The Deer-Forest Study, 2013–2020

Deer affect plants

Plants affect deer

Vegetation

Plant species compete for space and nutrients

Soil

Soil chemistry affects plants

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The Deer-Forest Study is a complex project that weaves together science from three different fields of study — wildlife, forestry, and soils — in a single research project. We knew when we started this project that it would be challenging, but the science behind our management of forested ecosystems is at a point where we need to look beyond single factors and focus on their interactions.

The front cover has a graphic that illustrates what the Deer-Forest Study is all about — deer, soils, vegetation and their interactions. The interactions, however, are the focus because that will tell us what factor is important and when it is important. Understanding the interactions will help wildlife and forest managers make better informed decisions.

We are still working hard to achieve all our goals and we have made great progress. This report provides insights into what we have accomplished, what we are currently working on, and what we can work on to continue to move the science and management forward. We also highlight in this report how The Deer-Forest Study has contributed to science beyond the goals and objectives of this study. We call it “Serendipitous Research!”

The Deer-Forest Study, to be successful, must be a long-term effort. Deer populations may respond quickly to management and soils barely change, but vegetation in forested ecosystems changes relatively slowly. We greatly appreciate the support of the Pennsylvania Game Commission and DCNR Bureau of Forestry for this research project.

Duane R. Diefenbach
Patrick J. Drohan
Marc E. McDill
Distance sampling has been used to estimate deer density but as typically applied has violated key assumptions: a) deer are uniformly distributed with respect to distance from the transect; and b) survey transects are randomly placed across the study area. These assumptions are violated when roads are used as transects because deer and habitats are not distributed randomly with respect to roads. For example, based on locations of GPS-collared deer, deer are more likely to be located away from roads (see Figure).

Amanda Van Buskirk, as part of her M.S. research, estimated deer densities on the study areas using a generalized distance sampling estimator that accounts for the non-uniform distribution of deer with respect to distance from roads. In addition, we have further generalized the estimator for study areas where there are both forested and open habitats where both the deer density gradient and detection functions may vary according to habitat type. Consequently, research from the Deer-Forest Study has benefitted research on study areas where chronic wasting disease is being monitored.
An important question we hope to answer is what are the key factors that influence the distribution and abundance of certain plant species, especially those that deer prefer to eat. To begin to address this question, Danielle Begley-Miller studied factors that might explain where she found Indian cucumber-root (*Medeola virginiana*), a flowering herb that deer love to eat. She looked at whether the area was fenced, soil conditions, and other environmental factors. What she found was surprising! As you might expect for a plant, the more available light the more likely the plant would be present at a site. However, she also found that as soil pH declined manganese (Mn) increased and you were unlikely to find the plant present. Manganese is an important metal for cellular processes of both plants and animals, but at high concentrations it is toxic. Danielle’s research shows that just because we don’t find Indian cucumber-root present does not necessarily mean deer ate all of them.

The probability of Indian cucumber-root being present at a site is positively related to the amount of available sunlight (canopy openness). However, if manganese is in the soil at high concentrations the plant is unlikely to be present regardless of available sunlight (yellow band in figure).
SOIL INFLUENCES DEER NUTRITION – IT’S NOT ALL ABOUT PLANTS

Calcium and the Ca:P ratio increase over the summer in forest herbs consumed by deer. Ca:P ratios <2.0 are ideal for ungulates (orange dashed line). Fortunately, these low ratios occur when demands for calcium are highest for lactating females.

Nico Navarro, as part of his M.S. research, was interested in how soils influence plant nutrient content, especially nutrients important to white-tailed deer. In spring, female deer diets may consist of mostly forest herbs – as much as 90% of their diet may consist of plants like Canada mayflower (*Maianthemum canadense*). Do plant nutrients differ between our northern and southern study areas? For some chemical elements there are important differences in plant nutrient content between the northern hardwoods and oak-hickory forests.

