Part I. Introduction to Managing Deer from an Ecosystem Perspective

Chapter 1. Introduction to the Report

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Chapter 1. Introduction

Deer play a role in ecosystems, particularly forests, in various ways including:

(1) Herbivory or predation on the plants they use as food

(2) Altering the physical habitat used by other animal species, plants, and other organisms in the ecosystem

(3) Altering plant species composition, richness (diversity), forest structure (see box on page 34), ecological processes, and ecosystem function

(4) Competing with other animals that use the same food resources

(5) As prey, providing food for large predators

Consequently, deer management has implications that go far beyond recreational hunting.

History of deer management in Pennsylvania

The history of deer management in Pennsylvania is one of overexploitation through unregulated hunting in the nineteenth century, followed by 100 years of overprotection, population increase, and habitat destruction. Deer were rare throughout the eastern United States by 1900[1] but they were scarce in Pennsylvania by 1895, when the Pennsylvania Game Commission (P.G.C.) was formed, in part to restore deer numbers.[2]

Regulated hunting, focusing primarily on protecting antlerless deer, became the hallmark of P.G.C.'s deer management program, which resulted in the herd's rapid recovery.[1] Deer densities were extremely high by the mid-1940s. Escalating alteration of forested habitats due to high-density deer populations was noted by Commission biologists who called for more aggressive antlerless deer harvests.[3] Antlerless deer, however, continued to be under-harvested and the state's deer population continued to grow.

In 1979, P.G.C. adopted deer density goals based on a nutritional carrying capacity model (see box on page 16) that estimated the amount of forage available to deer on a sustained basis in forested habitats. Again, there was a call by biologists to increase antlerless harvests to meet these goals, but instead the Commission maintained deer numbers at 50 to 100% above the recommended goal, where they remained through 1999[4] and then increased a further 20% by 2003.[5] As a result there is widespread concern in the state about severe degradation of deer habitat and negative impacts on Pennsylvania's forested ecosystems, agriculture, wood products industry, and the quality of life for many Commonwealth residents. At the same time, interest in ecosystem approaches to land and wildlife management has increased.

With the reorganization in 1999 of the Wildlife Management Bureau (with Dr. Gary Alt named chief of the newly formed Deer Management Section) and the support of agency policy makers, P.G.C. now has a more aggressive deer management program that, in theory, can effectively reduce deer densities in many parts of Pennsylvania. The challenge now is to tie deer densities to ecosystem management.

Task of the Deer Management Forum

The Deer Management Forum, first convened in October 2001 by Audubon Pennsylvania and the Pennsylvania Habitat Alliance, was asked to set forth a vision of what ecosystem-based deer management might entail in the Commonwealth's large forested areas. In particular, the group was asked to describe in a report how deer management might differ from current practices, if deer were managed within an ecosystem framework that aims to conserve biodiversity. Only with such a vision in hand could decision makers, should they be so inclined, take the steps that will be needed to move deer management in Pennsylvania further in the direction of ecosystem management.

To fulfill its task, Forum members reviewed the literature on deer impacts and management, as well as on the condition of Pennsylvania's forests and the stresses placed upon them. This literature review provides most of the support for the findings. The group also drew upon the experience Forum members have gained in studying and examining the wildlife and forested ecosystems of Pennsylvania. Fifteen meetings were held to prepare the report, many of which included presentations by outside speakers or Forum members with special expertise. Nine outside speakers addressed the group. Several additional scientists were interviewed. In addition, Forum members took several field trips.

Report organizing principle

This report is organized around the decision-support concept of adaptive resource management (A.R.M.).[6] A.R.M. is a science-based way of "learning by doing" that involves five steps:

(1) Set and quantify a resource management goal, based on a set of core values that most stakeholders can agree upon.

(2) Identify competing biological theories that are pertinent to meeting the overall management goal, and the management recommendations that follow from each theory.

(3) Based on past research and experience, pick what is initially believed to be the best combination of management actions (e.g., reducing deer density to 20 per square mile, avoiding the use of herbicides) and implement the combination in an experimental context.

(4) Make quantitative predictions of the results of management actions for each competing biological theory or model and compare the predictions against field data at regular intervals (e.g., every 3 years) using indicator species and other environmental indicators.

(5) Update the set of management actions, giving preference to the recommendations that flow from those theories (models) that performed best in the comparisons.[7]

The Pennsylvania Game Commission, along with wildlife agencies in other states, already relies on A.R.M. indirectly to set the waterfowl season, because the U.S. Fish and Wildlife Service uses A.R.M. to set its yearly targets for waterfowl harvest. Managing deer using an A.R.M. paradigm would be a more complex challenge. Nevertheless, the use of A.R.M. as a decision-support system provides a way to translate an abstract concept, "managing deer from an ecosystem perspective," into step-by-step operations that an agency or coalition of groups can implement. Furthermore, A.R.M. has the added potential to channel controversy into constructive predictions that can be tested and actually help to improve management over time.

Report content

Each chapter is relevant to one of the A.R.M. steps. The chapters in Part I deal with background information related to A.R.M. itself and to the first step in A.R.M., defining and quantifying the management goal. The report starts from the premise that management of white-tailed deer from an ecosystem perspective involves attempting, within the constraints of landowner objectives, to maintain or restore ecosystem structures and processes, not just healthy populations of deer.[8] Pennsylvania is taken as a illustrative example. To define typical ecosystem structures that need to be restored, the report reviews the natural history of Pennsylvania, the current state of the forests, and the extreme alteration of forests that has occurred with increased deer density in certain parts of the state. It concludes with a chapter that explores some of the root causes of our current ecological situation.

Part II begins by exploring the role of white-tailed deer in altering vegetation structure, along with the view that without reductions in deer density, neither recovery of greatly altered forest areas nor prevention of similar change in other areas is likely to be achieved. Alternative theories are discussed. Subsequent chapters go beyond the direct impact of deer to address the full theoretical basis and experience on which A.R.M. must be based, both in choosing yearly management actions and in making the predictions of outcomes that are crucial to updating management strategies for deer. These chapters include consideration of other factors that affect forest ecosystem structure, processes, and the manner and rate at which forests are likely to recover in different locations following reductions in deer browsing.

Part III discusses one of the important quantitative aspects of A.R.M., the measurement of progress. The first chapter presents a practical set of indicators that, if measured in the forests of Pennsylvania, would indicate the progress that was being achieved towards maintaining and restoring ecosystem structure and processes. These same indicators would be used to rank the success of biological theories in making predictions.

When a change in deer numbers is chosen as one of the planned management actions, managers and A.R.M. analysts also need to know whether the implemented deer harvest regulations actually change deer population levels. The second chapter in Part III reviews methods for measuring deer densities, a separate issue from measuring the progress of ecosystem recovery.

Implicit in the use of A.R.M. are the assumptions that (1) a suitable management structure, complete with qualified support staff or consultant expertise, can be put into place, and (2) a consensus among government agencies and stakeholders can be reached on defining a quantifiable goal that will embody the idea of managing deer from an ecosystem perspective. A.R.M. does not require consensus on the means to reach a goal — which is one of its strong points — but the goal itself must be well defined and quantifiable. Part IV takes up the important question of whether Pennsylvania currently has the capability to implement A.R.M. for deer. Can P.G.C., the Pennsylvania Department of Conservation and Natural Resources (D.C.N.R.), and private groups in the state build a consensus on goals and pull together the necessary expertise?

Information collected on management and stakeholder issues is presented in the two chapters that make up Part IV, one on government policy and one on stakeholders, including hunters, non-governmental organizations, and landowners.

Carrying capacity

Much confusion about deer management stems from the fact that more than one definition of "carrying capacity" is used, even among scientists and wildlife managers. The different meanings reflect very different philosophical and practical approaches to deer management.

• ***Ecological carrying capacity***

Ecological carrying capacity focuses on the interaction between a population of herbivores (plant-eaters, such as white-tailed deer) and the plants that they eat. It is defined as "the maximum density of animals that can be sustained in the absence of harvesting without inducing trends in vegetation."[9] At ecological carrying capacity, the rate of browsing is roughly equal to the rate of food-plant regrowth. The definition also implies that there are no major changes in plant species composition resulting from an increase in the density of an animal population to its carrying capacity.

• ***Nutritional carrying capacity***

In contrast, some highly simplified, deterministic models used in managing deer, elk, and moose throughout the United States focus instead on maximum sustained harvest yields (M.S.Y.). These models are used to estimate, from hunter harvest numbers and sometimes the physical condition of deer, where a population lies on the yield curve, which shows the hump-shaped relationship between deer population density and sustainable annual harvest (see Figure 9, page 160). Many managers who use these models believe that deer should be managed to stay near the peak (the nutritional carrying capacity) of the yield

(Box continued on next page.)

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curve, because near that point, both overharvest and underharvest (so-called management "errors") theoretically are automatically compensated by population responses of deer. The concept of nutritional carrying capacity disregards plant species composition and considers only the total availability of essential nutrients. From this perspective, the ideal deer habitat is fields of corn and other crops side by side with old fields or clearcuts overgrown with shrubs and tree seedlings. In fact, deer persist in high numbers partly because of the inadvertent input of resources as byproducts of human activity. Artificially high disturbance rates (logging), agricultural fields, and suburban gardens generate high-quality deer food in greater abundance or more consistently, or both, than processes that are not supported by humans, including those that perpetuate forests. The deterministic, single-species approach characterized by M.S.Y. has fallen out of favor with most scientists and many managers.[10]

• ***Cultural carrying capacity***

The maximum number of deer a habitat is physically equipped to support can be much higher than the number that will allow other forest management goals to be achieved. Management goals take more than the number of huntable wildlife into account. Forest management elements that are adversely affected by high deer densities include tree regeneration, conservation of rare plant species, and maintenance of habitat for watchable wildlife, rare animal species, and game other than deer. Cultural carrying capacity is a values choice, which takes into consideration the needs and concerns of a range of stakeholders.

