For additional copies of this booklet, please contact the author at tsimpson@MCCDistrict.org.

The author continues to work on issues related to oak reproduction. If you have any questions about the work or how it might be applied in a management context, please feel free to contact the author at the email address given above.
Acknowledgements:

I would like to acknowledge the generous support of this research by McHenry County Conservation District, in particular the support and leadership of Ed Collins, Director of the Division of Land Preservation and Natural Resources. Many people contributed to this research over the years, chief among them my research interns: Kevin Mulvey, Katie Cowlin, Matte Craffe, Emily Hansen, Steve Tillman, and Elizabeth Elliot-Hogg. Karen Lundell unearthed a key set of papers related to nut caching by blue jays. Dozens of Field Station interns participated in various aspects of the research as did several staff members of the LPNR Division. My thanks to all of them.
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SUMMARY:

Oak reproduction is often scarce or lacking in oak savannas and woodlands under ecological restoration, despite the fact that large canopy gaps created by the removal of invasive brush allow abundant sunlight to reach the ground surface. Understanding and facilitating natural reproduction is important to the progress of ecological restoration. In two experiments, we found that over 98% of the acorns in artificial caches located in dense, tall herbaceous vegetation were eaten by white-footed mice or meadow voles. In these and other experiments, we showed that predation of acorns by white-footed mice and meadow voles is much less in short-statured vegetation or bare, open areas than in corresponding areas of tall grass.

A survey of the spatial density of squirrel leaf nests in woods across McHenry County revealed that gray squirrels and fox squirrels are much less common in open canopy woods with tall, dense herbaceous vegetation than in closed canopy woods with sparse surface vegetation.

Thus, high populations of mice and voles correspond to low populations of squirrels. At least one reason why squirrels are rare in woods with dense, tall herbaceous vegetation is that acorns cached in these locations are more likely to be eaten by mice. We then conducted two experiments to investigate the effect of manipulating surface vegetation on the acorn-caching behavior of squirrels and blue jays. In both we found that squirrels and jays cached acorns in bare, open areas in preference to areas of tall vegetation. Land managers can encourage the establishment of oak seedlings by providing bare ground or short-statured vegetation at the time of acorn dispersal.

Index Terms: oak reproduction, acorn dispersal, acorn predation, white-footed mouse, meadow vole, squirrel, blue jay, caching
Introduction

This research began in the spring of 2009 at the conclusion of a prescribed burn. I was walking the edge of the burned area past a familiar stand of bur oaks, located in a familiar prairie restoration, when I turned to look and, for the first time, asked myself why there were no young oaks along the boundary between oak grove and prairie. The boundary had remained stable for over 20 years since the restoration of the prairie. The ground was bare and charred by fire, but close examination revealed not a single oak seedling of any size. Twenty years of abundant acorns, plenty of sunlight, and seemingly adequate soil, and not a single seedling to be seen. In the next few days, I walked along the perimeter of the burned area and found that oaks had failed to invade the prairie (about 24 hectares, 60 acres in size) anywhere along its boundary with oak woods. (I use the term woods as a general term to refer to groves of mature oaks, regardless of their stocking density.)

It is not difficult to find small clusters of oak seedlings in restored oak savanna landscapes of Glacial Park, but it is remarkable how rare these seedlings and young trees are in situations where they would appear to have more than sufficient light, water, and nutrients. This realization was quite disturbing to a teacher of natural history who had been assuring students for 25 years that oaks will reproduce freely if given a sunny place to grow free from invasive brush.

A growing number of ecological restoration managers in the Midwest are asking the same questions today concerning the lack of oak reproduction. The management solutions are straightforward in concept: either plant young oak trees or foster natural reproduction. The first is the more costly but also the more controllable. In addition, it can be organized, systematized, and replicated in much the same manner as modern agriculture and is subject to the same laws of scale and production efficiency. Modern forestry has utilized tree planting for the regeneration of economically valuable species for many decades, precisely because the timing and target species can be tightly controlled.

Natural reproduction methods will be the least costly but are also the least controllable. Years will pass between heavy acorn crops, and the actions of acorn-dispersing and caching animals are predictable only in a general way. We may be able to create the setting in which various ecosystem factors interact to produce young oak trees, but we cannot determine the outcome. If we are successful, the production of oak seedlings over the years will be high, but the result many years later may look quite different from our initial conception, with clumps and gaps in the spatial arrangement and a species composition that reflects innumerable and unplannable contingencies. However, if our goal is to create functioning oak woods that are as similar as possible to their historical counterparts, then fostering natural reproduction should be the first choice.
Alternatively, if our goal is to create an oak woodland with ten mature oaks per hectare, we could plant ten three-inch caliper balled-and-burlaped oak trees, deciding not only how many trees but where precisely to put them. We would need to protect each tree throughout its early life and replace individuals if they die. The two models for restoring oaks may look much the same to an untrained eye 75 years later, but through careful observation, the oak woodland relying on natural reproduction will teach us a great deal about the functioning of historical oak ecosystems—the second option, less so.

The paradox of ecological restoration is that we are trying to create an uncontrolled system, that is, one that generates endless novel arrangements but does so within the same boundaries that constrained the historical system. The principal difference is that, in the case of the restored system, we impose the boundaries intentionally. Natural reproduction methods fit this constrained but uncontrolled model best and planting three-inch caliper trees least.

Planting oak seedlings and saplings is a quick and direct way to return oaks to areas where they may have been absent for a century or more. Planting trees can be a positive communal activity that engenders support for the larger restoration cause. We have planted thousands of oaks in Glacial Park over the last 10 years for these and other reasons. Nevertheless, if we claim to be restoring oak savannas and woodlands, we must address the process that maintained oaks in the landscape for thousands of years. We will never know what a functioning oak woodland is like until we get this right.

This booklet presents a series of research projects and observations that, in total, produce a working model of oak reproduction in oak savannas and woodlands under ecological restoration. I then suggest strategies to foster the natural reproduction of oaks.

My colleagues and I conducted the research for this booklet on lands belonging to McHenry County Conservation District. We did much of the research in Glacial Park, a 3,500 acre natural area located in the northeastern corner of McHenry County.
Whenever I present this research, I have at least a few people tell me that there is no problem with oak reproduction in restored oak woods. Their objections fall into three categories.

First, many people contend that the small number of seedlings present in modern oak savannas and woodlands represents an adequate level of reproduction, or that the factors that facilitate oak reproduction occur uncommonly, hence we simply need to wait. Because oaks are long-lived, even very low rates of reproduction or reproduction at very long intervals, they argue, will prove enough to replace the adult oaks of today. Indeed, we have only been doing oak savanna and woodland restoration for 25 years, so we have not waited very long.

My response is that, if we must wait for the rare but inevitable episode of oak reproduction, then we should be able to determine why so few seedlings are establishing in the interim. If oak reproduction today is inadequate, then we need to understand why and how to ameliorate the situation. If one reads the public land surveys written by land surveyors of the Chicago Region in the early 19th century, one is struck by the frequency of their mention of oaks growing in shrub-like form. Oak shrubs were in fact one of the most common shrubs of our region. This is clearly not the case today. If the rate of reproduction today is in some sense adequate, it is certainly quite different from the rate of reproduction in the pre-European settlement landscape.

Second, it is often the case in Northeastern Illinois that oak woods will have a cohort of young oaks that date from the end of livestock grazing. In McHenry County these cohorts are often 25-40 years old, and any one stand of these young oaks is even-aged, that is, all of the individual trees started growth at approximately the same time. The claim is that this post-grazing cohort represents adequate reproduction.