The one question Nico did not think to ask when he began the study was how plant nutrient content changes over the growing season. Fortunately, he did look at his data and was surprised to see many plant nutrients changed throughout the summer. Most interesting was that in May when females are lactating the Ca:P ratio in Canada mayflower is ideal for ungulates. Another example of the interconnectedness of plants and animals in our forests.
Can DMAP units be too small? Can they be too big? When are they just right? Amanda Van Buskirk set out to answer this question as part of her M.S. research. Amanda developed a computer model that simulated the population dynamics and dispersal movements of deer. She was able to parameterize the model with Pennsylvania-specific rates based on decades of deer research. In particular, we know that female dispersal rates increase with increasing deer density. Would it be harder to create a localized reduction in deer density when more females disperse? Also, could the size and shape of the DMAP area influence the ability to locally reduce deer density?

Amanda discovered that DMAP areas are most likely to be effective if they are at least 5 square miles. At 1 square mile she found deer densities could increase almost as likely as decrease. Surprisingly, shape was not an important concern. This is good news for the Bureau of Forestry because their DMAP units average about 5 square miles.

**DMAP UNIT SIZE – THE GOLDILOCKS PRINCIPLE**

Research investigating the size and shape of DMAP units provides good news for the Bureau of Forestry. The shape of the unit does not reduce effectiveness, but units >5 square miles are more likely to successfully reduce deer densities. Most Bureau of Forestry DMAP units are of sufficient size. Although some DMAP units are long and linear, the shape should have little impact on their effectiveness.

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Danielle Begley-Miller tested the accuracy and consistency of field crews to collect vegetation measurements. First the bad news – field crews could not consistently assign the same deer browsing index level at our sampling sites. This is troubling because this index is used by the PGC to assess the impact of deer on forests and inconsistency among observers will mean it will take longer to detect real changes in the index.

The good news is that when using mil-acre plots for counting tree seedlings and herbaceous plants the field crews were highly consistent. This means that the data collected by Bureau of Forestry staffs under the Vegetation Impact Protocol should be highly reliable.
Mountains of Data

The Deer-Forest Study is unique in that it has collected detailed data on white-tailed deer (density, survival rates, harvest rates), vegetation, and soil conditions across 4 large study areas, each 25–40 square miles in size over a seven-year period. In addition, in 2018–2019 bird surveys were conducted at our vegetation plots.

DEER MOVEMENTS AND SURVIVAL AND HARVEST RATES

The Deer-Forest Study is closing in on 1 million deer locations (952,957) from GPS-collared deer monitored since 2013 where all data are curated on the Movebank platform. Movebank is a secure, online database system that allows all project collaborators access to GPS locations. By using this online database, other researchers have initiated collaborations. For example, these data contributed to a study published in the journal Science about how human activities have influenced movements of wildlife species worldwide.
Keeping Track of Data

VEGETATION: SPECIES COUNTS AND MEASUREMENTS

Two hundred permanent plots were established at randomly selected locations across the 4 study areas (50 per study area) where detailed vegetation data have been collected.

Overstory tree counts and basal diameter, sapling counts, and seedling counts are collected by species. Shrub species at different height and cover classes are recorded. On the forest floor, herbaceous plants are identified to species (in most cases) and counts made of species thought to respond to deer herbivory (e.g., Canada mayflower, Indian cucumber-root). Overstory data are collected on 24th-acre subplots, and data on smaller plants are collected on mil-acre and 300th-acre plots so that Deer-Forest Study data are collected at the same scale as USFS FIA plots and DCNR CFI plots. Additional plots with a similar design have been installed in “treatment areas,” where treatments such as understory herbicide treatments have been implemented to control competing vegetation.

