population size predicted under each model with that observed by a monitoring program. The current AHM process is passively adaptive, in the sense that there is no *a priori* consideration of how harvest decisions might affect discrimination among models. We contrast this approach with an actively adaptive approach, in which harvest decisions are used in part to produce the learning needed to increase long-term management performance. Our investigation suggests that the passive approach is expected to perform nearly as well as an optimal actively adaptive approach, particularly considering the nature of the model set, management objectives and constraints, and current regulatory alternatives. We offer some comments about the nature of the biological hypotheses being tested and describe some of the inherent limitations on learning in the AHM process.

Key words adaptive management, *Anas platyrhynchos,* decisions, harvest, hunting, learning, models, mortality, objectives, optimization, population dynamics, reproduction, regulations, stochastic control, survival, uncertainty

Despite considerable investment in scientific investigation, the sustainable exploitation of North American duck populations remains an uncertain endeavor. In response to this uncertainty, the United States Fish and Wildlife Service (USFWS) began applying the concepts of adaptive resource management (Walters 1986) to the regulation of duck harvests in 1995. AHM, as it has come to be known, explicitly recognizes that the consequences of hunting regulations cannot be predicted with certainty and provides a framework for making objective regulatory decisions in the face of that uncertainty (Williams and Johnson 1995). AHM also can help reduce uncertainty about harvest impacts through an iterative cycle of monitoring, assessment, and decision making (Johnson et al. 1993, Johnson et al. 1997).

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The difficulties in understanding the effects of hunting regulations on waterfowl populations have been well documented (e.g., Nichols and Johnson 1989), and several investigators have advocated an "experimental" approach that places a high premium on learning (e.g., Anderson et al. 1987). AHM, although intended to help managers learn more from the regulatory process, certainly is not the experimental approach envisioned by some. Rather, AHM emphasizes management *per se*, in which value is ascribed to information and understanding only to the extent that they contribute directly to the stated objectives of harvest management (Johnson et al. 1993, Williams and Johnson 1995). Perhaps not surprisingly, there continues to be some disagreement between managers and researchers about the appropriate emphasis on learning in the setting of waterfowl hunting regulations (Johnson and Case 2000).

Our objective is to provide some of our perspectives on learning in AHM as it has been practiced since 1995. Our focus is on the midcontinent population of mallards, which so far has been the principal target of biological modeling and the optimization of regulatory choices (Johnson et al. 1997). Specifically, we address 4 questions:

1) What are we trying to learn about the dynamics of the midcontinent mallard population?

2) How does learning occur in the AHM process, and what, if any, are its limitations?

3) Should we consider a more aggressive approach to learning than that currently employed in AHM?

4) Are we asking the right questions about population dynamics and the impacts of hunting regulations?

What are we trying to learn?

The specification of AHM models

The determination of sustainable levels of harvest depends on the ability to make reliable predictions of how population abundance will respond to various levels of harvest. These predictions, in turn, depend on the availability of quantitative models that describe relevant population dynamics and responses. In the case of AHM, these models must specify the effects of various hunting regulations and uncontrolled environmental factors on harvests and subsequent population size. Uncertainties about these effects are accounted for by the specification of a set of alternative models, which represent competing hypotheses of population dynamics. The challenge to the AHM process is to discriminate among these alternative models, given the confounding effects of environmental variation, partial controllability of harvests, and estimation error (Nichols et al. 1995). The goal of sustainable exploitation ultimately depends on this discriminatory ability and on the ability to specify models that can predict population responses over a range of real-world conditions.

Candidate models for the AHM process must meet 2 criteria (Williams and Johnson 1995). First, models must imply different harvest strategies, or there is no value (from a harvest-management perspective) in learning which model is the best predictor of population response. Second, models must describe different responses to harvest that are detectable by a monitoring program, or the AHM process will fail to identify the most appropriate model. Our experiences to date in constructing models for AHM suggest that the most useful models will be based on a combination of empiricism and ecological theory (Johnson et al. 1993). Unfortunately, data needed to describe and understand sources of variation in vital rates (i.e., mortality, reproduction, emigration, immigration) are lacking for many waterfowl species, especially at the large spatial scales at which harvest management is conducted. Perhaps more importantly, few working hypotheses exist regarding the ecological mechanisms responsible for density-dependence in waterfowl population growth. The paucity of these hypotheses is problematic because density-dependence provides the theoretical foundation for sustainable harvesting (Hilborn et al. 1995). For these reasons, specification of useful models remains one of the most challenging aspects of the AHM process.