I will talk more about the age-structure of oaks later, but these cohorts represent only a brief pulse of reproduction, after which oak regeneration stopped. In addition, these stands of young oaks in McHenry County are often composed almost entirely of Hill’s oak (Quercus ellipsoidales E.J. Hill) or occasionally red oak (Quercus rubra L.), even when the surrounding mature trees are predominantly bur oak (Quercus macrocarpa Michx.) and white oak (Quercus alba L.).

Third, oaks may not have reproduced naturally for many millennia. Native Americans utilized acorns for food and were dependent on the wildlife that ate acorns, and so it is entirely possible that they cultured the landscape in ways to benefit oak reproduction. If we accept that these societies actively managed landscapes for food and hunting, among many other uses, the conclusion may be at least partly true. They must have been aware of oak reproduction and appreciative of its importance. One might further speculate that they would have avoided activities detrimental to oak growth and reproduction. Beyond that, this would seem to be an undisprovable but also unprovable hypothesis.
Despite these objections, we should be able to find out what factor or factors are impeding oak reproduction in oak woods under restoration management. I began this research under the belief that:

1. The apparent lack of reproduction is an interesting phenomenon worthy of study.
2. We should be able to understand what factor or factors impede oak reproduction today.
3. If we are able to replace the missing part in our protocol for oak woodland restoration, we might discover other novel aspects of the ecology and management of oak woods previously unknown.

Black oak seedling at Illinois Beach State Park.

New growth on young bur oak.

Dr. Tom Simpson counting rings of ancient oak in Glacial Park.
THE AGE-STRUCTURE OF OAKS

My treatment of the age structure and diameter distribution of modern stands of oak deals only with Chicago Region landscapes. Our field work comes from DuPage County and McHenry County, but the timing and character of events over the last 200 years is broadly similar across the region. I introduce these data only to make two important points about historical oak reproduction. The first is that a stand of large oaks is usually even-aged. For instance, most older oak trees in the Chicago Area started growth in the early to mid 19th century. Upon close examination, one may find a second cohort of younger trees, which started growth in the years immediately following the end of livestock grazing. If most stands of oak are composed of only one or two even-aged cohorts, then there have been only one or two relatively brief periods of oak reproduction since the early 19th century.

The second point about age structure I would like to make is that there is little correlation between the age and diameter of oaks within a cohort, for instance the post-grazing cohort (Figure 1a and 1b). There is a three to seven-fold range of diameters within each of these sets of trees. Likewise, there is little relationship between age and diameter within the 19th-century cohort (Figure 1c). Therefore, the existence of a more or less continuous distribution of tree diameters in a stand of oaks does not imply a continuous distribution of ages, hence continuous reproduction over long periods of time. Rather the opposite is the case. In the history of most oak woodlands in the Chicago Region there have been only one or two major periods of reproduction separated by long periods when no reproduction took place. This seemingly minor point concerning the relationship of age and diameter is in fact very important. If you don’t see the problem (that oaks only rarely reproduce), you are unlikely to look for a solution.
Figure 1.
Age-diameter relationship among:

a. (top) a typical post-grazing cohort of Hills oak in McHenry County, IL;

b. (middle) a mid-20th century, post-grazing cohort of red oak at the Morton Arboretum, DuPage County, IL;

c. (bottom) a mixed stand of early to mid-19th century oaks, also at the Morton Arboretum, composed of white oak, red oak, and bur oak.

Tree ages were determined with an increment-coring tool. Note that diameter and age are not closely correlated in a, b, or c. The modest size-age correlation in 4b ($r = 0.4$) is due almost entirely to the two largest and two smallest observations.
The population of oak at the Morton Arboretum is clearly divided into two cohorts, and these two cohorts are strikingly different in species composition (Figure 2). Red oak dominates the younger cohort, whereas white oak dominates the older, settlement-age cohort.

The older cohort started growth in response to the disruption of Native American culture and resulting lack of periodic burning, which released oak seedlings and shrubs to grow. The cutting of older oaks by European-American settlers also contributed by increasing sunlight availability to the small oaks. The burst of reproduction ended when cattle and other livestock became so numerous in the woods that they ate all of the acorns and germinant seedlings. The younger cohort is a result of the abrupt end of grazing at the close of the agricultural period, which in the case of The Morton Arboretum began in the 1920s.

In McHenry County, Hill’s oak is much more common as a large tree than red oak and commonly takes the place of red oak in the post-grazing cohort. To demonstrate the spatial relationship of trees of these two cohorts, we GPS located all older trees in a 16-hectare (40-acre) oak woodland in northwest McHenry County. We then established a grid of sample points and at each point identified the nearest oak of the post-grazing cohort in each quarter (northeast, southeast, etc.). Older oaks are denoted by circles and younger oaks by grid squares. If we could not find an oak tree in the post-grazing cohort, the grid square is left blank.
In this McHenry County woodland, red oak dominates the post-grazing cohort only where it dominates the overstory (Figure 3). Hill’s oak or red oak dominate the younger cohort in much of the area where white oak is the most common overstory tree. Bur oak is common in the post-grazing cohort only where it dominates the overstory to the exclusion of other species and has lost out to Hill’s oak in some of those areas. White oak is extremely rare in the post-grazing cohort.

This woodland will change in the species composition of its oaks over the next century. White oak populations will decrease greatly. Bur oak will decrease in the number of trees and the area covered. Red oak will hold its own and Hill’s oak populations will expand a great deal. This is a typical species/age relationship for a McHenry County oak woodland, with the exception that red oak is more common in the steeply rolling topography here than is usual in the rest of the county. The sharp increase in Hill’s oak and decrease in white oak are common to almost universal in the county.

Whether this constitutes a problem is a matter of opinion, but it does represent a change in reproductive output from that time when the older trees were starting growth to the present. It provides yet another perspective on the phenomena of oak reproduction in modern woodlands.

Figure 3.
The spatial distribution of three species of oaks of the post-grazing cohort relative to the distribution of older oaks in a McHenry County woodland near Harvard, IL. (See text for an explanation of the methods used to construct the map.)
Common Answers to the Problem of Oak Reproduction

I present here seven commonly mentioned solutions to the problem of the lack of oak reproduction in modern oak woodlands.

**The Gap Hypothesis:** Oaks need abundant sunlight to grow and will reproduce when canopy gaps of the appropriate size appear. Prior to restoration activities, almost all modern-day oak woodlands have closed canopies and shady understories, and when gaps occur they are quickly filled by other tree species. Therefore, the way to stimulate oak reproduction is to create gaps and control the invasion and growth of other tree and shrub species.

This idea has been particularly common in forestry related research (Crow 1988, Lorimer 1984, Lorimer 1983, Larsen and Johnson 1998, Loftis 2004). Note that this is a two-part hypothesis:

1. Oaks require abundant sunlight to grow.
2. If you introduce sunlight into oak woods, oaks will reproduce.

The first part of the hypothesis is true according to all experiment and observation. The second part may need qualification: sunlight is necessary, but it may be insufficient on its own to stimulate oak reproduction.

After 25 years of restoration management, there are numerous gaps and edges in and around oak woods where oaks should be reproducing commonly and abundantly. In most cases this has not happened. Where oaks have reproduced, the pulse of reproduction was short, followed by years or decades with no seedling recruitment. Gaps are necessary for oak reproduction but are not sufficient to recruit oak seedlings in or adjacent to restored oak savannas and woodlands in the Chicago Region. The common exception to this are oak woods located on very sandy soils, such as the dunes along Lake Michigan. Here oak reproduction is often abundant when large canopy gaps are present (Figure 4). Later in this booklet I suggest a reason why oak reproduction is often abundant in sand soil and not in loam and clay loam soil inland of the lakeshore dunes.