Part V concludes the report with a specific example of how A.R.M. for deer might work in Pennsylvania's forests once an appropriate management structure is in place.

The report is structured to facilitate its use by a range of readers, including scientists, policy analysts, and policy makers. Summary findings and recommendations are placed at the end of each chapter. The most important findings and recommendations are compiled in the final chapter and encapsulated in the executive summary. Supporting material is given in appendices.

Limitations of the report

Although over-abundant white-tailed deer cause problems in agricultural areas and suburban areas, we have focused exclusively on forest tracts in excess of one square mile, consistent with our charge to study ecosystem management. As a result, issues related primarily to less forested areas, such as suburban sprawl, forest fragmentation, and the farm-forest interface, are not discussed. Nevertheless, many of the methods described here can be applied to those other areas.

This report has a tendency to focus on trees and other plants and forestry for a number of reasons. Primarily, the majority of the studies of deer impact on forested ecosystems have measured plants, not animals or other organisms. Plants are more easily located and measured. They do not hide to evade handling, they are attached to the specific sites where an impact is occurring, and they provide the basis of the habitat for the other species inhabiting a site. It is reasonable to assume, because animals are tied to suitable habitat, that the plants providing that habitat can be used as a surrogate measure for the recovery of the community as a whole.[11] Also, plants are generally less susceptible to seasonal or annual population fluctuations than other organisms and thus are better for observing trends in deer impact. In contrast, studies to assess the impact of deer on other wildlife have inherently high variability because the impact of deer on them is indirect, involving the removal of species of plants used for food or cover. Finally, many of the agencies charged with land and forest management that are concerned about the impact of deer on these resources are also charged with native plant management and have no regulatory authority over the animal populations on the lands they manage. A few studies have been done and others are underway to assess deer impacts on species other than plants, but it will take some time to develop the body of knowledge and data to document the definitive impacts of high deer densities on them.

Non-sustainable timber-cutting practices such as high-grading are having a detrimental influence on private forestlands across the state, although they are patchier and intermittent compared to deer overbrowsing. Acid rain is weakening the buffering capacity of soils statewide. We discuss these topics as they relate to deer management; however, consideration of policy measures to reduce non-sustainable timber-cutting and acid rain is outside the scope of this report. Nevertheless, the authors recognize that these are important topics and deserve the kind of policy attention that we in this report have given to the deer issue.

At least one reviewer wanted to see more social science in the report. In response, we added additional material to our discussion of the regulatory structure of deer management in Pennsylvania. Still, we recognize that management of deer from an ecosystem perspective is unlikely to be successfully implemented without the guidance of people with backgrounds in social science areas such as resource economics and sociology.

Endnotes

[1] McCabe and McCabe 1984

[2] Kosack 1995

[3] Latham 1950

[4] Legislative Budget and Finance Committee 2000

[5] M. Grund, unpublished data, 2003

[6] Lindenmayer et al. (2000) suggested that ecologically sustainable forest management requires perpetuating ecosystem processes, including chemical cycling and maintenance of biological diversity at all levels (genetic, species, landscape, and ecosystem). Because of the difficulty of measuring many ecosystem processes directly, they reviewed the use of indicators that could be monitored to determine whether goals were being met. They urged that adaptive resource management be employed to test the validity of any monitoring program.

[7] The theories themselves may be modified from time to time to take into account the results of the comparisons.

Endnotes

[8] Other definitions of ecosystem management are possible. For example, the Ecosystem Management Advisory Committee of the Pennsylvania Bureau of Forestry, D.C.N.R., defined it this way: "Ecosystem management is the implementation of practices that maintain or restore soil fertility, water quality, biological diversity, and other important indicators of ecological health" (from "Definition of ecosystem management for the Pennsylvania Bureau of Forestry," unpublished, November, 1998). Maintaining ecological integrity by protecting biological diversity and ecological processes is the general goal of ecosystem management, according to an extensive review of the historical development of the concept (Grumbine 1994).

[9] Krebs 1978

[10] Holt and Talbot 1978; Mangel et al. 1996

[11] When plant community recovery is successfully achieved in some areas, data can be collected on animals to check this assumption.

Chapter 2. The Adaptive Resource Management Approach

If any program to manage deer is to improve over time it must embrace, rather than ignore, the biological uncertainties. Adaptive resource management (A.R.M.) has been termed "managing in the face of uncertainty, with a focus on its reduction."[1] A more formal definition states that A.R.M. "describes the ability to make a sequence of decisions, in the face of uncertainty, that is optimal with respect to a stated objective, recognizing some constraints."[2] Implied in these definitions is that management can be improved if uncertainty is reduced. In calling for an adaptive management approach to managing deer in national parks, William Porter and Brian Underwood stated, "While the [National Park Service] cannot effectively achieve its goals without better science, neither can it wait for science to fully understand the dynamics of plant-herbivore interactions."[3]

A.R.M. is an alternative to more traditional ways of using scientific data in setting management regulations, namely those that rely solely on expert opinion within an agency or from outside in the form of expert advisory groups. A.R.M. is particularly appropriate in situations where differing interpretation of the scientific data has become a major obstacle to decision making. A.R.M. is not a substitute for broader reforms that have been suggested for wildlife management, such as formally evaluating management decisions against a set of agreed-upon criteria.[4]

An A.R.M. program links three components: (1) management objectives and decisions, (2) models of the system dynamics, and (3) a monitoring program to assess changes in the system being managed. The concept of a model may be unfamiliar to some readers (see box on next page), but its use in this report is essential to explain how management actions are actually adjusted in A.R.M. as new information about forest dynamics is gained.

Management objectives must be specific and quantifiable so that progress towards them can be given numerical ratings and success can be evaluated based on numerical goals. Objectives must be agreed upon by agencies and participating stakeholders as a precondition for A.R.M. to be implemented.[5] The long-term objective of managing deer from an ecosystem perspective is the recovery and maintenance of forest structure and diversity of indigenous animal and plant species, as well as ecological processes and forest ecosystem function. If the native herbaceous vegetation, shrubs, understory trees, and tree canopy are restored and maintained (presupposing that this is consistent with landowner objectives), we assume that other species dependent upon them will have the habitats they need to flourish.[6] We presume that any A.R.M. program for deer will begin with a short-term goal, such as showing improvement in forest structure. The ability to quantify goals, which is necessary for A.R.M., requires the judicious selection of indicators. There are candidate sets of indicators that are appropriate for Pennsylvania's forests (discussed

Definition of "model"

A predictive forest model is a set of verbal rules or mathematical equations that allow quantified predictions of how specific indicators of forest stand conditions will change over time based on a change in a variable of management interest, such as a change in deer density. Usually, forest models are based on a conceptual framework of how forest components interact.

The "input" to a predictive forest model is the starting condition of the stand and relevant variables, such as deer density.

The "output" from the model is a quantitative prediction of how the indicator will change at some time in the future.

For A.R.M. as used in this report, the model output must also include a value for the uncertainty in the prediction, such as a variance or standard deviation.

in Chapter 9). A set of several measures is more reliable than just one or two and those involving multiple species may better reflect broad trends than single-species measures (Lindenmayer et al. 2000); thus, to be effective, A.R.M. requires the simultaneous monitoring of several indicator species and one or more structural indicators (e.g., complexity of vertical layering in the forest, tree seedling density, shrub density). By definition, indicators are surrogates for the complete set of species in a community and the ecosystem processes that sustain them. As a result, research into the long-term appropriateness of the choice of indicators must parallel the monitoring of the indicators themselves.

Success in reaching the short-term goal (improving forest structure) would be declared when a statistically significant improvement in indicators of ecosystem integrity is detected and sustained over time. This by itself is a major challenge given the scientific difficulties in finding trends in complex, ever-changing ecological systems. Based on the analysis presented in subsequent chapters, it may take a decade or more to demonstrate that improvements can be both obtained and sustained.

As for the long-term goals, there exist quantitative indicators for commercially valuable trees that can be used to demonstrate long-term success,[7] but no such target magnitudes of change have been developed for other components of the forest ecosystem. However, it is vital to do so, for instance, by using expert panels such as the one convened for this report. Only with long-term targets in hand can the adequacy of short-term goals be assessed.

Although objectives chosen for A.R.M. should change only when or if new data render them obsolete, disagreement regarding models of the dynamics of the system being managed is permitted at any time. This is one way in which A.R.M. is an improvement over traditional management. Much of the uncertainty regarding managing deer to protect forested ecosystems revolves around how deer directly and indirectly affect the environment. Competing models of the dynamics of forested ecosystems might have different predictions regarding the effect of a specific management action. Those models that do the best job of predicting the outcome of a given management action are given more emphasis when future decisions are considered. This is why monitoring ecosystem responses to management actions is critical.