Conducting a study like this is a significant logistical challenge that involves hiring quality field technicians, providing housing and transportation for them, training them, and providing them with state-of-the-art tools for locating plots, measuring vegetation, and recording data. Over the seven years that vegetation data have been collected (2013–2019), we have developed a detailed, yet practical protocol for measuring the vegetation on our plots and a rigorous 2-week training program for our crews. During this training period, our crews learn to implement this protocol carefully and accurately, and to identify and measure over 170 taxa of plants. We have also developed careful quality control and data management procedures. Today, our vegetation database for the 200 permanent plots contains over 186,000 records of observations of small vegetation, including herbs, shrubs, ferns, and vines; and it contains over 64,000 records of seedlings, 6,000 records of saplings, and 31,000 records of trees (≥5” DBH).
Keeping Track of Data

SOILS pH, CATIONS AND METALS

Soils in forested systems are the least studied and understood, especially in the oak-hickory forests of central Pennsylvania. To date we have collected soils data by major horizons, such as pH, concentrations of major cations (Ca, Mg, K, P), concentrations of important metals (e.g., Mn, Al), that allow us to derive important elemental ratios (Ca:Al, Ca:P).

BIRDS

Point-count surveys (10 min) for songbirds were conducted at 45 vegetation sampling sites, with most sites samples more than once per season. These surveys will serve as baseline data for determining whether changes in the bird community are associated with any noted changes in vegetation.
In 2020, a new URL and website was created, https://deer.psu.edu, that improved the user interface (e.g., better search capabilities) and moderation of reader comments. The new website had over 23,000 page views just for the month of November 2020.

To date over 570 articles have been posted. Blog topics have included “field diaries” of the activities of our deer capture and vegetation crews, distillations of scientific publications made understandable for the general public, and movements of deer throughout the year in response to weather and deer behavior. The most popular story on the blog documented the movements of Buck 8917 and where and how he died.
<table>
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<td></td>
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<td>Number of page views of our most popular post</td>
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TESTING SOIL, HERBICIDE, AND DEER INTERACTIONS THROUGH EXPERIMENTAL MANIPULATION

Decades of research in Pennsylvania have shown that soil, deer, and plant competition each influence forest plant communities. The Deer-Forest Study is different because it is focused on understanding how these factors interact with each other to answer the question of when a given factor becomes dominant in influencing forest plant communities.

For her dissertation research, Dr. Danielle Begley-Miller set up an experiment where liming to change soil conditions, application of herbicide to reduce competing vegetation, and fencing to exclude deer herbivory were incorporated in a fully cross-classified experimental design. We continue to monitor these vegetation plots that will provide insights into the interactive effects of soil, competing vegetation, and deer browsing on understory plant conditions.

Each of our hypotheses — browsing by whitetailed deer, unfavorable soil conditions, and competing vegetation — have potential to explain current vegetation conditions in forested habitats across Pennsylvania. Pennsylvania forests face a variety of environmental challenges related to soil chemistry, as well as biotic interactions related to deer herbivory and interspecific competition. Plant communities rarely respond to abiotic conditions exclusively and are more likely to be influenced by a combination of abiotic and species coexistence mechanisms.
The Deer Impact Index (DII) is a subjective measure scored on a scale of 1 to 5 that is used to assess how deer browsing is affecting understory vegetation. Our research has shown that field technicians have difficulty consistently scoring a site, which means that observer variability reduces the statistical power of the technique to detect changes. Is there a better alternative, perhaps one that is more quantitative that does not depend on observer judgements? We can compare our fenced plots to unfenced plots to measure the effect of deer. We are investigating whether an index to available light can account for light differences. We then plan to investigate different quantitative measures that can be obtained from FIA or CFI data, such as cumulative height of seedlings.

DEER IMPACT INDEX: IS THERE AN ALTERNATIVE?

The Deer Impact Index is subjective and inconsistently scored by observers. We are looking at alternatives that are quantifiable and can be obtained from USFS FIA or Bureau of Forestry CFI data.
Ongoing Research

MANAGING COMPETING VEGETATION

Project lead: Dr. Autumn Sabo, Penn State Beaver

Treating competing vegetation with herbicides is believed to allow desired herbaceous plants and tree seedlings to increase. The Deer-Forest Study is testing this hypothesis.