*Figure 4.*
Black oak seedlings growing in a savanna with sand soil at Illinois Beach State Park.
Prescribed Fire: Frequent prescribed fires could eliminate oak seedlings and may be a principal cause for the lack of oak reproduction in oak woods under restoration management.

Fire certainly injures young oaks, but there is abundant historical evidence that frequent fires were a common part of the ecology of oak savannas and woodlands in pre-European settlement time. The abundance of black oak (*Quercus velutina* Lam.) reproduction at Illinois Beach State Park (Figure 5), a site regularly burned for the last 20 years, also would indicate that regular prescribed burning and oak reproduction are compatible.

In May of 2010, we planted 27 first-year oak seedlings in a tallgrass prairie next to the Research Field Station in Glacial Park. We then burned the area in May of the following year. The seedlings had broken dormancy and begun growth at the time of the fire. By the early spring, rodents had killed fifteen of the seedling. Of those seedlings alive before the fire (12), 75% (9) survived a late spring fire at one year of age.

In the early summer of 2015, we surveyed 170 oak seedlings after a prescribed fire the previous fall. The oaks were planted two to three years earlier as 5-gallon container seedlings. The area was seeded with native grasses and forbs at the time of the planting. The mortality rate for bur oak was 9% and for Hill’s oak 3%. Peterson and Reich (2001) reported that increasing fire frequen-
cies led to decreasing numbers of Hills oak seedlings yet fire had no effect of the numbers of bur oak seedlings. Hutchinson and Sutherland (2005) found that 2-4 prescribed fires did not significantly affect the density of hickory and oak seedlings.

Clearly, fires kill some oak seedlings. Smaller seedlings with lower food reserves may be more vulnerable and burning when seedlings are actively growing will result in higher mortality rates than burning in the dormant season. Even so, periodic prescribed fires may limit the height growth of seedlings and young trees but should not preclude the recruitment of oak seedlings. Recruitment of oak seedlings in a fire landscape should result in an abundance of oak seedlings, resprouts, and shrubs, yet these are clearly absent from most oak savannas and woodlands under restoration management today.

**The Fire-Nitrogen Hypothesis:** Frequent prescribed burning may increase levels of available nitrogen in the soil, restricting the growth of oak seedlings.

Taylor and Midgley (2018) compared the soil of an oak savanna in the Morton Arboretum in Lisle, IL, which had been annually burned for 30 years, to a nearby unburned woodland, and found that repeated low-intensity fires increased available nitrogen in the soil. They further speculated that this increase in nitrogen may limit oak reproduction in frequently burned oak savannas. Together with many if not most native herbaceous species, oaks are not nutrient demanding species, and it may be that slight increases in available nitrogen are detrimental to the growth of oak seedlings in competition with more nutrient demanding species. At the present time, however, it seems an unlikely explanation for such a pervasive phenomenon. Most oak savannas under restoration management are burned on intervals of three to five years or longer, hence any deleterious effect on oak seedling growth would be correspondingly less. Further, the hypothesis ignores the fact that oaks commonly fail to reproduce in unburned or rarely burned grasslands adjacent to established oaks. Lastly, it ignores the prevalence of fire in the Midwestern landscape over the last 10,000 years, a time in which oaks were the dominant tree species.

**Deer Browse:** Browse by large populations of white-tailed deer (*Odocoileus virginianus*) may eliminate oak reproduction in the modern landscape.

This may be true in areas where deer populations are very high. In our experience in McHenry County, however, while signs of deer browse over winter are common, young oaks typically sprout back the following growing season. Like fire, deer browse will deter height growth of small oaks but should not preclude the establishment of seedlings. Thus, fire and deer browse are important factors that need to be managed if oaks are to grow into the larger size classes, but they are important limiting factors only when there is an abundant supply of seedlings.
Soil Incompatibility: Human activities have so greatly modified the soils of our area that these soils may no longer support the growth of oaks.

Oaks are not especially demanding of nutrients and water relative to other tree species, but they do have an obligate relationship with mycorrhizal fungi in the soil. Mycorrhizae are the close association of plant root and fungus, and this symbiosis assists the plant in absorbing water and nutrients beneficial to its growth (Daughtridge et al. 1986). The fungal partners of oak are different from those of most other tree species in our area and are called ectomycorrhizal fungi. Dickie and Reich (2005) found that mycorrhizae beneficial to the growth of oaks were common near established oaks but sparse or absent in ex-agricultural fields distant from established oak stands. This question concerning the presence and importance of ectomycorrhizal fungi was, in fact, the first we tried to answer in our oak reproduction research.

In the spring of 2010, we inoculated 16 bur oak seedlings with ectomycorrhizal fungi and compared their growth to 16 un-inoculated seedlings. (The seedlings had not been inoculated at the nursery.) We planted the seedlings about 15 m from the edge of a woodland that included established oaks. This area was covered in brome grass (*Bromus inermis* Leyss.). Other than occasional prescribed fire, it remained unmanaged for the last 20 years. There were no naturally occurring oak seedlings in the area. In order to assess the effect of grass competition on the growth of oak seedlings, we used glyphosate herbicide to eliminate grass competition within one meter of four inoculated and four un-inoculated seedlings. At the end of the first growing season, we assessed the health and measured the height of each seedling. Neither inoculation or elimination of grass competition had a significant effect on the height growth or survival of the oak seedlings after one growing season. All subsequent experience has shown that un-inoculated oak seedlings will grow in almost any soil of the right moisture conditions in McHenry County, even when planted in the middle of large ex-agricultural fields far from established oaks.

Acorn Weevils: Weevils of the genus *Curculio* consume a significant percentage of acorns every year and may interfere with oak reproduction.

In order to address this issue, for eight years we collected acorns in lots of 100 of whatever species we could find. We stored them in plastic containers and to monitor for weevil emergence. Several weeks after the last emergence, we crushed the acorns and looked for weevils that had not emerged. On average, weevils infested about 29% of acorns in a given year (red oak 30.6%, Hill’s oak 22.8%, white oak 29.3%, and bur oak 31.8%), leaving on average 70% of the crop free of weevils. The intensity of weevil infestation is highly localized, and in any one year, bur oak acorns in one location can have infestation rates ten times as high as acorns from another location.
These infestation rates are within the range reported by other authors. Leiva and Alés (2005) found a 16.6% average infestation rate for Cucilio and Cydia (moth) larvae in holm oak (Quercus ilex L.) acorns in Mediterranean woodlands. In West Virginia, Dorsey et al. 1962 found infestation rates in untreated (with pesticide) red oak and white oak averaged 58%. Lewis (1992) found an average of 38% of coastal live oak (Q. agrifolia Nee.) acorns infested by for Cucilio larvae. These results and the knowledge that weevils and oaks have been living together for many hundreds of thousands of years makes acorn weevils an unlikely explanation for the current lack of oak reproduction (Leiva and Alés 2005).

Johnson et al. (1993) found that blue jays (Cyanocitta cristata) lost weight when fed an acorn-only diet, but sustained their weight with an acorn diet supplemented by five grams of weevil larvae per day. They concluded that, far from being a detriment to oak reproduction, weevils may be part of a three-way relationship (oak trees-weevil-blue jay) that facilitates oak reproduction. Espelta et al. (2009), however, cautioned that differences in weevil infestation among oak species could account for differences in acorn abundance and the recruitment of seedlings.