The set of models currently in use for AHM of midcontinent mallards consists of 4 alternatives, which result from combining 2 mortality and 2 reproductive hypotheses (Johnson et al. 1997). Rates of emigration and immigration are assumed to be negligible. Collectively, the models express uncertainty (or disagreement) about whether harvest is an additive or a compensatory form of mortality (Burnham et al. 1984), and whether the reproductive process is weakly or strongly density-

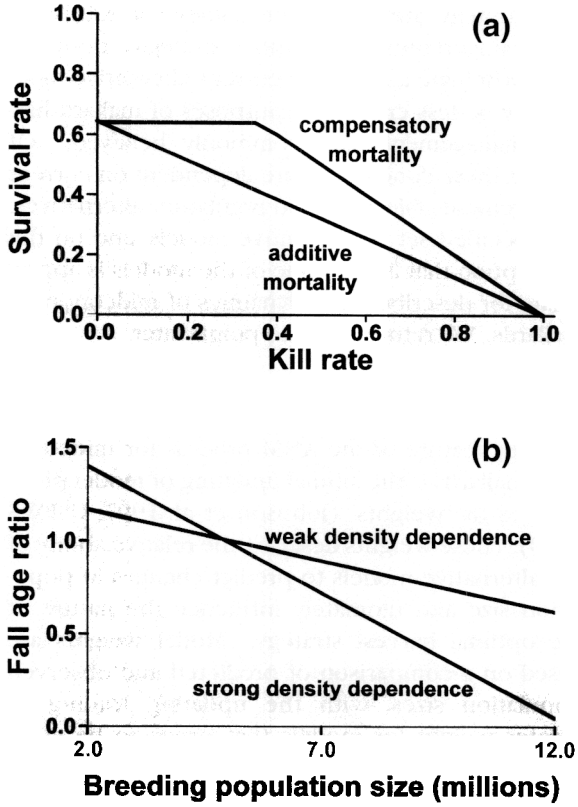

Figure 1. Alternative models of midcontinent mallards: (a) models of additive and compensatory mortality (adult females), and (b) models of weakly and strongly density-dependent reproduction for the average number of ponds in Prairie Canada (Johnson et al. 1997).

dependent (i.e., the degree to which reproductive rates decline with increasing population size; Figure 1). The model with additive hunting mortality and weakly density-dependent reproduction leads to the most conservative harvest strategy, whereas the model with compensatory hunting mortality and strongly density-dependent reproduction leads to the most liberal strategy. The other 2 models lead to harvest strategies that are intermediate between these extremes. Therefore, the probabilities (or "weights") assigned to the hypotheses of additive hunting mortality and strongly density-dependent reproduction can greatly influence the nature of the optimal harvest strategy (Johnson et al. 1997).

The expected value of perfect information

Once a set of alternative models has been specified, it is worth asking whether discrimination among these models has value relative to the stated objectives of harvest management. A relatively high value indicates that an adaptive approach to harvest regulation, in which learning is an inherent goal of management, is a worthwhile endeavor. In calculating this value, the idea is to compare the expected performance of management if the most appropriate model were known with the performance expected under the best nonadaptive strategy. This value is referred to as the expected value of perfect information (EVPI, Hilborn and Walters 1992).

We calculated EVPI using the current model set for midcontinent mallards by applying the optimization algorithms and software described by Lubow (1995) and Johnson et al. (1997). We first derived an optimal harvest strategy for each of the 4 alternative models and then simulated annual harvests under each model assuming its associated optimal harvest strategy were followed. We then calculated an unweighted average (α) of the model-specific mean harvests. The average α represents the expected performance of management if the most appropriate model were known.