We are continuously monitoring 8 paired treatment-control areas as part of the Deer-Forest Study where treatment areas were sprayed with broadcast herbicide, or mowed, or received basal bark herbicide treatments. Dr. Autumn Sabo is focusing on two research questions:

1) What is the efficacy of treatments for reducing competing vegetation and encouraging tree regeneration desirable for timber or wildlife? And 2) How do treatments otherwise impact plant community composition on the forest floor? Preliminary analyses indicate that the aggregate heights of desirable tree seedlings often rebound beyond pre-treatment levels two to three years post-treatment, although responses vary by tree species. After analyzing how the composition and structure of treatment areas varying in deer pressure shift in comparison to un-treated stands, we will be better able to evaluate when and where to devote resources to understory vegetation management. Short-term findings will address the prime regeneration window. Longer-term results will provide insights about slower forest processes including self-thinning and transitions to shade-tolerant species that may, eventually, reduce competing vegetation abundance naturally.
Light availability is a vital factor in tree regeneration, thereby influencing stand development. However, measurements of light penetration to the forest floor are difficult and expensive to procure and process. An index of light availability based on data commonly gathered during forest mensuration would be useful both to researchers and forest managers. Using data from several projects in Northern Hardwood forests in the Upper Midwest, we are investigating the possibility of using measurements of basal area to predict light availability. Light attenuation may be influenced by leaf morphology, crown position, and crown structure. Along with basal area, we can also categorize trees by leaf type, diameter (as an indicator of height class), and shade tolerance. Ultimately, we hope to develop an index that can be used to distinguish between light environments suitable for reproduction of different species. Regeneration failure is sometimes attributed to deer herbivory, but there remains confusion over the interaction of light environment and depredation. We intend to use data from studies using deer exclosures to determine the index values at which the effect of reduced light eclipses the influence of deer herbivory.

The amount of sunlight reaching the forest floor has a large influence on vegetation growth. Developing a simple model to predict light availability at a site could help researchers separate the effects of light availability and deer herbivory.

The data for examining these questions comes from studies in Wisconsin and Michigan. However, our final product will be based on data from a portion of the Deer-Forest Study in Bald Eagle and Rothrock state forests. Data available include measurements of overstory, saplings, seedlings, and percent canopy closure. Because we expect seedling response to light to take several years to develop, we will use seedling data from 2018, which is 5 years after treatment and initial light measurement. The amount of data available from the Deer-Forest Study will allow us to both develop and test the model.
Researchers have used GPS technology to track adult male deer to make inferences about mate-seeking behavior and identify when and where breeding events occur. However, none of these studies have had both female and male deer radio-collared in the same area. We tested whether methods used by other researchers were able to detect events when we knew a male and female traveled together during the breeding season. We found none of the methods correctly detected these paired movements, which means that inferences from these previously published papers may need to be viewed with caution.

Do methods that solely use the movements of a single sex actually detect breeding events? Deer-Forest Study data, where we tracked both males and females, suggest they do not. Researchers should be cautious when making inferences about breeding behavior solely from movements of one sex.

Therefore, movement data from both sexes is needed to identify mating events.
Amanda Van Buskirk’s recent thesis research on estimating deer density has provided a robust method for obtaining direct deer density estimates. However, we also have accumulated additional information about survival and harvest rates that can be incorporated into an Integrated Population Model. Such a model would provide more accurate population estimates that would provide stronger inferences about changes in deer density effected by use of DMAP.