**Passenger Pigeons:** Now extinct, the passenger pigeon once numbered in the billions as recently as the mid-19th century. Acorns were a principal food source and this close association may have fostered oak reproduction.

Webb (1986) has suggested that passenger pigeons (Ectopistes migratorius) played a role in long-range seed dispersal for oaks and other nut-bearing trees. Pigeons consumed acorns in large numbers, but unlike blue jays and squirrels, they did not cache acorns in the surface soil. If they dispersed acorns, it was the result of pigeons dying with acorns in their crop after flying some distance from the parent tree. This is possible, but we have no evidence by which to judge the effectiveness of this method of dispersal. Passenger pigeons may have played a role in acorn dispersal and oak reproduction, but squirrels and blue jays may have played a much more important role—we simply don’t know.

Pigeons often roosted in such large numbers that they broke tree branches, dramatically changing the canopy architecture of large areas of oak woods (Ellsworth and McComb 2003). This disturbance increased sunlight intensity for germinant oak seedlings. Thick guano deposits in these same woods, however, may have been toxic to seedlings and young trees, which would have had a negative effect on oak reproduction. It is impossible to sort through multiple influences, most of which vanished with the passenger pigeon a century ago, and arrive at a single model of the pigeon’s role in oak reproduction. We simply do not know whether pigeons played an important much less a necessary role in acorn dispersal or oak reproduction. My tendency is to put untestable hypotheses to the side and ask whether changes in modern landscapes can facilitate oak reproduction, and to progress from these more certain foundations.
The Oak Life Cycle

At the conclusion of the first year of work, in the winter or 2009-2010, we had sufficient evidence to set aside the gap hypothesis and the mycorrhizae hypothesis. My seasonal technician Kevin and I went over the life cycle of oaks (Figure 6a) and quickly eliminated growth, flowering, and acorn maturation as possible problems. By all accounts, these take place adequately in modern landscapes. Acorns will germinate and grow into trees if protected. Oak trees will grow in a wide variety of soils and landforms, including ex-agricultural soil, and they grow in competition with a wide variety of native and non-native herbaceous species. In restored oak savannas, woodlands, and prairie edges, they often have abundant available sunlight. Mature trees periodically produce acorns in great abundance.

It seemed clear to the two of us that a problem must be located in the life stages of acorn dispersal, caching, and survival through to germination and establishment (Figure 6b.) Even at this early stage of the work, fire and acorn weevils seemed highly unlikely explanations. This realization pointed us in the direction of the animals that eat acorns and the animals that gather, disperse, and store acorns in surface-soil caches. That critical moment of insight guided the next eight years of work.

Figure 6.
The life cycle of oaks.
"...a problem must be located in the life stages of acorn dispersal, caching, and survival through to germination and establishment... (which)...pointed us in the direction of the animals that eat acorns and the animals that gather, disperse, and store acorns in surface-soil caches."
The Role of Mice and Voles as Acorn Predators

Acorns are nutritious and seasonally abundant food source for many animals. Oaks typically produce abundant acorn crops only at intervals of several years, separated by years of very low nut production. Thus they present a moving target for predator populations, which crash in years of low acorn production and are then at a low ebb when trees mast heavily the following year. We focused our attention on white-footed mice (Peromyscus leucopus) and meadow voles (Microtus pennsylvanicus) in this research for several reasons.

1. They are the most abundant vertebrate species in wooded and grassland ecosystems in McHenry County respectively, and acorns are a preferred food source for both.
2. They are active all winter and thus compete with acorn caching animals like blue jays, gray squirrels (Sciurus carolinensis), fox squirrels (S. niger), and southern flying squirrels (Glaucomys volans) for fresh acorns in the fall and cached acorns for the remainder of the year.
3. Most importantly, they compete for acorns with squirrels and jays in late winter and very early spring, a time when the food reserves of squirrels and jays are lowest and they are most susceptible to starvation.

The eastern chipmunk (Tamias striatus), in contrast, is abundant in many oak woodlands and consumes large numbers of acorns, but is inactive over winter. Deer mice (Peromyscus maniculatus) are present in both woodlands and grasslands, but they are much less common than white-footed mice and meadow voles.

Spatial Distribution of Mice and Vole Populations Relative to Habitat Structure

In the fall of 2009, we ran a small experiment in which we planted white oak acorns at the edge of a tallgrass prairie in Glacial Park, with several sets exposed to rodent predation and several sets protected by ½-inch mesh hardware cloth. The unprotected acorns suffered almost complete loss to rodent predation (Figure 7). The size of the holes dug by the predators, much too small to be dug by chipmunks or squirrels, pointed to either white-footed mice or meadow voles. This was our first evidence that mice and/or voles might play an important role in oak reproduction.

In 2011, we compared the feeding intensity of mice and voles in open oak savanna, which featured a thick, tall herbaceous vegetation, with that in a matched oak woodland with the surface vegetation closely mowed. We used 10 plastic trays filled with sand and baited with 100 sunflower seeds each. We then covered each tray with chicken wire to prevent feeding by larger mammals. Greater persistence in feeding should result in few seeds remaining, and lesser feeding persistence should result in more seed remaining (Brown 1992). Across
four experimental sites and 12 total nights (average three nights per site) we found average seed predation of 36.3% in woodlands with tall grass and 2.5% in mowed woodlands. Fanson (2010) noted a similar trend, with white-footed mice preferring to feed in areas of dense cover and avoiding areas of sparse cover because of the perceived high risk of predation in open areas.

Next, we used live trapping to directly assess differences in white-footed mice populations in three restored oak woodlands with dense herbaceous vegetation with those in three un-restored brushy woods sites with sparse, short herbaceous vegetation. Using trap-frequency data, we calculated a minimum population size for each site. After a total of 450 trap-nights (30 traps x 5 days x 3 sites) in restored woodland and 450 trap nights in brushy woods, we found that the minimum population size of mice in restored woodlands was higher than that in brushy woods, though the difference was not statistically significant. Mice respond to vegetation structure at a small spatial scale (1-10 m²), and at this scale the shrub-layer vegetation of brushy woods is often quite heterogeneous. This habitat variation and corresponding variation in mice populations complicated the task of finding differences between restored woodlands and brushy woods.

We did find that in the restored woodland sites, the mice population estimates were closely and positively correlated (r=0.90) with the cover of herbaceous vegetation below one meter in height. We also found that, for brushy woods sites, mice population estimates were most closely and positively correlated (r = 0.63) with the cover of woody vegetation below one meter in height. In both cases, mice populations were higher in areas of dense surface vegetation than in areas of more sparse vegetation.

Meadow voles are voracious predators of acorns. There is very little in the literature concerning vole predation on acorns, perhaps because voles are primarily creatures of grassland and only rarely enter oak woods. Vole predation on acorns becomes critical, however, when one considers the ability of oaks to successfully colonize adjacent grassland.

In a 2012 study, quite similar to the 2011 study mentioned previously, we used acorns as the food item and compared mowed and unmowed grassland (Figure 8). For six nights, we baited each of 20 sand-filled trays with 20 acorns each and placed 10 trays in mowed areas and 10 trays in unmowed areas. Trays were covered in chicken wire screens to deter feeding by larger mammals. On average 14.7% of acorns were removed from the trays in unmowed grassland and 0.08% from trays in mowed grassland. In both studies, feeding intensity of these small mammals (meadow voles, white-footed mice, and deer mice) were closely related to vegetation structure. Bare areas and closely mowed vegetation deterred mice and vole feeding.