We then derived the best nonadaptive harvest strategy by equally weighting the 4 models and deriving an associated optimal harvest strategy. In effect, this produces optimal harvest decisions for the manager who is completely uncertain (and expects to remain so) about the most appropriate model (Johnson et al. 1997). We then calculated the expected performance of this nonadaptive strategy by simulating its use with each of the 4 alternative models. As before, we calculated an unweighted average (β) of the mean annual harvests expected under each of the models. The average β represents the best performance that could be expected in the face of continuing model uncertainty. The difference between α and β is the EVPI associated with the current model set for midcontinent mallards.

We calculated the EVPI for midcontinent mallards under 2 different scenarios. In the first, we used a management objective to maximize long-term cumulative harvest and assumed perfect control over mallard harvest rates. In the second scenario, we used a management objective to maximize long-term cumulative harvest, but added a constraint in which harvest is devalued whenever mallard population size is expected to fall below the goal of the North American Waterfowl Management Plan (Johnson et al. 1997). The current objective for midcontinent mallards specifies a relative value of harvest as a proportionally decreasing function of the difference between the goal and expected population size (USFWS 2000). We also relied in the second scenario on the current speci-

Table 1. Expected model-specific annual harvests of midcontinent mallards under the case of model certainty and the best non-adaptive strategy (model uncertainty). Case 1 refers to an objective to maximize long-term cumulative harvest and perfect control of harvest rates. Case 2 refers to an objective to maximize long-term harvest, subject to a constraint on population size, and the current regulatory alternatives. Model designations are: ScRs = compensatory mortality and strongly density-dependent reproduction, ScRw = compensatory mortality and weakly density-dependent reproduction, SaRs = additive mortality and strongly density-dependent reproduction, and SaRw = additive mortality and weakly density-dependent reproduction.

		Model-specific annual harvests (millions)				
Case	Strategy	ScRs	ScRw	SaRs	SaRw	$\bar{x}$
1	Model certainty	3.23	3.52	1.70	1.50	**2.49**
	Model uncertainty	3.09	3.45	1.69	1.39	2.40
2	Model certainty	1.65	2.21	1.28	1.42	1.64
	Model uncertainty	1.65	2.21	1.28	1.32	1.62

fication of 5 regulatory alternatives, by using the harvest-rate mean and variance associated with each of those alternatives. These regulatory alternatives (and their associated harvest rates for adult males) are: liberal ($\bar{x}$=0.130, SE=0.032), moderate ($\bar{x}$=0.111, SE=0.027), restrictive ($\bar{x}$=0.066, SE=0.014), very restrictive ($\bar{x}$=0.053, SE=0.011), and closed ($\bar{x}$=0.009, SE=0.003) (USFWS 2000).

For the first scenario (i.e., maximize long-term cumulative harvest, and perfect control over harvest rates), the calculated EVPI was about 90,000 harvested mallards/year (Table 1). This figure is considerably less than that reported by Johnson et al. (1993), probably because we were able to derive a much more effective nonadaptive strategy. In any case, an annual harvest of 90,000 mallards likely represents about $16 million in associated economic output (Southwick Associates 1995). Thus, there would seem to be significant value in identifying the most appropriate model of mallard population dynamics. In contrast, however, the EVPI for the second scenario (current management objective and regulatory alternatives) was only about 20,000 harvested mallards/year, representing an economic output of about $4 million.

Clearly, the value of discriminating among alternative models relies not only on the models themselves but on the stated objective(s) of management and on the ability of managers to regulate harvest. Nonetheless, we admit to being surprised at the relatively low EVPI using current management objectives and regulations and by the relatively good performance expected from the nonadaptive strategy. This strategy appears to be somewhat robust to model uncertainty, and adaptive strategies designed to discriminate among the current alternative models may be less critical for purposes of mallard harvest management than commonly believed. Of course, these conclusions are dependent on current management objectives and regulatory alternatives, the specified set of alternative models, and on the assumption that at least one of the models is appropriate for describing the dynamics of midcontinent mallards. We return to these points later.

How does learning occur?

A key feature of the AHM process for midcontinent mallards is the annual updating of model probabilities or "weights" (Johnson et al. 1997, USFWS 2000). These weights describe the relative ability of the alternative models to predict changes in population size and ultimately influence the nature of the optimal harvest strategy. Model weights are based on a comparison of predicted and observed population sizes, with the updating leading to greater weight for models that prove to be good predictors (i.e., models with relatively small differences between predicted and observed population sizes; Figure 2). These comparisons account for sampling error (i.e., partial observability) in population size and pond counts, and for partial observability and controllability of harvest rates (Williams et al. 1996, USFWS 2000).