The benefit of IPMs is that they use data from one year to help estimate deer density the following year. This eliminates biologically implausible changes in deer density that occur from sampling error. Because the PGC deer program uses the PASAK model, which estimates deer abundance independently each year, research into developing an IPM for the Deer-Forest Study has potential benefits for population monitoring for the PGC deer management program.
We have learned that it takes about 3 years before all DMAP permits sell out when either a new DMAP unit is created or permit numbers are increased. Also, we have been sending annual surveys to hunters on our study areas to find out their hunting effort, attitudes, and opinions about their deer hunting experience. Unfortunately, we have not been able to find a collaborator to dive into these data and learn more about how hunters use DMAP and what hunters do and do not know about this program. Sufficient data are available for a Ph.D. student to develop a dissertation research topic.

Our research has shown that short-term deer exclusion (2 years) does not explain much about where deer-preferred plants occur or are absent. Since the Begley-Miller et al. (2018) paper we have collected more soils data and can expand this research across all 4 study areas. Also, we have longer periods of deer exclusion that could be evaluated. We have a new measurement of Dr. Begley-Miller’s experimental plots from 2018 (five years after establishment and four years after treatments) that may show effects that were not evident at 2 years after treatment. In addition, we have yet to analyze the data from the deer exclusion subplots on the 200 permanent plots.
The fawn survival study contributed to a meta-analysis of fawn survival studies conducted throughout North America and discovered some previously unknown patterns in survival rates and cause-specific mortality. An important finding was that fawn survival increases the more agriculture that exists on the landscape. Previous researchers had suggested that habitat conditions might influence survival, but individual studies were unable to find consistent patterns.
MEASURING STRESS

Fawns with higher levels of stress hormones have lower survival rates. The source of this stress is unknown but was not related to abundance of predators on the landscape.

Predation is the primary cause of mortality in white-tailed deer fawns throughout the range of the species. However, a study in Delaware found that when no predators were present fawn survival was only 50% – not much different from places were 2 or more predators were present! This suggests that predators may consume a lot of fawns but predation may not be the ultimate cause of fawn mortality. Tess Gingery, as part of a side project with her M.S. degree, found that fawns with higher stress hormone levels had lower survival rates. And fawns that lived in areas with higher predator densities did not necessarily have higher stress levels. This study may explain why Delaware, with no predators, has similar fawn survival rates as Pennsylvania.
We modified micro-GPS units and attached them to regular VHF fawn radiocollars. For the first time, we obtained hourly locations for fawns <1 month of age. This research has found that fawns have larger home ranges than previously thought. When compared to current methods used to assess fawn movements and home range, we found that the GPS location data provided completely different insights into fawn habitat use.
Females and fawns take advantage of human disturbance to avoid predators.

Predators influence prey in numerous indirect ways, causing prey to view space as a dynamic landscape of fear. One way to characterize this landscape is through examining habitat use, as both predator and prey attempt to meet nutritional needs while avoiding risky areas. Because habitat use can also be influenced by anthropogenic disturbance, it is vital to determine how predator-prey distributions change as natural habitat continues to be encroached upon.

We used camera traps to examine the distribution of predators (black bear, coyote, bobcat) and white-tailed deer fawns to human-modified habitats. We found that fawns had higher local site use probabilities outside the state forests, as opposed to black bears. Coyotes shifted in their response to proximity to anthropogenic disturbance based on whether the state forest was surrounded by natural habitat or by human-modified habitat.

We found clear evidence of dams and their fawns taking advantage of the 'human shield' present outside the state forests. Our study provides new perspective to a concurrent study that showed fawn survival was positively correlated to the amount of human-modified habitat and suggests that the landscape of coexistence (that between predators and humans) can influence the landscape of fear perceived by prey.
Perceived predation risk by deer varies across such factors as space, time, and predator species. However, in an increasingly human-dominated world, researchers also need to take into account how anthropogenic disturbance influences interactions among predators and prey. We examined how white-tailed deer fawn antipredator behavior differed in a multi-predator system with black bear, coyotes, bobcats, and humans, and how that behavior changed over an anthropogenic disturbance gradient. We used camera trap data on the Deer-Forest Study research areas.