In October of 2011 we placed 252 bur oak acorns along transects divided among three restored oak woodlands in Glacial Park. We did this in order to...
directly estimate predation on acorns after dispersal. In previous decades, the exotic and invasive woody plants had been removed from each woodland and the sites burned on a three-year rotation. Herbaceous growth was abundant in each. Every five meters along each transect we placed a cache of four acorns in a square pattern with a small metal tag at the center. We used a metal detector to relocate the caches. There were 21 caches on each transect. We placed half of the acorns beneath tree leaves but on top of the mineral soil. The other half were buried about 1-2 cm below the mineral soil surface.

Three weeks later we checked all transects for predation of acorns. All 126 acorns left on the ground surface and below leaf litter were gone. Of the acorns buried, four (3.2%) survived. Overall the predation rate over the three-week period for buried and surface-cached acorns was 98.4%. Live trapping in succeeding years revealed that white-footed mice and eastern chipmunks were the most likely acorn predators. Gray and fox squirrels were relatively rare in these woodlands.

We followed this two years later with a similar study using acorns of four oak species (bur oak, white oak, Hill’s oak, and red oak), caching the acorns in mowed and unmowed grassland. We established four 65 m-long transects in mowed and four in unmowed grassland. We placed caches of four acorns at five-meter intervals along each transect (12 caches/transect). We buried acorns 1-2 cm deep in 15 cm square arrangement with a metal landscaping staple at the center. We alternated species of acorn along the transect line. There were 384 acorns total, 96 acorns of each species, and 48 of each species in each mowing treatment.

We returned to these transects the following June and checked for the survival of acorns. We defined survival as an intact acorn whether or not it had germinated. Overall, only 0.5% of the acorns cached in un-mowed, tall grass survived (bur oak 2.1%, all others zero). Of those cached in mowed grassland, 88.6% survived in June of the following year (red oak 86.5%, bur oak 80.8%, Hill’s oak 91.7%, and white oak 95.5%). Of the four acorns originally placed at each cache in the mowed area, an average of 3.54 survived predation and 1.67 germinated as of June 2014. Only 0.46 were alive in September of 2014. The sharp decline between June and September of 2014 was coincident with the regrowth of grass and, presumably, reinvasion of the area by meadow voles.

For both acorn caching experiments, survival of buried and surface-cached acorns in tall herbaceous vegetation was less than 2%. Mowing the grass prior to acorn burial in the second experiment increased acorn survival to 89%. Regrowth of grass in the second experiment during the summer of 2014 produced a loss of nearly 75% of the germinant seedlings. Clearly, mice and vole predation on acorns and recently germinated seedlings was very high.
Acorn Dispersers: Squirrels and Blue Jays

The paradox of oak reproduction is that it is actually common, it is simply uncommon in the oak savannas and woodlands where we expect to see it. At the time when most of this research was underway, I lived in the town of Libertyville among a scattering of old bur oak trees. Oak seedlings appeared each spring in my lawn, and I commonly saw young oaks growing from people’s border plantings and garden beds. Each fall I watched gray squirrels gathering and caching acorns in the lawns and then moving the nuts from one place to another. Squirrels are paranoid about the security of their food supplies, so they commonly re-cache nuts several times through the late fall and early winter, until the ground freezes or is snow covered. There is little sign of squirrels digging for buried nuts when the ground is frozen or snow-covered, but squirrel holes reappear with the spring thaw.

After closely watching squirrels for years, I have never yet been able to find where they stored a nut. They are masters at camouflaging the site of burial. On the other hand, it is easy see where they remove an acorn, because they make no effort at hiding an empty hole. The abundance of these squirrel holes indicates where squirrels are actively caching and re-caching nuts. What is particularly interesting about this story is that squirrels are abundant in suburban landscapes, and they routinely choose mowed turf-grass areas for caching nuts.

In 2009 we decided to look for squirrels in both restored oak savannas and woodlands and in brushy, degraded oak woodlands throughout McHenry County. We used the density of leaf nests as an index of squirrel abundance. We walked trails through these areas and recorded all nests within a specified distance from the trail. We calculated the sample area from the length of the trail and the width of the sample area. We found that squirrel nest densities are much higher, by a factor of 5-8, in brushy degraded woods than they are in restored oak savannas and woodland (Table 1). At two locations (Nippersink C.B. and Harrison Benwell), we measured leaf-nest densities before and after brush removal, and in both cases the number of nests plummet after the removal of the brushy understory of shrubs and small trees. Clearly, gray squirrels and fox squirrels were disappearing

<table>
<thead>
<tr>
<th>Brushy Oak Woods</th>
<th>Sample Area (ha)</th>
<th>Nest Number</th>
<th>Nests/ha</th>
<th>Cleared Savanna</th>
<th>Sample Area (ha)</th>
<th>Nest Number</th>
<th>Nests/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harrison Benwell</td>
<td>19.5</td>
<td>63</td>
<td>3.2</td>
<td>Harrison Benwell</td>
<td>22.0</td>
<td>9</td>
<td>0.4</td>
</tr>
<tr>
<td>Nippersink C.B.</td>
<td>10.1</td>
<td>29</td>
<td>2.9</td>
<td>Nippersink C.B.</td>
<td>10.1</td>
<td>6</td>
<td>0.6</td>
</tr>
<tr>
<td>DeCarlo-Olson</td>
<td>10.8</td>
<td>31</td>
<td>2.9</td>
<td>Glacial Park</td>
<td>18.5</td>
<td>5</td>
<td>0.3</td>
</tr>
<tr>
<td>Rush Creek</td>
<td>31.5</td>
<td>54</td>
<td>1.7</td>
<td>Prairieview</td>
<td>3.9</td>
<td>3</td>
<td>0.8</td>
</tr>
<tr>
<td>Marengo Ridge</td>
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<td>39</td>
<td>2.5</td>
<td>Silver Creek</td>
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<td>6</td>
<td>0.7</td>
</tr>
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<td>Coral Woods</td>
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<td>1.8</td>
<td>Average</td>
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<td></td>
<td></td>
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<td>2.5</td>
<td>Average</td>
<td></td>
<td></td>
<td>0.5</td>
</tr>
</tbody>
</table>

Table 1. A comparison of the densities of squirrel leaf nests between oak woodlands in McHenry County with a dense understory of invasive small trees and shrubs (brushy woods) and those cleared of invasives (savanna).
from our oak woods after clearing the exotic and invasive understory. If we were restoring the structure and composition of the oak woods, why were these native animals disappearing?

To better understand the habitat preferences of gray squirrels, we radio collared 12 gray squirrels and followed their movements, recording locations every week throughout the year. We captured and released the squirrels in an area where they had access to both brushy woods and restored woodland from which the understory of invasive brush had been removed. Our goal was to determine if the squirrels preferred one structure of vegetation or the other. We collected 233 squirrel locations over a two-year sample period between 2013 and 2014. After adjusting for the sizes of brushy and restored woodland habitats and their distance from the trap and release site, we found that squirrels showed a statistically significant preference for the brushy woods habitat (chi square test, p<.05). This confirmed the results from the nest density study done earlier.

One reason why squirrels are so abundant in suburban landscapes is the abundance of ideal acorn-caching habitat—mowed turf grass. As we said in the discussion of white-footed mice populations, brushy woods are structurally quite variable, but most feature areas within them that are sparse or absent vegetation in less than one-meter height class, hence should offer opportunities for caching acorns.