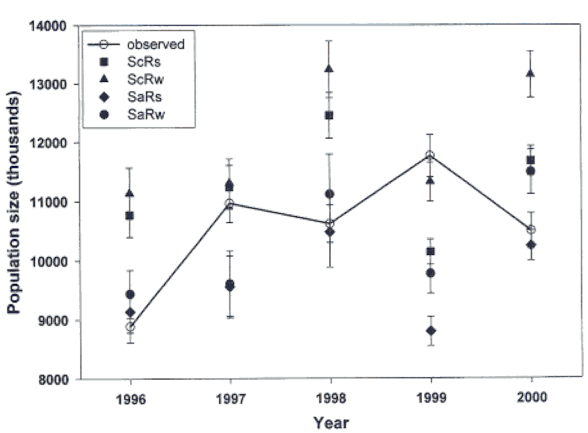

Figure 2. Estimates of observed mallard population size (line with open circles) compared with predictions from 4 alternative models of population dynamics (ScRs = compensatory mortality and strongly density-dependent reproduction, ScRw = compensatory mortality and weakly density-dependent reproduction, SaRs = additive mortality and strongly density-dependent reproduction, SaRw = additive mortality and weakly density-dependent reproduction). Vertical bars represent one standard deviation on either side of the estimated population size.

The updating of model weights is based on Bayes Theorem:

$$p_{t+1}(\text{model } i \mid \text{data}) = \frac{p_t(\text{model } i)\; p_{t+1}(\text{data} \mid \text{model } i)}{\sum p_t(\text{model } j)\; p_{t+1}(\text{data} \mid \text{model } j)} \quad (1)$$

where p_t(model i) is the probability in year t that model i is "correct." A key assumption is that at least one of the alternative models is an appropriate description of population dynamics and remains so throughout the process. Data describing the state of the system in year t+1 consists of breeding population size (N_{t+1}) and number of ponds in Prairie Canada (P_{t+1}). Equation (1), then, tracks through time the probability that each of the candidate models is the best predictor of observed changes in population size. Under the current approach, data on pond numbers are not helpful for model discrimination because all 4 candidate models use the same auto-regressive model to predict pond numbers (Johnson et al. 1997).

We can rewrite the conditional probability in equation (1) as:

$$p_{t+1}(\text{data} \mid \text{model } i) = f\,(N_{t+1}^{\text{data}} \mid \hat{N}_{t+1}^{(i)}), \quad (2)$$

where N_{t+1}^{data} comes from the Breeding Waterfowl and Habitat Survey (Smith 1995), $\hat{N}_{t+1}^{(i)}$ is the predicted observed size of the population based on model i, and f denotes a probability density function. This probability density function is derived empirically from the structure of model i, from assumed sampling distributions for pond abundance in year t and for population size in years t and t+1, and from variation in harvest rates under a given regulatory decision (USFWS 2000).

When the AHM process was initiated in 1995, the 4 alternative models of population dynamics were considered equally likely, reflecting a high degree of uncertainty (or disagreement) about harvest and environmental impacts on mallard abundance. Model weights shifted markedly in 1996 and again in 2000 (Table 2). The rapid shift of model weights is to some extent a reflection of the limited components of variation that are included in the distribution of predicted populations under each model. These variance components include sampling variation in observed population size and pond numbers, and either the sampling variation in observed harvest rates (1996, 1999–2000), or the total (i.e., sampling + temporal) variation in the prediction of harvest rates under each regulatory alternative (1997–98). The sources of uncertainty incorporated in the current updating procedure are consistent with those acknowledged in the process of identifying an optimal policy. However, the survival and recruitment components are treated as deterministic and thus ignore residual error from the regression models. We currently are addressing how to properly incorporate this uncertainty into the updating process, in light of the fact that only one survival (additive) and one recruitment model (weakly density-dependent) were derived directly from either maximum-likelihood or least-squares estimation based on data. The other 2 models were derived partially from data and partially by fixing parameters to reflect the ecological theory that gave rise to them. Therefore, some models in the set were derived with fewer sources of variation than others. We have just begun to explore ways in which to modify the updating procedure to account for these variance components. The inclusion of these additional variance components in the updating procedure will slow the movement of model weights and perhaps be more reflective of actual rates of learning.