The form of A.R.M. that we present in this report is based on the model of waterfowl management developed by the U.S. Fish and Wildlife Service.[8] In this form of A.R.M., decision makers give an initial weighting to the models in making quantitative decisions such as how many antlerless deer harvest permits will be authorized in a given year. For instance, if the Pennsylvania Game Commission (P.G.C.) assigned a 90% weight to the consensus view that white-tailed deer are hurting forest structure and a 10% weight to theories that white-tailed deer were relatively unimportant, as we recommend later in the report, then the initial number of permits under A.R.M. would end up close to the recommendation that would be made under the consensus view alone. There are many possible weighting schemes that could be used, including a weighted-average approach (this term will be defined later) when the management action includes quantitative components such as numbers of permits. Alternatively, an all-or-nothing approach could be used in which the agency would fully adopt for a given year the model with the greatest weight. In any case, the assigned model weights would be adjusted in future years based on how well each model did in predicting the outcome of the management action. The adjustments can be made using professional judgment, probability theory,[9] or some combination of the two. The exact values of the initial weights are not crucial, because the system is self-correcting. Furthermore, the weights can be adjusted to account for multi-criteria outcomes that include goals or constraints other than ecosystem management. For example, the rate at which progress in forest recovery occurs can be adjusted by raising or lowering the quantitative decisions (e.g., antlerless permits) to account for agency funding or other constraints.

In many, perhaps most, cases it is desirable to update the models themselves from time to time based on the results of the monitoring program. This could be done after each evaluation was completed, so that models would be optimized for their next evaluation several years later. In addition, totally new models might be proposed, which could also be considered at the start of a new monitoring period.

A quantitative example of applying A.R.M. to deer in large forested areas is presented in Tables 1 and 2 and the next five paragraphs. Those readers not interested in such detail may want to skip to the paragraph following Table 2.

A hypothetical example of A.R.M. in action with two competing models (I and II) is shown in Tables 1 and 2. The area of application is assumed to be a region where 6,000 deer harvest permits have been issued annually for many years, keeping the deer densities above P.G.C. targets. Model I is based on research into the effects of deer on forest structure and processes. If the model is correct, then deer harvest permits should be increased to 12,000 per year in order to start the forest on the way to recovery. In our example, we take Model II to be the "null hypothesis," that is, the theory that no management action under consideration will change anything. Scientists often use the null hypothesis as a standard of comparison against the theory that a particular research effort is designed to test. Under model II, the number of deer harvest permits would be left at 6,000 per year. To begin the A.R.M. process, managers make an initial professional judgment, with the help of expert advice, of the likelihood that each model is

Table 1. Example of updating model weights in adaptive resource management with two competing theories. A highly simplified indicator is used for illustrative purposes only; a real-world A.R.M. program would include the monitoring of a larger set of indicators.

year	measurement of the ratio of *Rubus* cover to fern cover in stands with high levels of light reaching the forest floor, as an indicator of forest recovery [a]	prediction made 3 years previously [a]		model weight [b]	
		Model I	Model II	Model I	Model II
Year 0 (initial yr)	10 ± 3 [a]			0.7 [c]	0.3 [c]
Year 5[d]	12 ± 3	14 ± 5	10 ± 3	0.64	0.36
Year 8	15 ± 3	17 ± 6	10 ± 3	0.68	0.32
Year 11	17 ± 4	16 ± 6	10 ± 3	0.80	0.20
Year 14	19 ± 4	18 ± 6 [e]	10 ± 3 [e]	0.93 [e]	0.07 [e]

[a] The number after the ± is the standard deviation of the listed value. A ratio is used in order to cancel out growth effects in recently thinned stands due solely to increased light reaching the forest floor.

[b] In computing updated weights, Bayes's theorem[10] is used assuming a normal distribution. Let P(M|D) be the desired updated weight (conditional probability), given the most recent monitoring data, D. Bayes's theorem states that $P(M|D) = P(D|M) \times \frac{P(M)}{P(D)}$, where P(M) is the model weight before the new data are obtained (the prior estimated relative probability of the model being correct). P(D|M) is the probability that the data, D, would be obtained, assuming the model is correct, e.g., the normal distribution using the model's mean and standard deviation. P(D) is the net probability of the data occurring. P(D) can be determined by normalizing the updated weights, P(M|D), which must sum to unity over all models.

[c] Subjective relative weight used to start the process. The sum of the model weights is always unity.

[d] Measurements following the first baseline measurements in year 0 are delayed to allow deer populations to catch up to changes caused by an increase in antlerless deer harvest permits.

[d] Model I would do slightly better by the end of year 14, if the standard deviation of its predictions were reduced, whereas Model II would do slightly better if its standard deviation were increased.

correct. In the example considered in Table 1, Model I is considered more likely to be correct and is given an initial weight of 0.7 whereas Model II is given an initial weight of 0.3.

Using the initial weights, the actual number of deer harvest permits allocated for the next 3 years is set to 10,200 (= $0.7 \times 12{,}000 + 0.3 \times 6{,}000$). Next, predictions of what will happen to the forest in the management area 3 years after the deer harvest permit allocation is raised from 6,000 to 10,200 are made by each model. In our hypothetical example, we use only one, highly simplified indicator of forest recovery, namely, the ratio of the percent of ground covered by a set of shrub species in the genus *Rubus* (blackberries, raspberries, dewberries), which are highly preferred by deer, to the percent of ground covered by the unpalatable herbaceous species hay-scented fern and New York fern, as measured in stands with high levels of light reaching the forest floor.

Model I predicts that the ratio will increase each year with a magnitude that depends on the average decrease in deer density over the period. Model II predicts that the average cover ratio will be the same after 3 years, that is, the increase in deer harvest permits from 6,000 to 10,200 will make no difference to the ecosystem indicator. As a result, we have a clear difference in predictions that can be tested by *Rubus* and fern monitoring data, which we assume is collected at year 5 and every 3 years thereafter. At the end of year 5, the predictions of the models are

Table 2. Example of changes in allocation of deer harvest permits following updating of model weights (same example as in Table 1)

year	permits that would be allocated if a model were assumed 100% correct		model weights (from Table 1)		allocated permits (based on weighted average) [a]
	Model I	Model II	Model I	Model II	
Year 0	12,000	6,000	0.7 [b]	0.3 [b]	10,200
Year 5[c]	12,000	6,000	0.64	0.36	9,800
Year 8	12,000	6,000	0.68	0.32	10,100
Year 11	12,000	6,000	0.80	0.20	10,800
Year 14	12,000	6,000	0.93	0.07	11,600

[a] The permit allocation is kept the same for 3 years.

[b] Subjective weight used to start the process

[c] Measurements following the first baseline measurements in year 0 are delayed to allow deer populations to catch up to changes caused by an increase in antlerless deer harvest permits.

compared to the data and new weights are assigned to the models (Table 1). The new weights are used to update the number of deer harvest permits allocated for years 6 through 8. In this example, the process continues for 14 years and probability theory is used to update the model weights rather than professional judgment or some combination of the two.

Based on the data collected in year 5, the null hypothesis model, Model II, does better than the biological model, Model I, at predicting the outcome of the chosen, short-term indicator of forest recovery and improves its relative weight (Table 1). As time goes by, however, Model I does better. It recovers its high weight and eventually far outdistances Model II, achieving a (relative) weight of 0.93 by year 14. Note that, in ARM, alternative models do not have to be based on totally different theories. They could have the same basic structure and differ solely in the choice of parameter values.

The way that the model weights affect a management action (allocated deer harvest permits in this example) is shown in Table 2. Based on the initial, subjective weight assigned to the models, the initial allocation of deer harvest permits for a hypothetical zone is set in this example to 10,200. In the following year, the number decreases slightly to 9,800, because Model II did better in predicting the outcome of the monitoring program. However, by the fourth comparison to field data, the allowed number of permits is quite close to that which would be chosen if Model I were assumed to be 100% correct.

The models used in an A.R.M. program do not have to be complicated, in fact, in most cases, the simpler they are, the better. However, each model must include a prediction of its rate of error (e.g., a standard deviation) to be included in the reweighting process. Obviously, for A.R.M. to work, the aim of the monitoring program must be to collect the data required to evaluate the predictions of each model. A.R.M. is an iterative process as subsequent management decisions are made: (1) a management action is proposed based on past model weights, (2) each model predicts the outcome of the management action, (3) data are collected to evaluate the model predictions, and (4) the model that did the best job at predicting prior outcomes is given the greatest influence in guiding the next revision to the management action. Note that weights are assigned to the model, not to the indicator species used to test the model. This is particularly important to bear in mind when multiple species are used as indicators.[11]

Adaptive resource management is not a panacea, and although simple it is not necessarily readily implemented without strong agency commitment. A.R.M. focuses on particular management problems; its contribution to general knowledge usually ranks as a lower priority than is typical in scientific research. Opinions vary on the other ways in which A.R.M. differs from traditional research in science. Many view the quasi-political process of gaining and retaining the support of diverse, often antagonistic groups of stakeholders as an integral part of A.R.M.[12] Some practitioners are willing to accept lower standards of scientific rigor, viewing

Institutional conditions favoring adaptive resource management[15]

- There is a mandate to take action in the face of uncertainty.
- Decision makers are aware that they are experimenting.
- Decision makers care about improving outcomes over biological time-scales.
- Preservation of pristine environments is no longer an option, and human intervention cannot produce desired outcomes predictably.
- Resources are sufficient to measure ecosystem-scale behavior.
- Theory, models, and field methods are available to estimate and infer ecosystem-scale behavior.
- Hypotheses can be formulated.
- Organizational culture encourages learning from experience.
- There is sufficient stability to measure long-term outcomes; institutional patience is essential.