At least two other factors may contribute to this bias in the distribution of gray squirrels and fox squirrels. Squirrels are known to eat soft fruits in summer, and brush-filled woods may offer additional food sources, such as the fruits of honeysuckle (*Lonicera* sp.), mulberry (*Morus* sp.), cherry (*Prunus* sp.), autumn olive (*Eleagnus umbellata* Thunb.), hawthorn (*Crataegus* sp.), crabapple (*Malus* sp.), and others. Brushy woods may also offer greater protection from predators, especially hawks and owls. And it must be pointed out that our restored oak savannas are usually lacking native shrubs, hence the food and cover provided by these. It is entirely possible that all of these factors play a role in the present distribution of squirrels. Results of the squirrel nest-density study and the radio-collar experiment are consistent with the hypotheses that squirrels seek out areas with bare ground or short stature vegetation for acorns caching, but we cannot rule out other causes.

*Right: Attaching a radio collar to a gray squirrel. Held firmly in the dark of the canvas handling cone, the squirrel does not struggle. The procedure takes under two minutes.*
A Working Hypothesis Concerning Oak Reproduction

As early as 2011, we formed a preliminary hypothesis concerning oak reproduction:

Hypothesis:
1. Caching of acorns by squirrels and blue jays is essential to oak reproduction.
2. Squirrels and jays preferentially cache acorns in areas of bare ground or short herbaceous vegetation to avoid the risk of mice and vole predation on their food supply. They avoid caching acorns in areas of tall herbaceous vegetation in order to avoid predation of those acorns by mice and voles.
3. In order to encourage acorn caching in and adjacent to restored oak savannas and woodlands, we need to create bare ground or short vegetation around the time of acorn dispersal and caching.

Our work on the feeding behavior and habitat preferences for mice, voles, and squirrels provided some support for the first two parts of the hypothesis. What remained was to show that creating short-structured vegetation or bare ground would indeed cause squirrels and jays to cache acorns in those places.
OBSERVATIONS AND EXPERIMENTS IN OAK REPRODUCTION

In the fall of 2014, we plowed and tilled with a tractor-mounted agricultural disc a one-acre site in preparation for an oak barrens restoration. Our plan was to seed prairie and plant 5-gallon container oaks and hazel. The area was located adjacent to a stand of bur oak and the soil was bare at the time of acorn dispersal. On several occasions that fall, we inadvertently chased fox squirrels out of the area, and we made a mental note to watch for volunteer oak seedlings the next spring. In May of 2015, we found more than 300 recently germinated bur oak seedlings in the project area. None of these seedlings occurred beneath the crown of seed-bearing oaks, so seed-caching animals—presumably the fox squirrels we had seen the previous fall—must have put them there. We searched the surrounding brome grass and found no seedlings.

Clearly the squirrels were attracted to the bare, open site for acorn caching—this despite the added risk of predation by raptors upon entering these areas. We were unable to find any direct reference to this squirrel behavior in the literature, but several researchers have noted that blue jays prefer to cache acorns in bare open microhabitats (Darley-Hill and Johnson 1981, Pons and Pausas 2007, Johnson et al. 1997, Bossema 1979). This incident seemed to confirm our hypotheses concerning squirrel behavior, but we had yet to show that we could actually produce the same phenomenon by intentional management.

In the fall of 2014, we established twelve 10 x 10 m plots in white oak woodlands in Glacial Park. Six plots were located in a 0.4 ha section of oak woodland cleared of all woody undergrowth (savanna), and six were located in adjacent woods with the brushy undergrowth in place (brushy woods). We then completely removed the herbaceous ground vegetation from three plots in savanna and three in brushy woods (Figure 9). We did not remove herbaceous vegetation from three savanna and three brushy woods plots for use as controls. The result was bare ground exposed in all six denuded plots, 80-100% herbaceous cover less than 1 m tall in three control savanna plots, and 15-40% herbaceous cover in three control brushy woods plots. All plots were under the crowns of mature white oak trees. The acorn crop in 2014 was moderate to heavy.

We returned to these sites in the summer of 2015 to determine the density of oak seedlings in control and treatment plots. Across both savanna and brushy woods, seedling numbers in the denuded plots were significantly higher (ANOVA, p < .05) than the control plots (Table 2). There was no significant difference between savanna and brushy woods plots. None of the oak seedlings originated from acorns that germinated on the surface of the soil, meaning that nut-caching animals had dispersed and buried the acorns in these locations.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seedlings/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Savanna</td>
<td>367</td>
</tr>
<tr>
<td>Brushy Woods</td>
<td>283</td>
</tr>
<tr>
<td>Denuded Plots</td>
<td>567</td>
</tr>
<tr>
<td>Non-Denuded Plots</td>
<td>83</td>
</tr>
</tbody>
</table>

Table 2: Estimates of seedling densities per hectare in the Denuded Plot experiment. The difference between savanna and brushy woods plots in not statistically significant, whereas that between the denuded and non-denuded plots is significant (p<.05)
This last point concerning the active dispersal of white oak acorns by animals is important for understanding white oak reproduction. White oak seedlings may grow from acorns passively dispersed and subsequently buried by leaf fall. Several authors have noted that squirrels prefer to cache acorns of the red oak group to those of the white oak group, because the acorns of the red oak group remain dormant over winter whereas those of the white oak group germinate in the fall (Smallwood et al. 2001, Fox 1982). The cotyledons of actively growing seedlings rapidly lose their nutritive value to the squirrel. This last statement concerning the timing of germination is not true of all oaks of the white oak group in our area, as bur oak (Q. macrocarpa Michx.) in the Chicago Region exhibits winter dormancy for most of its acorns (Burns and Honkala 2002).

Both authors note that squirrels will bite the embryo end of the white oak acorns to kill the embryo before caching, in order to prevent germination before they retrieve the acorn. Fox (1982) does note that this notching behavior is not universal and that juvenile squirrels in particular often do not notch the acorn before caching. The denuded-plot experiment confirms that:

1. Squirrels (either gray squirrel or fox squirrel) and/or blue jays actively disperse white oak acorns.
2. Either jays are the effective dispersal agent of white oak acorns or squirrels do not notch all of the acorns they cache.
3. Bare-soil areas are preferred to tall herbaceous vegetation for caching.
We then tested the usefulness of late-summer burning in creating bare-ground habitat for acorn caching animals. In the summer of 2015, we established four 12.5 x 32 m research plots (400 m²) in cool-season grass vegetation within 50 m of established (>100 year old) oak woodland in Glacial Park. All plots were on former pasture/hayfield sites, whose vegetation at the time of plot establishment was primarily smooth brome (Bromus inermis Leyss.), a common cool-season grass introduced during the farming era.

We divided each plot into two 6.25 x 32 m treatment areas (200 m²). We mowed a four-meter wide band around each plot to serve as a firebreak when burning and afterward to provide a mow-only treatment comparison (400 m²). Around the periphery of the mowed area the grass was left uncut to serve as a control (400 m²) (Figure 10). On August 19th the interior 12.5 x 32 m plots were mowed and then burned on September 2nd (mow-only and control areas were not burned). Grass quickly resprouted in the burned area. In order to maintain a bare-ground condition, on September 17th we ran an agricultural disc though one of the two 6.25 x 32 m burn treatment areas for each plot and then sprayed the same areas with a 1% glyphosate solution one week later. The result was a four-way vegetation contrast:

1. Untreated brome grass (control).
2. Mowed but not burned or disced (mowed on 8-19 and 9-11).
3. Summer-burned brome grass with short grass regrowth but absent any thatch
4. Burned, disced, and herbicided ground, which was nearly bare of vegetation.