Anthropogenic disturbance influenced spatio-temporal co-occurrence across multiple scales, often increased spatiotemporal overlap among species, and interactions became neutral or weaker in anthropogenically disturbed environments. For example, bears and fawns, coyotes and adult male deer, and bobcats and fawns all had greater temporal overlap in public forests surrounded by agriculture and development. Factors that influenced deer vigilance (e.g., distance to forest edge and predator relative abundance) in public forests surrounded by agriculture and development did not when the surrounding matrix type was forest. We demonstrated how anthropogenic disturbance influences predator-prey behaviors.

VIGILANCE IN RESPONSE TO PREDATORS

Predator relative abundance has no effect on vigilance behavior in white-tailed deer in agricultural regions but vigilance increases with increasing predator abundance in forested environments.

Vigilance in response to predators

Serendipitous Research
**SPATIAL GENETICS**

Topographic features influence gene flow. Areas of high gene flow in this figure follow the topography in the Ridge and Valley Region of Pennsylvania, Maryland, and West Virginia.

Research in Pennsylvania on dispersing deer has shown that roads and rivers are barriers, albeit permeable. Genetics data collected from deer on the Deer-Forest Study contributed to a study showing how topographic barriers were associated with genetic discontinuities.


**MOVING IN THE ANTHROPOCENE**

The Deer-Forest Study contributed to a worldwide study of mammalian movements as it relates to human activities. Animals move less in areas where humans have a greater impact on the environment.

The Deer-Forest Study contributed data for a study on animal movements relative to the amount of human disturbance. The research used data from animals around the world collected by over 100 researchers. The findings were published in the journal Science and showed how human activities reduced the movements of mammals.

People

PIs

• Dr. Duane R. Diefenbach, Unit Leader, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University

• Dr. Marc E. McDill, Associate Professor of Forest Management, Pennsylvania State University

• Dr. Patrick J. Drohan, Associate Professor of Pedology, Pennsylvania State University

COLLABORATORS

• Dr. Autumn Sabo, Assistant Professor of Forest Ecology, Penn State Beaver

• Dr. Frances E. Buderman, Assistant Professor of Quantitative Wildlife Ecology, Pennsylvania State University

• Dr. Margaret Brittingham, Professor of Wildlife Resources, Pennsylvania State University

• Dr. Phillip Jones, Post-doctoral researcher

STAFF

• Tess M. Gingery, Research Associate

• Alyssia Church, Movebank database support

• Lilly Bean, vegetation database support

AGENCY COLLABORATORS

• Dr. Christopher S. Rosenberry, Pennsylvania Game Commission, Wildlife

• Dr. Bret D. Wallingford, Pennsylvania Game Commission, Deer and Elk Section

• Jeannine Fleegle, Pennsylvania Game Commission, Deer and Elk Section

• Emily Domoto, Department of Conservation and Natural Resources, Bureau of Forestry

CURRENT AND FORMER GRADUATE STUDENTS

• Dr. Danielle Begley-Miller, Ph.D. in Wildlife and Fisheries Science, 2018.


• Asia Murphy, Ph.D. in Ecology, expected 2021.
PUBLICATIONS


IN PREPARATION OR SUBMITTED TO JOURNAL


Navarro, N.; Drohan, P.J., Diefenbach, D.R., McDill, M.E. Northern Appalachian ecological site differences in soil chemistry and carbon: implications forest management.


THESES AND DISSERTATIONS

Van Buskirk, A. 2020. Estimating the effects of changes in harvest management on white-tailed deer (Odocoileus virginianus) populations. Thesis, Pennsylvania State University, University Park, PA, USA.

Navarro, N. 2018. Using soil chemical properties and white-tailed deer (Odocoileus virginianus) forage nutrients to refine forested, northern Appalachian ecological sites. Thesis, Pennsylvania State University, University Park, PA.