After 5 years of AHM, model weights for midcontinent mallards reflect considerable support for the

Table 2. Annual changes in model probabilities (weights) associated with alternative models of midcontinent mallard population dynamics. All models had a probability of 0.25 in 1995.

Mortality hypothesis	Reproductive hypothesis	Model probability 1996	1997		1999	2000
Additive	Strong density dependence	0.65479	0.53015	0.61311	0.60883	0.92176
Additive	Weak density dependence	0.34514	0.46872	0.38687	0.38416	0.07822
Compensatory	Strong density dependence	0.00006	0.00112	0.00001	0.00001	0.00001
Compensatory	Weak density dependence	0.00001	0.00001	0.00001	0.00700	0.00001

hypotheses of additive hunting mortality and strongly density-dependent reproduction. There are 2 important caveats to this conclusion, however. The first involves a recognition that the updating procedure assesses relative, not absolute, model performance. It is at least possible that one or more models might receive much of the weight over time, yet still produce predictions that are numerically much different from observed population size. If all candidate models are poor predictors of absolute changes in population size, then a high probability associated with the best model of the set will not be very comforting to managers. This dilemma underscores the need for continuing efforts to build more reliable models by relying on traditional demographic research.

The second caveat involves the issue of replication and randomization of regulatory "treatments," and the associated impact on inferential strength (Nichols and Johnson 1989). In AHM, application of different regulatory alternatives occurs nonrandomly over time because of the dependency of regulations on system state (i.e., population size and pond numbers). Therefore, years with different regulations are characterized by systematic differences other than that associated with the regulatory treatment. This statistical confounding limits the confidence one can have that the weights associated with alternative models are reflective of actual ecological relationships.

Should we consider a more aggressive approach to learning?

The current AHM process is passively adaptive, in the sense that learning (if any) occurs as a by-product of the regulatory process. The reader should be aware, however, that our definition of passive adaptive management is fundamentally different from that of Walters (1986) in that we explicitly consider alternative models of system dynamics. Nonetheless, in the current practice of AHM there is no *a priori* consideration of how a particular regulatory choice might affect our ability to discriminate among alternative models. A major advantage of this process, nonetheless, is the explicit accounting for uncertainty represented by a set of alternative models, and the association of these models with annual, empirical measures of their predictive ability. The primary disadvantage of a passively adaptive process, however, is the failure to recognize that some regulatory strategies are more informative than others and that regulations can be used proactively to reduce certain sources of uncertainty.

Development of an actively adaptive strategy involves a tradeoff between short-term management performance and the long-term value of knowing which alternative model of population dynamics is most appropriate (Walters 1986). The idea is to determine the regulatory strategy that will provide the best long-term performance, recognizing that long-term performance is influenced by hunting regulations and by the rate at which we can learn about regulatory effects. Optimal actively adaptive policies can be determined with a generalization of the current AHM process by accounting for the dynamics of model weights (Johnson and Williams 1999). In the actively adaptive process, temporal transitions in the model weights are a function of regulatory actions, much as temporal changes in population size are a function of regulations. The management objective also is modified in such a way as to emphasize learning when uncertainty is high, and harvest when uncertainty is low. Computational details of the actively adaptive approach are beyond the scope of this paper, so the reader is referred to Williams (1996*a*, *b*) for information on theory and computing algorithms. Generalized software for solving problems in adaptive optimization is available from Lubow (1995, 1997).

Because of the different perspectives on learning embodied in passively and actively adaptive approaches, we were interested in how the associated regulatory strategies for midcontinent mallards might differ. As we have said, model discrimination in the current AHM process occurs passively, and we were interested to know whether an actively adaptive regulatory strategy would exhibit harvest actions that are designed to help discern the most appropriate model. Therefore, we computed optimal passively and actively adaptive regulatory strategies and compared state-specific harvest decisions for a range of population and pond sizes. We conducted this comparison for both of the scenarios described in our earlier calculations of EVPI. As before, our comparisons are based on equal weights for all models, because it is under this condition that the passively and actively adaptive strategies will exhibit the greatest differences. There is no difference, of course, between a passively and actively adaptive policy in the face of model certainty (Johnson and Williams 1999).