The initial plan was to rely on adjacent oak stands for a supply of acorns. The oak woodland adjacent to the experimental area is predominantly bur oak and shagbark hickory (Carya ovata Mill.) with a minor component of Hill’s oak. Bur oaks produced very few acorns that year. In particular, the bur oaks adjacent to the experimental area produced few if any acorns. We gathered acorns from bur oak trees in other areas of the park in order to supplement the acorn supply. To reduce loss to small rodents, we put the acorns in 30 x 40 cm wire trays standing 40 cm above the ground on metal conduit posts (Figure 10). The trays were located at one corner of the mowed perimeter on the side nearest the established oak woodland. We added acorns to the trays every few days until October 5th, when our acorn supply was exhausted.

Due to the small supply of acorns and that our primary interest was in the response of nut-caching animals to changes in vegetation, we decided to expand the boundaries of the study and include nuts from shagbark hickory and black walnut (Juglans nigra L.). Both species produced abundant nuts in 2015. We placed the hickory nuts and walnuts in the same wire trays for two weeks in late October.
On May 31, 2016, we surveyed for oak, hickory, and black walnut seedlings. Oak seedling densities were significantly higher (ANOVA, p < 0.05) in the disced areas than in burn-only, mow-only, and tall-grass treatments (Table 3a). Shagbark hickory seedlings were more common than oaks in the disced treatment, due entirely to their abundance in plot 1, next to which a mature hickory produced a heavy nut crop (Table 3b). All hickory seedlings in plot 1 were located outside of the drip line of the crown of the nut-producing tree, hence the nuts were transported and cached by animals. We found only three black walnut seedlings, and that was in the burn and disc area of plots 1 and 2 (Table 3c). All of the oak seedlings were Hill’s oak, even though we had supplied only bur oak acorns in the supplemental feeding trays. Evidently, the Hill’s oaks growing in the nearby woods produced a sufficient supply of acorns, even though we were unable to find any the previous fall.

We could not determine what animal species cached the Hill’s oak acorns, but on two occasions in the fall of 2015, we found a blue jay feather in the disced and herbicided treatment areas. Several of the Hill’s oak seedlings were more than 60 m from the nearest Hill’s oak seed-producing tree. Due to the nuts large size, squirrels probably cached the walnuts and hickory nuts.

These two experiments indicate that nut-caching animals have a strong preference for caching nuts in areas of bare ground. This concurs with Johnson et al.
(1997) and Harrison and Werner (1984), both of who found that blue jays avoided caching nuts in tall grass. Both authors theorized that blue jays avoid caching nuts in sites where other nut predators would likely rob their cache. It seems reasonable to speculate that an animal dependent on cached food supplies would avoid caching acorns in areas of tall herbaceous vegetation where mice and vole predation on buried acorns is very high.

Based on these experiments, the failure of oak reproduction in restored oak woodlands and adjacent grasslands would seem to be due, at least in part, to the manner in which the structure of herbaceous vegetation mediates the competition between acorn-caching animals and acorn predators. Clearing invasive brush as a part of oak woodland restoration increases light availability, which stimulates rapid growth of the herbaceous vegetation. The increased height and density of this layer leads to higher populations of white-footed mice (Larsen 2012). Squirrels and jays then avoid the area as a site for caching acorns. The story is much the same in adjacent grassland, where thick herbaceous vegetation supports a large meadow vole population, which in turn discourages acorn caching by squirrels and jays. Whether squirrels and jays respond directly to vegetation structure or to the presence and abundance of mice and voles, we do not know. Nevertheless, when we experimentally produced bare ground patches, squirrels and/or jays responded by caching acorns and other nuts.

<table>
<thead>
<tr>
<th>Hill's Oak</th>
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<th>Mow</th>
<th>Tall Grass</th>
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</tr>
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<td>Average</td>
<td>37.5</td>
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</tbody>
</table>

Table 3.

a. (top) Hill's Oak; b. (middle) Shagbark Hickory; c. (bottom) Black Walnut
Estimates of seedling densities per hectare by species, plot, and treatment for the Summer Burn Experiment. The burn-disc treatment has significantly more seedlings (p<.05) than burn only, mow, or tall grass.
This avoidance of tall grass for nut caching by both squirrels and jays is peculiar because it subjects the animals to an increased risk of predation while they are in these bare, open areas. For evolution by natural selection to produce such a risk-taking behavior, mice and voles must have presented an important threat to jay and squirrel survival over very long periods of time. Further, it implies that both bare-short herbaceous vegetation and dense-tall vegetation and corresponding low and high mice populations were a part of the world in which these behaviors evolved.

Early in this research project, we entertained the idea that mice and vole populations in modern times are simply much larger overall than those of the pre-European settlement past, perhaps because of disruptions to predator populations, and that the large mice populations simply overwhelm and outcompete squirrels and jays for acorns. Oaks thus lose their seed dispersal agents.

We have no way of knowing whether populations of mice and voles are higher or lower today than in the distant past, but there is no evidence that that difference, if it exists, is decisive in the reproduction of oaks. Given the rodent population numbers of today, bare ground or short-grass vegetation causes vole and mice feeding to drop to negligible levels. Squirrels and jays respond to the same situation by caching acorns.

Short-term fluctuations in mice and vole populations, however, may lessen or increase the effects of spatial variation in acorn-caching opportunities. For instance, white-footed mice populations drop sharply following years of poor acorn crops (Elkinton et al. 1996 and Jones et al. 1996). We can imagine a model in which mice populations rise in the months following a large acorn crop and fall after poor crops. If a small acorn crop precedes a large crop, then the mouse population will be low (in response to the poor crop) at the time of the large crop. If we introduce into this model a mechanism to create patches of bare ground and short-grass vegetation, the result will be a prime opportunity for oak seedling establishment. Whether meadow vole populations respond similarly to fluctuations in acorn abundance is unknown.
EXPLAINING HISTORICAL OAK REPRODUCTION

These results raise a fascinating set of questions concerning how acorn dispersal and caching occurred during the roughly 11,000 years in which oak species dominated the arboreal flora of the Chicago Region, but prior to the plow, agricultural disc, and mower. We speculate that late summer or early fall fire and/or large-herbivore grazing may have created bare-ground at the time of acorn dispersal and, thus, an opportunity for acorn caching by squirrels and jays. Our experimental use of late-summer fire may have been sufficient without disc tillage and herbicide application if we had burned two or three weeks later.

It is commonplace for most prescribed burning to occur in the spring during March and April and again in fall in late October and early November. This is partly due to the availability of prime fuel conditions and suitable weather and partly due to the management demands of the summer season. There is considerable historical evidence that Native Americans burned the landscape throughout the late summer and fall seasons.

We have already mentioned that one commonly finds a post-grazing cohort of young oaks in McHenry County oak woodlands. Intense grazing typically creates woodlands with an open savanna structure but with very closely cropped surface vegetation. The subsequent removal of grazing animals would seem to produce an ideal opportunity for acorn caching by squirrels and jays, if only briefly before the regrowth of a dense herbaceous layer. One might envision an oak woodland landscape in which short intense periods of localized grazing created a patchwork of opportunities for acorn-caching animals. Subsequent grazing or landscape fires might then stop the growth of most but not all of these seedlings.