A.R.M. as any systematic attempt to manage natural resources by conducting a series of field trials of alternative management practices, regardless of how rigorously they are carried out.[13] However, as standards of rigor decrease, the risk of erroneously rejecting hypotheses that are actually true increases exponentially. Many, perhaps a majority of practitioners believe that the higher risks of failing to apply rigorous methods of experimental design, data collection, and statistical analysis do not justify the lower costs and are too likely to lead to higher costs and harmful mistakes in the long run.

Achieving an effective institutional framework is one of the challenges of A.R.M. that sets it apart from ordinary research (see box above). In a cautionary note about A.R.M.'s "promises and pitfalls" it has been noted that "An institution's ability to respond to and generate new knowledge is a function of two factors: access to the information and *the will and capacity to utilize that information*"[14] (emphasis added).

Two major challenges exist in implementing A.R.M. for deer in Pennsylvania. First, disagreement over management objectives must be settled in the political arena before A.R.M. can proceed. Second, even though deer harvest regulations are established on an annual basis, vegetation responses may take years or decades. This leads to delayed feedback, which presents difficulties when deer harvest decisions need to be made annually. Feedback is delayed not just because of the lag in the vegetation's response to changes in deer populations, but because the full impact on deer population following changes in permit allocations, particularly antlerless deer harvest allocations, is itself delayed. As a result, major feedback may not be received until 6 years after the start of a deer A.R.M. program, although after the first 6 years, feedback useful for fine-tuning management decisions will be received on a regular basis.

Delays resulting from the use of A.R.M. are to be expected. For example, when the U.S. Fish and Wildlife Service first applied adaptive management to waterfowl, there were two models in competition. One version predicted that reproductive rates would depend strongly on waterfowl density. The other version predicted only a weak relationship between reproduction and density. It took 5 years before one model clearly had outperformed the other.

With delayed feedback, the choice of the initial weights becomes more important than it would be in a situation of rapid feedback. Incorrect weights take longer to subside from the system. In effect, the choice of initial weights represents a 6-year commitment to a particular set of models. Consequently, in the case of deer A.R.M., decision makers cannot relax and pick an arbitrary set of weights, letting the process correct errors in a few years. Decision makers need to listen carefully to the arguments in favor of various theories of forest response to deer populations and make careful judgments about which models deserve the highest weights in setting the level of management action (e.g., annual deer harvest permit allocations). The crucial role of the initial models is a major reason that, in subsequent chapters, we review in detail for the benefit of the reader the literature on deer and forest dynamics.

Despite the complication of delayed indicator response, A.R.M. brings rigor to the decision-making process. It provides a framework for the optimal use of information and the objective evaluation of competing scientific views, such as the importance of deer vs. acid rain in forest ecosystem degradation. This results in a greater understanding of the system being managed and ultimately, better management.

Findings on the adaptive resource management approach

(1) Adaptive resource management (A.R.M.) is a science-based methodology that is well suited to managing deer from an ecosystem perspective while accommodating disagreements over models of forest dynamics or causes of forest alteration. The A.R.M. approach provides for testing competing scientific models or hypotheses about how forests function while, at the same time, providing a framework for regular management decisions to be made and implemented based on the best available information. A.R.M. involves five steps:

- (a) Set and quantify a resource management goal, based on a set of core values that most stakeholders can agree upon.
- (b) Identify competing biological theories that are pertinent to meeting the overall management goal, and the management recommendations that follow from each theory.
- (c) Based on past research and experience, pick what is initially believed to be the best combination of management actions (e.g., reducing deer density to 20 per square mile, avoiding the use of herbicides) and implement the combination in an experimental context.
- (d) Make quantitative predictions of the results of management actions for each competing biological theory or model and compare the predictions against field data at regular intervals (e.g., every 3 years) using indicator species and other environmental indicators.

(e) Update the set of management actions, giving preference to the recommendations that flow from those theories (models) that performed best in the comparisons.

(2) Two major challenges exist in implementing A.R.M. for deer in Pennsylvania. First, management objectives must be determined in the political arena before A.R.M. can proceed. Second, recovery of the structure, diversity, and function of forest ecosystems may take years or decades. Evaluating progress over a multi-year time frame presents difficulties when deer harvest goals need to be set annually.

(3) Managing white-tailed deer in large forested areas from an ecosystem perspective involves attempting, within the constraints of landowner objectives, to maintain or restore ecosystem structures and processes, not just healthy populations of deer. An appropriate short-term goal to use in A.R.M. is the demonstration of a statistically significant improvement in forest structure.

(4) The ability to quantify a goal, which is necessary for A.R.M., requires the judicious selection of indicators. Intermediate to long-term goals must include target magnitudes of change in measurable indicators of ecosystem recovery.

Recommendations on the adaptive resource management approach

(1) A.R.M. should be chosen as the framework for implementing management of deer from an ecosystem perspective. The science-based approach of A.R.M. will allow agencies to begin applying remedies based on the best available information while updating their operational theories as new data become available.

(2) Quantitative guidelines for long-term program success applicable to all components of the forest ecosystem need to be developed, just as they have been for commercially valuable trees. This could be done as part of the A.R.M. process, using an expert panel approach similar to that taken to produce this report.

(3) Research into the long-term appropriateness of the choice of indicators needs to parallel the monitoring of the indicators themselves.

Endnotes

[1] Williams and Johnson 1995

[2] D. R Anderson,National Biological Service, Fort Collins, Colorado, personal communication, 1995 (cited in Williams and Johnson 1995: page 431)

[3] Porter and Underwood 1999

[4] Griese et al. 2000

[5] Kendall 2001

Endnotes

[6] The committee presumes that recovery and maintenance of other species, including vertebrates, invertebrates, and beneficial fungi and other microorganisms will follow if severe stress on plant life is addressed. This assumption can be tested for some organisms (e.g., birds) as part of the long-term monitoring that needs to accompany any set of policy measures implemented with the aim of achieving recovery and maintenance of natural ecosystem structures and processes.

[7] Marquis et al. 1992

[8] Johnson et al. 1993

[9] A Bayesian probability adjustment can may be made as follows. If the monitoring data show a mean value A of a predicted parameter, A, and a model predicted a value, B, with uncertainty characterized by the modeler as normally distributed with standard deviation σ, then the updated relative weight for that model is determined by multiplying the old weight by the normal probability function,

$$\left(\frac{1}{\sqrt{2\pi\sigma^2}}\right)^{-\frac{1}{2}\left(\frac{B-A}{\sigma}\right)^2}$$

(Table 1, footnote b, Johnson et al. 2002; Pearl 2000). If there are multiple predictions for all the models, an equivalent multiplier is used for each prediction. The entire process is repeated each time new monitoring data are available. A model that is good enough to make the difference between the measured and predicted value comparable to or smaller than its assigned standard deviation σ will do well in the reweighting, particularly if its is small. In the all-or-nothing approach, it could happen that theories not included in the initial weighting did quite well. In that case, they would have to be given an initialized, post-facto weight before the Bayesian updating was performed.

[10] Pearl 2000; Johnson et al. 2002

[11] In the multiple-indicator case, the simplest approach to weighting models by performance would be to treat all indicators as equal. In this approach, the net weight for a model would be the product of the individual weights computed separately for each indicator, as described in the text for the example of *Rubus*:fern cover ratio. Other variations are possible, for instance, giving special ranking to those indicators that are thought to be the best surrogates for recovery of forest structure and processes. In all cases, the net weights are assigned to the competing models and do not indicate any value assigned to a particular species.

[12] James N. McNair, Head, Quantitative Population Biology Section, Patrick Center for Environmental Research, Academy of Natural Sciences of Philadelphia, personal communication, 2002

[13] James N. McNair, Head, Quantitative Population Biology Section, Patrick Center for Environmental Research, Academy of Natural Sciences of Philadelphia, personal communication, 2002

[14] McLain and Lee 1996, cited in Schaeffer 2001

[15] Lee 1993 and National Research Council 1996, cited in Schaeffer 2001

Chapter 3. A Brief History of Penn's Woods

Our report starts from the premise that the management of white-tailed deer in large forested areas from an ecosystem perspective will involve attempting, within the constraints of landowner objectives, to restore or maintain ecosystem structures and processes and not just healthy populations of deer. To help define the ecosystem structures and processes that need to be restored or maintained, in this chapter we review the relevant natural history of Pennsylvania and the current state of the forests.

The land that greeted the earliest Europeans to arrive in Pennsylvania was primarily forested, broken only by rivers and lakes, clearings associated with Indian villages and occasional large-scale windstorms, and scattered openings of grassland, shrubland, marsh, and shrub swamp. Early accounts of the landscape of the interior of Pennsylvania contain frequent references like this descriptive passage by Fortescue Cumming while crossing Tuscarora Mountain in 1807, "... view to the westward, though extensive, was cheerless and gloomy, over a broken and mountainous or rather hilly country, covered with forests, chiefly of the dark and sombre pine ..." Another passage referred to extensive grasslands and gallery-type forests in which one could "drive a carriage unhindered," apparently the product of Native Americans' regular use of fire to manage the landscape.[1]

Despite its immensity, however, that forest was a fairly recent product of the geological evolution of Pennsylvania's landscape. Eighteen thousand years ago the northeastern and northwestern corners of the state were covered with ice, and tundra and open, boreal woodlands covered the remainder of the state.[2] As the ice receded, species that had lived only to the south during the most recent ice advance began gradually repopulating the state, a process that is still ongoing.