The actively adaptive strategy is different from the passive strategy when the management objective is

to maximize long-term cumulative harvest and when there is perfect control over harvest rates (Figure 3*a*). Harvest decisions in which the actively adaptive strategy was more conservative than the passively adaptive strategy were evident at high levels of mallard and pond abundance. The actively adaptive strategy was more liberal than the passively adaptive strategy at population sizes around 6–7 million. However, most differences were relatively minor and never exceeded an absolute difference in harvest rate of 0.08 for any combination of population size and pond numbers. The mean difference in harvest rate across all system states was <0.01.

When the management objective was constrained by the population goal of the North American Waterfowl Management Plan, and when current regulatory choices were substituted for perfectly controlled harvest rates, the pattern of differences between the passively and actively adaptive strategies changed dramatically (Figure 3*b*). Much less of the state space contained differences of any kind, with those differences being restricted mostly to population sizes <5 million. For population size <5 million, the actively adaptive strategy was often more liberal than the passively adaptive strategy. The mean difference in harvest rate across all system states was again <0.01, although the maximum difference was slightly greater (0.1) than in the first scenario. These results suggest that a passively adaptive strategy may perform nearly as well as an actively adaptive strategy over the long term.

Our comparisons of actively and passively adaptive strategies are consistent with our calculations of EVPI, suggesting that the importance and most appropriate approach to learning in the management process depends critically on management objectives and associated constraints. While it might seem reasonable to advocate an aggressive, experimental approach to resolve uncertainty about the effects of harvest (e.g., Anderson et al. 1987, Conroy and Krementz 1990), managers must be careful not to turn large-scale management into a research endeavor. In effect, implementation of a regulatory experiment means temporarily replacing traditional harvest objectives with an objective to learn. As a consequence, there is a potential loss of short-term harvest opportunity associated with regulatory experiments that managers typically have found unacceptable. In contrast, the focus of AHM is on neither learning rates nor short-term harvest, but instead on regulations that provide an optimal balance of short- and long-term harvest benefits.

Are we asking the right questions?