The abundant oak reproduction in very sandy soils (mentioned earlier), may be due to the lack of available of water for plant growth. This often produces patches of exposed sand with no vegetative cover, hence favorable habitat for acorn caching. In loam and clay loam soil, bare areas are rapidly colonized by tall herbaceous plants.

In the discussion of the age structure of oak stands, we mentioned that Hill’s oak and red oak dominate the post-grazing cohort in McHenry County and that white oak and bur oak are underrepresented, even in situations in which white oak and bur oak compose the majority of seed producing trees nearby. As mentioned previously, both Hill’s oak and red oak acorns have a high tannin content and feature winter dormancy, whereas acorns of white oak and bur oak have a low tannin content. White oak germinates in the fall and bur oak is usually
dormant over winter. The cause of the dominance of Hill’s oak and red oak in the post-grazing cohort must be either:

1. A strong preference among squirrels and jays for caching Hill’s oak and red oak acorns versus those of white oak and bur oak.
2. The differential post-dispersal survival of acorns and seedlings of the two groups.

We have demonstrated that squirrels and/or blue jays cache white oak and bur oak in appropriate bare habitats. These facts do not support the idea that squirrels and jays disperse only Hill’s and red oak acorns.

Ranchers, however, have long known that cattle can eat large quantities of acorns, even to the point of poisoning themselves, and that individual animals differ in their taste for acorns. Tannin is largely responsible for acorn toxicity (Basden and Dalvi 1987). Cattle may select acorns based on the large difference in tannin content between the red oak and white oak groups. In addition, the tannin content of the leaves of red oak and Hill’s oak is higher than that of white oak and bur oak, hence cattle may further discriminate between the two groups in the seedling stage.

(below)
Cattle grazing in an oak woodland pasture.
MANAGEMENT RECOMMENDATIONS

We suggest here a few management techniques that may stimulate the establishment of oak seedlings.

1. The use of mowing and late-summer burning in and adjacent to stands of seed-bearing oaks may stimulate the caching behavior of squirrels and jays. For our mowing experiments, we used a tractor-mounted rotary woods mower, and the grass was 7.5-12.5 cm (3-5 inches) tall after mowing.

2. Likewise grazing large numbers of livestock for short periods may produce opportunities for acorn caching. Whenever possible, one should apply fire or grazing treatments in the year of a heavy acorn crop and seasonally timed to produce maximum bare or short-grass habitat at the time of acorn dispersal.

3. Timing the removal of invasive shrubbery and small trees to produce bare-ground conditions may also stimulate oak seedling establishment, if it is done in the year of an abundant acorn crop and immediately prior or during the period of acorn dispersal. Likewise if thinning overstory oaks is timed similarly, and one creates patches of bare ground or short vegetation, one may produce a crop of oak seedlings. In either case, the increase in sunlight intensity will enhance the survival and growth of the seedlings.

4. Prairie restoration on ex-agricultural fields adjacent to stands of mature oaks often leads to a cohort of young oaks in the prairie border. This is due to squirrels and/or jays caching nuts in the bare ground of the adjacent field. Timing prairie-restoration activities to correspond to years of heavy acorn crops will allow the establishment of a large cohort of oaks, which will create a more natural transition between prairie and oak savanna/woodland. In prairies already established, late summer burning or mowing may stimulate oak recruitment. Also, moving away from sod-forming grasses, such as big bluestem (*Andropogon gerardii* Vitman) and toward shorter-statured bunch grasses, such as little bluestem (*Schizachyrium scoparium* Michx.) and prairie dropseed (*Sporobolus heterolepis* A. Gray) may encourage the creation of unvegetated gaps and openings suitable to attract acorn dispersers.
CONCLUSION: The Case for Change

In the decades following European-American settlement, prairies disappeared under the plow as oak woods were converted to wooded pastures for domestic livestock or cleared and the ground put into crop production. The wood of oaks was valuable for a variety of uses, including firewood, railroad ties, building construction, and oak-plank roads. Farmers not only grazed stock in remaining woods but seeded aggressive, exotic grasses to replace the rapidly disappearing native plants. The bare, often disturbed soil created by heavy grazing offered prime habitat for the rapid spread of weedy plants unpalatable to livestock. While the old oaks were rapidly disappearing, a new generation of oaks sprouted from oak seedlings and shrubs already established at the time of settlement. The burst of reproduction didn’t last long though, as acorns and young oaks were preferred food for cattle. Oak reproduction almost completely stopped during the most intensive phase of the agricultural era, extending roughly from the 1870s and 80s into the mid to late 20th century in most parts of the Chicago Region (Figure 11).

The removal of livestock from oak woods occurred abruptly as land transitioned from farm to public conservation agencies or to corporate and residential holdings. With neither fire nor cow to slow their growth, invasive shrubs and trees rapidly invaded oak woods and transformed open savanna and woodland into dense forest. A brief surge of oak reproduction accompanied this change in land use, but it ended shortly after it began. Native plants of the old oak savanna, which survived the century or more of livestock grazing, rapidly disappeared in the dense shade. Oaks in the modern landscape are under threat from diseases such as bur oak blight, oak wilt, shoestring fungus, and sudden oak death, and from insects such as gypsy moth.

Oak woodlands and prairies that survive today have suffered so many abuses over the last 200 years that we quite naturally think of disturbance as bad. It is not surprising that, when people began restoring oak woodlands in the late 1980s, they understood restoration as an activity that repaired the damage and disturbance of the past and then protected the land from further disturbance. A healthy oak woodland we believed was one with a thick and diverse growth of native sedges, forbs, and grasses. We had every reason to believe that removal of invasive brush and use of fire would restore both the ground flora and provide the necessary opportunities for oak reproduction. Many very talented and intelligent people have made enormous strides over the last 30 years in oak savanna and woodland restoration.

This model of a verdant oak savanna, lush with the growth of native herbaceous plants does not need replacement, but it does need revision based on an emerging understanding of the intricacies of oak reproduction. The oak woodlands of the Chicago Region and the Midwest were part of cultural landscapes for over 10,000 years, were burned frequently by the native inhabitants in the summer and fall, and were grazed by elk and bison. We do not know how the frequency and intensity of these and other events combined to present opportunities for acorn caching by squirrels and jays. If we manage to provide these
opportunities, we may find other problems that prevent oak reproduction. Even so, without an abundant supply of seedlings, issues such as deer browse and fire, which effect height growth of seedlings and young trees, are of little importance.

In McHenry County more than 90% of witness trees recorded by the public land survey in 1840 were oaks. Oak and hazel were nearly ubiquitous in the shrub layer. Oak has dominated the arboreal pollen record across the Midwest for the last 11,000 years. Species that are often unable to reproduce in adequate numbers in modern landscapes were doing so over millions of acres and thousands of years.

The search for a solution or solutions to this problem must be a joint effort of scientists and land managers. The range of situations routinely confronted by restoration managers is far greater than that captured in a limited number of scientific experiments. For this reason, ecological restorationists should begin to work these ideas into their practice. When dozens to hundreds of practitioners are experimenting succeeding and failing together and talking to one another, the solutions will emerge. There is no reason to believe that if we continue to do restoration in the future only as we have done in the past that we will produce abundant oak reproduction.

Figure 11.
The reduction in the cover of oak ecosystems in McHenry County since European settlement in the early 19th century. McHenry County lost half of its oak woods by 1872; by 1939, 81% were gone, and by 2005, 86% were gone (MCCD 2009).

Circa 1837 (143,000 acres)  Circa 1872 (72,200 acres)

Circa 1939 (26,600 acres)  Circa 2005 (18,000 acres)
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