Influence of Native Americans

Fossil pollen and charcoal residues preserved in bogs and lake sediments all across the eastern half of North America show the beginnings of wide-scale burning as far back as 2,000 or 3,000 years ago. Native Americans found they could improve the ease of travel, hunting, and defense and promote the growth of animal and plant species prized as food by wielding fire as a powerful land-management tool.[3]

Evidence exists that Native Americans managed vast areas of forest with fire to create open, park-like forests and also to clear fields where they grew corn, beans and other crops. The oak-dominated forests that persist today and native grasslands, most of which disappeared soon after Native Americans were ousted from the land, almost certainly owe their existence to traditions of large-scale burning among some groups of people for centuries or thousands of years before the arrival of Europeans.[4]

Native American populations were much larger before contact with Europeans introduced smallpox and other diseases, and the extent of land affected by their management was large.[5] When the first European settlers arrived, extensive clearings were described in the Cumberland Valley, Penns Valley in Centre County, the Wyoming Valley, southern York County, and other sites.[6] Later travelers in these same regions described a forested landscape apparently the result of successional growth.[7]

Cutting down the trees

As European settlers claimed the land, taming the wilderness meant cutting down trees and eradicating some forest wildlife, especially large predators, to make room for farms, towns, and villages and assure the safety of settlers and their livestock. Wood not needed for fuel or building material was often burned early in the process of clearing the land — after all, there was a seemingly unlimited supply.

In Pennsylvania, the clearing for farming and cutting trees for commercial uses that began with the first European arrivals had, by 1900, reduced the forest cover from 90 to 95% of the land area to 32%.[8]

Early lumbering

Tall, straight, and suitable for ships' masts, the eastern white pine was the first large-scale target of waves of loggers in Pennsylvania's forests. Beginning in the 1760s, white pine logs 120 feet long and 4 feet in diameter (or larger) were cut in the hills of northeastern Pennsylvania, fastened together in huge rafts, and floated down the Delaware River to Philadelphia to provide masts for British ships.

A second wave of timber harvesting focused on hemlock bark, which was used in the leather-tanning industry. Hemlock logs were cut and the bark stripped. Charcoal making was another forest industry that thrived before the discovery of coal as a fuel. In areas near early iron furnaces, colliers harvested trees (mainly oaks) and stacked them in conical piles built in the woods. The piles of logs were covered with earth and burned to produce charcoal, which was then hauled by wagon to the iron works. Because small trees as well as large were used for charcoal making, timber could be harvested on a 25-year rotation in most areas. An iron furnace required 20,000 to 35,000 acres of forest to support it on a sustainable basis.[9] Today, it is not unusual to come across level circular areas about 40 feet in diameter scattered in forests where charcoal making occurred.

The chemical wood industry and the indiscriminate removal of forests

The invention of the geared logging locomotive set the stage for the removal of forests between 1890 and 1930 across the entire state. The railroad logging era, as it is known, allowed loggers to reach Pennsylvania's vast interior. Rail beds were constructed up every hollow far into forests unreachable by water transport. Today many of the old railroad beds are the basis for a network of hiking trails.

During the railroad logging era, technology was employed not only to harvest vast areas, but also to utilize everything regardless of species or size. What was not usable as lumber was treated by slow heating and distillation in chemical factories, which produced acetate of lime, wood alcohol, wood tar, charcoal, and gases. Wood products including barrel staves, lath, shingles, boxes, and kindling were produced in hastily built factories located in temporary towns that sprang up throughout the northern tier of Pennsylvania. Old photographs record the boom days at Masten, Golinza, Laquin, and many other sites that today are only names on a map, a few old foundations, or perhaps the site of a hunting camp.[10]

The removals were massive and indiscriminate; fires started by sparks from the logging locomotives frequently followed, burning rapidly and fiercely through the slash. The resulting scenes of devastation generated concern by groups throughout the state and led to the formation of the Pennsylvania Forestry Association. A campaign led by Dr. Joseph Rothrock resulted in the formation of a Division of Forestry within the Pennsylvania Department of Agriculture in 1895 and the appointment of Dr. Rothrock as the first Forestry Commissioner.

Development of a system of forest reserves, now known as state forests, began in 1897 with the acquisition of abandoned cut-over lands that were sold at tax sales. By 1904 the system held about a half million acres; today state forest lands total 2.1 million acres.

Impact of pests and diseases

Pennsylvania's forests have been profoundly affected by pests and diseases introduced from different parts of the world. The chestnut blight fungus, first discovered in New York City in 1904, swept through Pennsylvania in less than one decade, reducing American chestnut, which had previously been the most abundant tree across much of the state, to minor status. The gypsy moth, which spread into the state following its accidental release in eastern Massachusetts in 1869, reduced the abundance of oaks by feeding on them in preference to all other species. Beech bark disease, which appeared in Nova Scotia about 1920, still is spreading across the northern and western half of the state. Typically, the largest, oldest trees are the most susceptible; the full impact of beech bark disease has not yet been realized. Dutch elm disease and dogwood anthracnose have taken their toll. The most recent invader, hemlock woolly adelgid, is killing our state tree, the eastern hemlock, in southern and eastern parts of the state. Mild winters have

Vertical structure in forests

In forest ecology and forestry, the term understory refers to all of the forest layers beneath the canopy, or topmost layer. We follow the common practice of dividing the forest into four major vertical layers above the surface of the ground. Shrubs and herbaceous plants are generally confined to the two lowest layers but trees (and woody vines) may be present in any or all layers. In forests with low or moderate deer densities, the understory layers typically include seedlings, saplings, and "pole-size" trees of species that are capable of eventually growing into the canopy. Certain tree species, such as flowering dogwood, striped maple, American hornbeam, eastern hophornbeam, and downy serviceberry, never grow large enough to occupy the canopy of a mature forest.

The four layers (including common synonyms for each) are:

- **canopy**, overstory, dominant trees, upper canopy, upper layer, major trees
- **subcanopy**, understory trees, lower canopy, intermediate canopy
- **shrub layer**, understory shrubs
- **herbaceous layer**, herbaceous flora, herbaceous species, ground layer, ground-layer vegetation, forest-floor plants

allowed the adelgid to spread rapidly westward. (Further discussion of these diseases and insects is in Chapter 6.)

Recent outbreaks of native insects such as elm spanworm, forest tent caterpillar, eastern tent caterpillar, and cherry scallop-shell moth have caused extensive tree death in some parts of the state. Research is ongoing to understand the underlying causes of a recent decline of sugar maple in Pennsylvania.[11] Low levels of magnesium combined with excessive stress, for example from insect defoliation, have been associated with sugar maple decline.[12] On soils with low or intermediate concentrations of base cations, the situation is also worsened by high levels of acidic deposition.[13]

Major forest types

Pennsylvania contains about 16.7 million acres of forestland.[14] Nearly all current forests are second- and third-generation stands that developed after extensive forest removals between 1890 and 1930, when deer densities were very low.[15] Though generally even-aged, many stands contain scattered residuals from the previous generation and some may contain up to four age classes.

The climate, rainfall, and soils support forest growth throughout most of the state with the exception of scattered areas that are too wet, low in soil nutrients, fire-prone, or dry and rocky. From an ecological perspective, 62 tree-dominated natural community types have been described for Pennsylvania.[16] According to the most recent reconstruction of potential natural vegetation (Figure 4B, page 126),[17] the major forest communities represented in the state are beech-maple forest (parts of Erie, Mercer, Lawrence Counties), mixed mesophytic forest (parts of Greene and Fayette Counties), oak-hickory-pine forest (extreme southeastern Somerset and York, southern

Bedford and Fulton, and southwestern Franklin and Lancaster Counties), northern hardwoods (the high plateaus, Allegheny Mountains, and most of northwestern Pennsylvania) and Appalachian oak forest (the remainder of the state, including portions of the northern tier).

In the following descriptions of the major forest types across the state and throughout this report, common names of plants and other organisms are used. The corresponding scientific nomenclature is indexed in Appendix E.

Beech-maple forests, sugar maple-basswood forests

The common canopy trees of beech-maple and sugar maple-basswood forest communities are sugar maple, red maple, American basswood, American beech, white ash, yellow birch, sweet birch, and yellow-poplar. Understory trees and shrubs include flowering dogwood, pawpaw, eastern hophornbeam, spicebush, witch-hazel, and bladdernut. These forests have a rich and diverse herbaceous flora that includes black snakeroot, blue cohosh, wood geranium, hepatica, wild leek, jack-in-the-pulpit, spring-beauty, yellow trout-lily, bishop's-cap, rattlesnake fern, and many others.

Mixed mesophytic forests

The most species-rich forest type represented in the state is the mixed mesophytic forest, which reaches its greatest development in the Great Smoky Mountains and elsewhere in the southern Appalachians. Canopy dominance is often shared by many species, in Pennsylvania most often including yellow-poplar, sugar maple, American beech, American basswood, northern red oak, cucumbertree, yellow buckeye, Ohio buckeye, white ash, and black cherry. Understory trees and shrubs include flowering dogwood, pawpaw, umbrella magnolia, redbud, witch-hazel, and wild hydrangea. If not severely impacted by deer, this forest, which often occurs on sites with rich, limestone-based soils, has an incredibly diverse herbaceous flora that includes large white trillium, Virginia bluebell, wild blue phlox, dwarf larkspur, blue-eyed-Mary, wood anemone, foamflower, wild-ginger, squirrel-corn, Dutchman's-breeches, toadshade, black snakeroot, and many more.