In AHM, the set of alternative models is intended

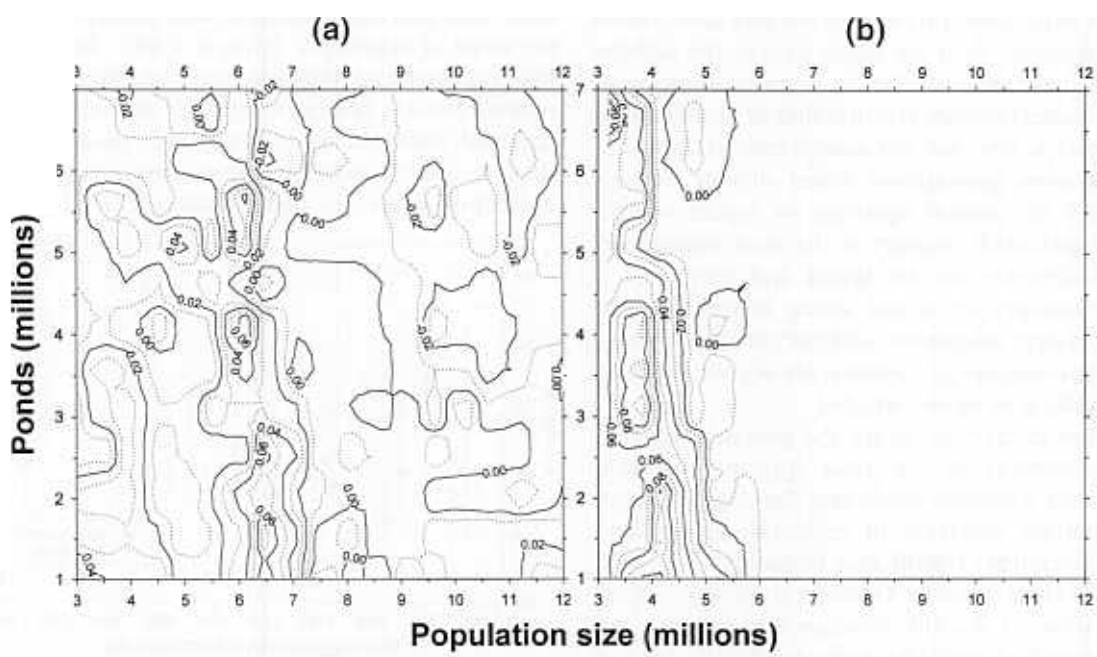

Figure 3. Comparisons of passively adaptive versus actively adaptive harvest strategies for midcontinent mallards, in which contour lines represent the difference between the optimal harvest rate for the active and passive strategies: (a) using an objective to maximize long-term cumulative harvest and assuming perfect control over harvest rates, and (b) using an objective to maximize harvest, but where harvest is constrained by the population goal of North American Waterfowl Plan, and relying on current regulatory alternatives.

to capture key uncertainties about how harvest and uncontrolled environmental factors affect waterfowl abundance. The hope is that at least one of the models in the model set will do a reasonable job of predicting changes in population size over a range of real-world conditions. It is worth asking, therefore, whether the current model set for midcontinent mallards meets these criteria. We continue to believe that the current model set was a reasonable choice, considering key questions about the mortality and reproductive processes it embodies and the empirical basis for estimating model parameters. Whether any of the models turn out to be reliable predictors over the long term remains to be seen, but we are encouraged to date by observed population sizes that are mostly within the range of model predictions. In fact, one of the models has done a remarkable job of predicting the observed population size in 3 of the last 5 years.

Nonetheless, we do recognize limitations in the current model set. A major concern is one we expressed as early as 1993 (Johnson et al. 1993). Despite the ability of a model set to cover the range of possible responses to harvest, it may still represent a poor model set if the most appropriate model appears to change over time. For example, if the capacity to compensate for hunting losses through reduced natural mortality depends on a density-dependent process (as virtually all scientists agree it must), then we might expect the additive hunting mortality model to appear appropriate when mallard density (i.e., number of birds/limiting resource) is low, and the compensatory model to appear most appropriate when density is high. Whether the annual updating of model weights could track such changes in the most appropriate model depends on the speed and frequency at which changes occur, our ability to observe (estimate) system responses, and the extent to which important sources of variation are accounted for in the updating of model weights.

We are concerned about the potential for temporal instability in the most appropriate model because of evidence suggesting the degree of additive hunting mortality in midcontinent mallards varies over time (Smith and Reynolds 1992; W. L. Kendall, United States Geological Survey, unpublished data). A possible solution is to model a density-dependent mortality process directly, so that mortality after the hunting season is expressed as a function of post-harvest mallard density. Unfortunately, our efforts to date in this regard have failed to demonstrate a clear relationship between natural mortality and population size, which we use as a surrogate for density (Figure 4). Our failure to demonstrate such a relationship could mean that population size is a poor surrogate for density, measures of population size or density are unavailable during the right time(s) in the annual life cycle, or estimates of annual survival are so imprecise that detection of biologically relevant patterns is impossible. Of course, another explanation is that mortality in mallards is largely a density-independent process and hunting mortality has been mostly additive to other sources of mortality over the range of historic experience.

Specification of ecologically realistic models is only half the battle. How does one choose realistic model alternatives that are consistent with available data, yet suggest different harvest strategies? The approach used with the midcontinent mallard model set was to specify a particular mathematical form for the survival and reproductive processes, and then estimate the associated parameters from extant data. Uncertainty about the most appropriate model was characterized by selecting alternative values of key parameters within the confidence limits of the parameter estimates. We are increasingly concerned, however, that uncertainty about system behavior within the limits of historic experience may be less important to management than uncertainty about system behavior outside the range of experience (Walters 1986). Runge and Johnson (In press) demonstrated that the nature of optimal harvest strategies depends strongly on the specified functional form of the ecological relationships involved in demographic processes, even when alternative forms are indistinguishable with extant