Oak-hickory-pine forests

Oak-hickory-pine forests are most common on dry ridgetops, rocky sites and south-facing slopes. This community is dominated by chestnut oak, scarlet oak, pignut hickory, blackgum, sweet birch, and Virginia pine in the canopy. Before 1910, American chestnut was a dominant and commercially important component of these forests, but the accidental introduction of the chestnut blight fungus in 1904 reduced chestnut to a minor forest understory component in a few decades. Where deer numbers are low, dry oak forests often have a dense shrub layer of black huckleberry, mountain-laurel, lowbush blueberry, and maple-leaf viburnum. Forest-floor plants include teaberry, pipsissewa, trailing-arbutus, Pennsylvania sedge, wild sarsaparilla, bracken fern, pink lady's-slipper, and whorled loosestrife.

Northern hardwoods

The northern hardwood forest occupies the northern third of the state and extends south at high elevations along the Allegheny Front. It also occurs farther south on north-facing slopes and ravines. Major canopy tree species are sugar maple, red maple, and American beech; black cherry is also an important component of many stands. Northern hardwood stands where more than 25% of the total basal area[18] of all trees is in black cherry are referred to as black cherry-northern hardwoods[19] (in the wood products industry, this type is known as Allegheny hardwoods). Associated tree species in northern hardwoods include eastern hemlock, eastern white pine, white ash, yellow-poplar, sweet birch, yellow birch, cucumbertree, American basswood, and northern red oak. Understory trees in northern hardwood forests typically include striped maple, mountain maple, American hornbeam, eastern hophornbeam, American mountain-ash, Allegheny serviceberry, and downy serviceberry. Shrubs formerly abundant in the northern hardwood forest included hobblebush, American yew, mountain winterberry, rosebay rhododendron, and witch-hazel; in most of northern Pennsylvania they have been severely reduced or eliminated by deer. Typical herbaceous species include Canada mayflower, starflower, Indian cucumber-root, painted trillium, purple trillium, large round-leaved orchid, shining clubmoss, and marginal wood fern, but these too have been severely impacted by deer in many areas. New York fern and hay-scented fern, formerly minor components of the northern hardwood forest understory, are not favored deer food and have proliferated where deer have eliminated the normal diversity of species.

Appalachian oak forests

Appalachian oak forests (called Appalachian mixed hardwoods or oak-mixed hardwoods in the wood products industry) are the most common community in the southern two-thirds of the state. Common canopy species include northern red, white, black, scarlet, and chestnut oaks in mixture with pignut, mockernut, shagbark, and bitternut hickory, red maple, yellow-poplar, sweet birch, black cherry, cucumbertree, and eastern white pine. In areas with low deer populations, the subcanopy and shrub layers often include mountain-laurel, black huckleberry, lowbush blueberry, flowering dogwood, beaked hazelnut, redbud, eastern hophornbeam, and maple-leaf viburnum. Common forest floor herbaceous species include bellwort, Solomon's-seal, Solomon's-plume, mayapple, blue cohosh, wood ferns, purple trillium, violets, and yellow trout-lily. The dominance of oaks in these forests is partly the result of long-term, recurring fire discouraging competing tree species, most of which are less tolerant of fire than oaks.[20]

Additional forest types

Several other forest types occur in specialized environments. Although they occupy relatively small areas, they add significantly to the overall biological diversity of Pennsylvania.

Coastal plain forests

In the southeastern corner of the state, in the narrow sliver of the Atlantic Coastal Plain physiographic province that parallels the Delaware River, coastal plain forest canopies contain sweetgum, willow oak, southern red oak, and sweetbay magnolia above a shrub layer of sweet pepperbush, swamp dog-hobble, and pinxter-flower azalea. The herbaceous layer features many coastal plain rarities including Maryland meadow-beauty, New York aster, and coast violet.

Glacial bog forests

In the northeastern and northwestern corners of the state, in areas covered by ice during the most recent glaciation, peat deposits support bog forests of a northern character dominated by black spruce and tamarack. Shrubs include Labrador-tea, highbush blueberry, sweetgale, bog-laurel, bog-rosemary, and northern arrowwood. Characteristic herbaceous species include pitcher plant, round-leaved sundew, many sedges, and rare orchids such as dragon's-mouth, yellow fringed orchid, white fringed orchid, rose pogonia, and grass-pink.

Barrens

Serpentinite rock, which occurs in a band of outcrops stretching across southern Delaware, Chester, and Lancaster counties, supports forests of pitch pine or Virginia pine, eastern redcedar, post oak, blackjack oak, sassafras, scrub oak, and dwarf chinkapin oak interspersed with grasslands dominated by little bluestem, Indian grass, big bluestem, prairie dropseed, moss-pink, barren chickweed, and serpentine aster, with a high diversity of other native grass and forb species.

Shale barrens and limestone barrens of the Appalachian Ridge and Valley physiographic province harbor drought-tolerant species including eastern redcedar, Virginia pine, Table Mountain pine, chinkapin oak, post oak, and hackberry. Redbud and fragrant sumac are frequent in the subcanopy and shrub layers. Herbaceous species include side-oats gramma, Indian grass, little bluestem, hoary puccoon, false-gromwell, bird's-foot violet, and shale-barren ragwort.

Pitch pine-scrub oak barrens occur on ridge tops and other fire-prone sites. Ranging from dry to moist, these habitats have a dense shrub layer that includes sheep-laurel, sweet low blueberry, and rhodora; the herbaceous layer includes the globally rare variable sedge, white fringed orchid, dwarf cornel, and climbing fern.

Riparian forests

Riparian areas throughout the state, where periodic flooding is a limiting factor, are characterized by forests of American sycamore, silver maple, boxelder, American elm, slippery elm, black willow, green ash, red maple, and shellbark hickory. River birch occurs along rivers and streams in the eastern part of the state but not in the west. River floodplains are also rich in shrubs, woody vines, and herbaceous species. Those native to Pennsylvania include silky dogwood, frost grape, spicebush, poison-ivy, spotted jewelweed, pale jewelweed, clearweed, wood nettle, great nettle, and jumpseed. Floodplain forests are especially prone to invasion by introduced species, including multiflora rose, Japanese honeysuckle, Morrow's honeysuckle, Tatarian honeysuckle, Japanese stilt grass, Japanese knotweed, giant knotweed, garlic mustard, and lesser celandine.

Swamp forests

Bottomlands and other areas with a year-round high water table are habitats for several swamp forest types. Red maple and blackgum dominate the most common, widespread swamp type. Swamps dominated by pin oak or swamp white oak are mainly in the southern half of the state and those dominated by eastern hemlock, mainly in the northern half. Red maple and black ash-dominated swamps occur mainly where the groundwater is rich in base cations, overlying calcareous (limestone, dolomite) or mafic (diabase) bedrock. Red spruce swamps occur in glaciated northeastern Pennsylvania. Swamp forests along Lake Erie are the only location where pumpkin ash occurs. Other characteristic tree species in swamp forests include yellow birch, eastern white pine, American elm, slippery elm, and bitternut hickory. The shrub layer often includes highbush blueberry, winterberry, spicebush, northern arrowwood, southern arrowwood, smooth alder, speckled alder, or swamp azalea. Common herbaceous species include skunk-cabbage, cinnamon fern, sensitive fern, arrow-leaved tearthumb, halberd-leaved tearthumb, and sedges.

The forest today

Despite dire predictions by Rothrock and others, Pennsylvania's forests did recover in the years following the devastating removals around the turn of the nineteenth century. Trees came back not only on cut-over lands, but also on abandoned farmland; today second growth forests cover 59% of the state's land area. Only a few fragments of the original forest remain. The Allegheny National Forest in northwestern Pennsylvania includes the only sizeable tract of old-growth forest, 4,080 acres in the Tionesta Scenic and Natural Area. Some 30 smaller fragments are fully or partially protected in state forests, state parks, Allegheny National Forest, and lands owned by public utility companies and conservation land trusts.[21] The Snyder-Middleswarth

State Forest Natural Area preserves over 300 acres of old growth and three tracts in Cook Forest State Park total nearly 300 acres. Several protected stands top 100 acres in size, including Woodbourne Forest and Wildlife Sanctuary (The Nature Conservancy), Otter Creek Natural Area (Holtwood Environmental Preserve, PPL Corporation), Detweiler Run, The Hemlocks, and Alan Seegar State Forest Natural Areas (Pennsylvania Department of Conservation and Natural Resources), and Hearts Content Natural Area (U.S. Forest Service).

Pennsylvania's publicly owned forestlands include 2.1 million acres of state forests and 277,000 acres in 116 state parks. State game lands, administered by the Pennsylvania Game Commission, contain another 1.4 million acres in the public domain. Pennsylvania's only national forest, the Allegheny National Forest, contains just over a half million acres. By far the largest proportion (70%) of forested land in the state is privately owned.

The wood products industry remains an important part of Pennsylvania's economy, totaling nearly $5 billion per year and providing about 100,000 jobs. The most valuable single timber product is black cherry, which is used mainly for veneer by the furniture industry. Oaks and other hardwoods are also important. The resilience of Pennsylvania's forests and their ability to regenerate naturally have long sustained the Pennsylvania wood products industry. But problems resulting from high deer density and fire suppression have affected the abundance of many commercially important species, especially oaks.[22] Extensive burning by Native Americans may have made possible the expansive oak forests found by early Europeans. Fires that followed clearcutting allowed oak forests to become reestablished[23]. But now, oaks are being replaced by red maple in many areas.[24] Research by the Pennsylvania Bureau of Forestry and the U.S. Forest Service suggests that oaks may become reestablished under a regime of deer exclusion followed by fire to reduce competition from faster-growing species such as red maple, sweet birch, black cherry, and pin cherry.[25]

Most forested landscapes in Pennsylvania consist of a mosaic of 70- to 110-year-old stands that originated after catastrophic disturbances, most often heavy logging but also, in some areas, fire and windfall. Stand structure often closely approximates a single cohort (i.e., they are even-aged), although remnant trees from older cohorts are sometimes present. Forest stands typically contain species representing a range in shade tolerance. Stands usually have a stratified canopy (trees occupying both subcanopy and canopy levels) and an irregular diameter distribution.[26] Fast-growing, shade-intolerant species dominate in the larger diameter classes and occupy only the upper layer. In contrast to the situation in most old-growth forests, slower growing, shade-tolerant species are most often concentrated in the smaller diameter classes and understory layers. Woody species composition in second-growth forests can differ from the pre-European-settlement forest composition due to successional status, site conditions, and disturbance history.[27]

The types of disturbances currently affecting second-growth forests differ from those that initiated their development in the nineteenth or early twentieth century. Ordinary windstorms, occasional ice storms and hurricanes, and rare, localized downbursts and tornadoes are still a factor as they have always been,[28] but fire has been drastically reduced. Introduced insects and diseases have altered the successional pathways of some forest types by virtually eliminating certain species, thus creating unprecedented favorable environmental conditions for others.[29] White-tailed deer populations have grown beyond the forest's ecological carrying capacity in most of the state (see box on page 16 and Chapter 11) and have changed species composition and reduced species diversity, mostly in layers beneath the canopy, through selective browsing.

Despite the presence of a diverse overstory, tree regeneration typically is severely limited in Pennsylvania forests.[30] A statewide survey of the regeneration of commercially important species, part of the U.S. Forest Service's recent Forest Inventory Analysis (F.I.A.), concluded that "by every measure, the regeneration picture in Pennsylvania is bleak based on findings for the first panel [year] of regeneration measurements"[31] (see Table 3).

Even where regeneration is ample, the tree seedlings present typically represent fewer species than the overstory due to dense deer populations and the deer's feeding preferences for some species of tree seedlings over others.[32] This is particularly important in stands that may be subject to future canopy thinning or removal by cutting or natural events, because most tree species that grow into the overstory after disturbance must be present as established seedlings before the overstory is removed.[33] Thus, removal of the overstory under present conditions frequently results in regeneration failure or new forests of lower diversity, unless heroic measures are taken. For example, northern hardwood forests frequently regenerate to ferns and grasses, striped maple, or near monocultures of American beech, sweet birch, or black cherry. A

Table 3. Regeneration of trees of value to the wood products industry in Pennsylvania forests.[34] The overall trends are assumed to apply to the majority of native tree species (all of Pennsylvania's indigenous trees are listed in Table 4, with those having significant commercial value marked by an asterisk).

silvicultural region	percent of stands with regeneration of species with high commercial value	percent of stands with regeneration of any species with commercial value
Eastern broadleaf–east	22	50
Plateau	24	45
Central Appalachian	30	44
Eastern broadleaf–west	45	58

monoculture of any species is not a preferred outcome, even if the needs of the wood products industry alone are taken into account, partly because monocultures are much more susceptible to mass mortality from outbreaks of insect herbivores or diseases.

Mixed oaks, in the presence of a high deer density and the absence of occasional fire, frequently regenerate to ferns, mountain-laurel, rosebay rhododendron, flowering dogwood, sassafras, sweet birch, blackgum, red maple, or yellow-poplar. Aside from the commercial losses, a once-magnificent part of Pennsylvania's natural heritage is disappearing as oak forests succumb to a more homogeneous forest dominated by red maple.[35] The vast forests dominated by oaks, American chestnut, and hickories that formerly covered two-thirds of the state sustained a higher total biomass — and in all likelihood a higher diversity — of animal life, with their massive crops of fat-, carbohydrate- and protein-rich nuts and acorns, than the low-diversity woods that are taking their place.

Tree establishment and survival are affected by a variety of factors in addition to deer browsing, including propagule (seed) supply, seedbed conditions, sunlight, competition with other plants, small mammal and insect predation, diseases, non-sustainable forestry, incidence and severity of fire, and soil physical and chemical properties.[36] However, unlike deer overbrowsing, most of these factors rarely limit regeneration of large numbers of species simultaneously over large areas, or for periods of decades or longer. Exceptions may include non-sustainable timber-cutting practices and acidification of soils by atmospheric deposition of pollutants.

In areas such as northwestern Pennsylvania where overbrowsing has been a factor since the 1920s,[37] there may be little in the way of local sources of propagules (seeds, spores, and vegetative reproductive organs such as bulblets) remaining for the shrub and herbaceous species native to the forest understory, which far outnumber tree species in overall diversity. Further exacerbating the situation is the fact that most forest herbs do not have long-distance dispersal mechanisms. The primary means of reproduction for many species is vegetative spread by horizontal roots (rhizomes) or trailing stems (stolons) and the seeds of many others are dispersed by gravity or ants.[38]

Studies of seeds lying dormant in the soil of the region's forests hold out little hope that this "seed bank" will contribute significantly to the recovery of plant species diversity following release from deer overbrowsing.[39] However, there is some hope based on recent work at Hearts Content Natural Area that suppressed individuals of some shrubs and herbaceous species may be present at very low densities even in heavily browsed areas.[40] Some species are still present in local refugia such as large boulders, the tops of which can support small patches of forest floor species,[41] and steep-sided rock outcrops. The prospects for suppressed plant remnants are greater in areas where deer overpopulation is a more recent phenomenon.

Deer threaten the regeneration of all forests throughout the state. Fencing to exclude deer is now a standard practice on state forest lands when timber is harvested. Fencing is necessary to allow new trees to become established and grow beyond the browse line (the height deer can reach, which is about 5 feet). According to the state forester, Dr. James Grace, 20,000 acres of state forest land are fenced at present, but the total could easily be 50,000 if the need were adequately addressed.[42] Optimum timber harvest levels have not been met due to the inability to fence and treat more acres.

Findings on the history of Penn's Woods

(1) Pennsylvania's forests regrew after the massive cutting that occurred between 1890 and 1930. Trees came back not only on cut-over lands, but also on abandoned farmland; today second-growth forests cover 59% of the state's land area. Only a few fragments remain of the pre-European-settlement forest.

(2) Today's forests, most of which are in the 70- to 110-year-old category, differ from the forests that greeted the first Europeans in several important ways. Three hundred- to 400-year-old giants are found in only a few remnant old-growth groves. Oaks and eastern white pine are not as abundant as they once were and American chestnut has been relegated to a minor role in the understory due to the impact of the introduced chestnut blight fungus.

(3) In the areas that have been affected the longest by high deer densities , the diversity of canopy tree species has decreased. Even in some areas that have sustained high deer densities for just a few decades or less, understory tree and shrub layers have been diminished in species diversity, height, and density or completely eliminated, and the formerly diverse ground layer has been reduced to ferns and a few other species that are either not preferred by deer or resilient to repeated browsing.

(4) Pennsylvania's forests also have been profoundly affected by pests and diseases introduced from other parts of the world.

(5) Sixty-two tree-dominated natural community types have been described for Pennsylvania by ecologists. To the wood products industry, the major forest categories of interest are the northern hardwood and Appalachian oak-mixed hardwood forests. The northern hardwood forest is the main forest type in the northern one-third of the state and extends southward at high elevations along the Allegheny Front and down the spine of the Appalachians in western Pennsylvania into Maryland and West Virginia. The main forest type in the southern two-thirds of the state is oak-mixed hardwood.

(6) The U.S. Forest Service's F.I.A. data show that among four tree-harvest regions covering Pennsylvania, desired levels of regeneration were found in only 22 to 45% of the total forest area.

Endnotes

[1] Cumming 1810; Maxwell 1910

[2] Watts 1979; Martin 1958

[3] Maxwell 1910; Day 1953; Thompson and Smith 1970; Webster 1983; Dent 1985; Denevan 1992; Casselberry and Evans 1994; Black and Abrams 2001

[4] Marye 1955; Russell 1983; DeSelm 1986; Abrams 1992; Clark and Royall 1996; Clark et al. 1996; Delcourt and Delcourt 1997, 1998

[5] Dobyns 1966, 1983; Denevan 1992

[6] Bates and Richard 1887; Losensky 1961; Cook 1887; Schoepf 1788; Marye 1955

[7] E.g., Maximilian 1834

[8] deCoster 1995

[9] Bining 1938

[10] Kline et al. 1970-1978; Marquis 1975

[11] Kolb and McCormick 1993; Long et al. 1997; Horsley et al. 2000, 2002

[12] Bailey et al. 2004; Horsley et al. 2000

[13] Drohan and Sharpe 1997

[14] McWilliams et al. 2002

[15] Marquis 1975, 1992

[16] Fike 1999

[17] Küchler 1964

[18] Basal area is the area occupied by tree trunks in an imaginary plane 1.4 m (4 feet 7 inches) above the ground.