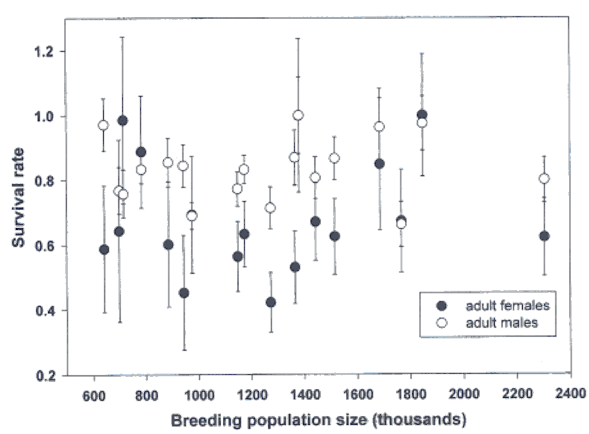

Figure 4. Estimates of February–August survival rates of adult mallards banded in southwestern Saskatchewan, plotted against population size in May, 1968–86. Vertical bars represent one standard error on either side of the prediction.

data. For example, while it is commonly assumed that a compensatory-mortality hypothesis leads to greater optimal harvest rates than the additive-mortality hypothesis, Runge and Johnson (In press) found this to depend on the form of the reproductive function. Useful model sets, therefore, must consider not only uncertainty about parameter values conditioned on a particular functional form, but the possible form of ecological relationships outside the range of experience. Ecological theory will be critical to the specification of such alternatives.

A related concern is the dependence on linear models to describe relationships between population density and vital rates (e.g., the reproductive models for midcontinent mallards). Such models imply a symmetric logistic growth curve, where the maximum population growth rate (and sustained yield) is attained at a population density half of the carrying capacity, K. Nonlinear relationships between vital rates and population density lead to maximum growth rates that are shifted to one side or another of $K/2$. The critical dependency of optimal harvest strategies on the form of density dependence suggests that we must seek a better understanding of the ecological mechanisms responsible for internal regulation of population size. Fowler (1981) provided a good rationale for considering life-history strategies of species when hypothesizing the nature of density-dependent population growth. Unfortunately, theory is not enough. The development of useful models of density dependence in waterfowl continues to be hampered by uncertainty concerning the most likely environmental limiting factor(s), and by a paucity of demographic and environmental data at the necessary spatial and temporal scales (Johnson and Case 2000).

Conclusions

In the strictest sense, AHM is about management rather than research. It is about making reliable predictions of responses to harvest and not about identifying *per se* the ecological mechanism(s) responsible for that response. In a larger sense, however, we also recognize that AHM is about making management and research more of a collaborative venture, and about seeking the kind of detailed understanding that ultimately can lead to more reliable predictions. We cannot emphasize strongly enough, however, that the importance of learning (and the approach to it) in the AHM process depends critically on the objectives and constraints of management and on specification of key uncertainties in population response. More aggressive approaches to learning, such as short-term regulatory experiments, may have significant benefits, but are likely to be politically unacceptable.

We believe the current model set for midcontinent mallards effectively expresses key uncertainties in the mortality and reproductive processes. Nonetheless, we continue to have concerns about the limited hypotheses of density-dependent population growth it embodies, and about the manner in which alternative models were specified. We believe the model set could be improved by formulating more mechanistic models of the mortality and reproductive processes (Johnson et al. 1993), and by considering plausible forms of those models outside the historic range of system states. Traditional field studies and a greater reliance on ecological theory will be essential to this endeavor. Productive investigations of density-dependent processes also will rely on the development of cost-effective methods and protocols for habitat and environmental monitoring. We also believe it is likely that relationships between vital rates and population density will need to be investigated at a scale smaller than the population level. Population-level models rely on a great deal of averaging of small-scale effects, and the ability to recognize important ecological patterns and relationships can be lost.

The learning process in AHM as represented by Bayes Theorem is a logical, unbiased approach to discriminating among alternative models. It does, however, have its limitations. We must assume that the most appropriate model remains so over time or that changes will be gradual enough that they can be recognized by shifts in model weights. As we have explained, the rate at which model weights can change depends on the components of variation accounted for in the updating process. The desire for responsive model weights, therefore, must be weighed against the need to account for sources of variation that may be common to all alternatives in the model set. Finally, the updating process determines only relative model performance, which is based solely on comparisons over time. Clearly, it would be unwise to rely exclusively on the AHM process for inference about population dynamics and the impacts of harvest. Traditional modes of inquiry will continue to be essential in the search for sustainability.

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