[19] Fike 1999

[20] Tome 1854; Abrams and Nowacki 1992; Brose et al. 2001

[21] Erdman and Wiegman 1974; Bjorkbom and Larson 1977; Pennsylvania Bureau of Forestry 1979; Smith 1989

[22] Other forest stresses are discussed in Chapters 5 and 6.

[23] Abrams 1992

[24] Abrams 1998

[25] Van Lear et al. 2000

[26] Oliver and Larson 1996

[27] For example, in a 1940s forest vegetation assessment of old growth in Kentucky's Cumberland Mountains, Braun (1950) estimated that 84% of the overstory consisted of 10 species, dominated by American beech, sugar maple, American chestnut, and eastern hemlock. In 1988, the U.S. Forest Service reported that 10 different species accounted for 83% of the overstory, which is now dominated by oaks, yellow-poplar, hickories, and red maple (Steinman 1999). Disturbances to the late-successional forests observed by Braun, such as chestnut blight and logging, created growing conditions favorable to the early-successional species that currently dominate.

[28] Lorimer 1977, 1980; Runkle 1982; Frelich and Lorimer 1991

[29] E.g., Fajvan and Wood 1996

[30] Marquis et al. 1992

[31] McWilliams et al. 2002

[32] Allegheny National Forest 1995

Endnotes

[33] Grisez and Peace 1973

[34] Data from McWilliams et al. 2002

[35] Abrams 1992, 1998

[36] Kozlowski 2002

[37] Fronz 1930

[38] Bierzychudek 1982; Sobey and Barkhouse 1977; Beattie and Culver 1981

[39] Leckie et al. 2000; Pickett and McDonnell 1989

[40] Ristau 2001

[41] Rooney 1997

[42] Dr. James R. Grace, State Forester, Bureau of Forestry, Pennsylvania Department of Conservation and Natural Resources, personal communication, 2002

Chapter 4. Some Root Causes of Our Current Ecological Problems

The roots of the deer problem

White-tailed deer have been a symbol of wild eastern North America throughout the region's recorded history and even before. From prehistoric Native Americans to twenty-first-century nature enthusiasts and hunters, deer glimpsed in the woods have thrilled people with their grace and stateliness, and venison at the campfire and table has provided savor and sustenance. Unfortunately, deer-human interaction in the last two centuries has a dark side: in the 1800s, overexploitation and near-extinction, and in the 1900s, overprotection and resultant habitat destruction by now-teeming populations.

There is a widespread impulse to blame recent policies and management actions, or inaction, for the current deer situation, but the ultimate causes run much deeper and have been around for a very long time. Profound changes to the landscape and to interactions among wildlife species brought about by humans are responsible for the current high densities of white-tailed deer and their pervasive effects on the rest of the ecosystem. These changes are persistent and difficult to reverse, which means that there is no quick fix. Any remedy for the deer problem will require persevering with carefully targeted efforts indefinitely.

The arrival of Western civilization in Pennsylvania, beginning in 1643 with a small settlement of Swedes in present-day Delaware County, has been more like a geologic force than merely one species' population shift. Within 200 years of arriving, Europeans had cut down most of the forest and converted vast areas to crops and pasture. Industrialization since about 150 years ago has accelerated the pace of change, adding urban sprawl, strip-mining, and other large-scale landscape transformations.

From the deer's perspective, this has been a bonanza. White-tailed deer is an "edge" species. The patchwork of forest fragments interspersed with farmland and suburban lawns and gardens that cover much of present-day Pennsylvania could hardly be more ideal habitat it is capable of supporting far greater deer populations than the mostly forested landscape of 1643.

The increase in Pennsylvania's deer population from the beginning to the end of the twentieth century was mirrored by the buck harvest (see Figure 3, page 122). Statewide, the buck harvest increased nearly 160-fold from 1915 to 2001[1] while the human population grew by a factor of only 1.5 in the same time period.

Although much of present-day Pennsylvania has been transformed into ideal deer habitat over the last few hundred years, major human impacts on Pennsylvania's wildlife, including deer, can be traced back much further, almost as far back as our species' first arrival on the scene at least 13,000 years ago. Contrary to a long-held popular belief, research by paleontologists[2] and recent work by paleoecologists[3] strongly suggest that early human impacts on eastern North American ecosystems were profound. The effect that is most obvious from the fossil remains was the extinction of more than two dozen species of "megafauna" — large mammals — within a few centuries of the arrival of the first humans. An effect not easily detected in the fossil record is a cascade of ecological changes that almost certainly resulted from the removal of the largest herbivores (grazers and browsers) and most of the large carnivores. Megaherbivores and large predators are often keystone species where they survive in present-day ecosystems. A keystone species is one whose effects are much greater than would be expected from its relative population abundance, and whose removal causes the loss of many other species in a community.

Many Pennsylvanians know that gray wolves and mountain lions, before they were exterminated in the nineteenth century, preyed on deer. Fewer are aware that, for millions of years — more than 99% of white-tailed deer's existence as a species — Pennsylvania's native fauna also included American cheetah, Studer's cheetah, jaguar (which survives only in tropical America), dire wolf, Armbruster's wolf, grizzly bear (now confined to western North America), lesser short-faced bear, and giant short-faced bear.[4] The giant short-faced bear was the largest land predator the earth has seen since the demise of the dinosaurs. There is every reason to presume that white-tailed deer were preyed upon by all of these species.

Ironically, *Homo sapiens* — the original cause of large predators' disappearance from Pennsylvania — is the only species still present in the state that is capable of maintaining the population density of white-tailed deer in balance. Deer populations are likely to be reduced most effectively by hunters shooting adult females.[5] However, predation by humans, as currently practiced by hunters and managed by state wildlife agencies, differs in key ways from the predation that regulated deer numbers throughout the species' evolutionary past. Wild predators on deer in North America typically minimize risk to themselves and magnify their chance of success by taking fawns in preference to adults,[6] does in preference to bucks,[7] and deer weakened by age, starvation or injury in preference to robust, healthy individuals.[8] Furthermore, there are two components to predators' effects on deer foraging: numerical and functional. Hunters can reduce the numerical abundance of deer but they are much less effective than predators in shifting deer behavior to avoid large portions of remote areas and reduce foraging times.[9] Recent studies of the effects of wolf reintroduction in Yellowstone National Park have documented cascading effects of the restored carnivore-herbivore interactions. Increased predation risk caused elk to avoid stream corridors, allowing woody plants to regenerate and thus restoring riparian function. Beaver colonies, which had been missing from the area for 50 years, reappeared and aquatic food webs, including birds and other fauna, were reestablished.[10] It is not a trivial challenge and may not be fully practical to find ways in which hunting can be managed in the long term to mimic the way populations have been regulated for millions of years by native predators, and still retain its appeal to hunters.[11] Nonetheless, we assume that until hunters are given adequate tools, it would be premature to conclude that recreational hunting cannot do the job (see Chapter 13).

Findings on the root causes of our current ecological problems

(1) For millions of years — more than 99% of white-tailed deer's existence — the species' population was subject to regulation by a diverse array of predators, including not only the gray wolf and mountain lion but also the American cheetah, Studer's cheetah, jaguar, dire wolf, Armbruster's wolf, grizzly bear, lesser short-faced bear, and giant short-faced bear.

(2) Deer are an "edge" species. The patchwork of forest fragments interspersed with farmland and suburban lawns and gardens that covers much of present-day Pennsylvania could hardly be more ideal habitat, capable of supporting far higher deer populations than the mostly forested landscape of 1643, at the beginning of European settlement.

(3) As a result of the elimination of large predators in the 1700s and 1800s, humans are the only species still present in Pennsylvania capable of maintaining the population density of white-tailed deer in balance with its habitat. Active intervention by humans to keep deer populations below levels that severely alter the composition and diversity of forests will have to be sustained forever, assuming that it is impractical to restore the full complement of predators across the entire range of white-tailed deer in the state.

Endnotes

[1] Pennsylvania Game Commission 2002b

[2] Cope 1871, 1899; Wheatley 1871; Hay 1923; Guilday 1971; Kurtén and Anderson 1980; Williams at al. 1985

[3] Graham and Lundelius 1984; Guthrie 1984; Martin and Klein 1984; McDonald 1984; Owen-Smith 1987; Grayson 1991; Stuart 1991; Zimov et al. 1995; MacPhee and Marx 1997

[4] Cope 1871, 1899; Wheatley 1871; Hay 1923; Guilday 1971; Kurtén and Anderson 1980; Williams at al. 1985

[5] See pages 221 and 222 for discussion of an often-mentioned alternative.

[6] Mech and Karns 1977; Nelson and Mech 1986; Pierce et al. 2000

[7] Nelson and Mech 1986; Bleich and Taylor 1998; Pierce et al. 2000

[8] Mech and Karns 1977; Ackerman et al. 1984; DelGiudice 1998; Pierce et al. 2000

[9] Dr. William J. McShea, Research Scientist, Conservation and Research Center, Smithsonian Institution, personal communication, 2003

[10] Ripple and Beschata 2003, 2004

[11] See Chapter 15 on hunter satisfaction.