

Lessons from the Prairie

Research at The Nature Conservancy's
Tallgrass Prairie Preserve



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1. Introduction

SINCE ITS 1989 INCEPTION, the Tallgrass Prairie Preserve (TGPP) has been a focal point of ecological research in Oklahoma. Researchers from Oklahoma State University, the University of Tulsa, the George M. Sutton Avian Research Center and several other institutions have been actively involved in studying the flora, fauna, and forces that characterize and shape the tallgrass prairie landscape. Their research represents the breadth of both basic and applied ecological science. To date, more than 160 scientific publications have been produced from research done at the TGPP (Figure 1).

As more and more researchers undertake projects at the TGPP, it is increasingly important to understand the preserve's scientific background and to have a ready reference of the important findings so far discovered. The purpose of this document is to summarize and explain the body of research accomplished at the TGPP and to provide the history of the preserve. In addition to summarizing research, this document also includes an annotated bibliography of all known scientific publications resulting from work accomplished at the TGPP.

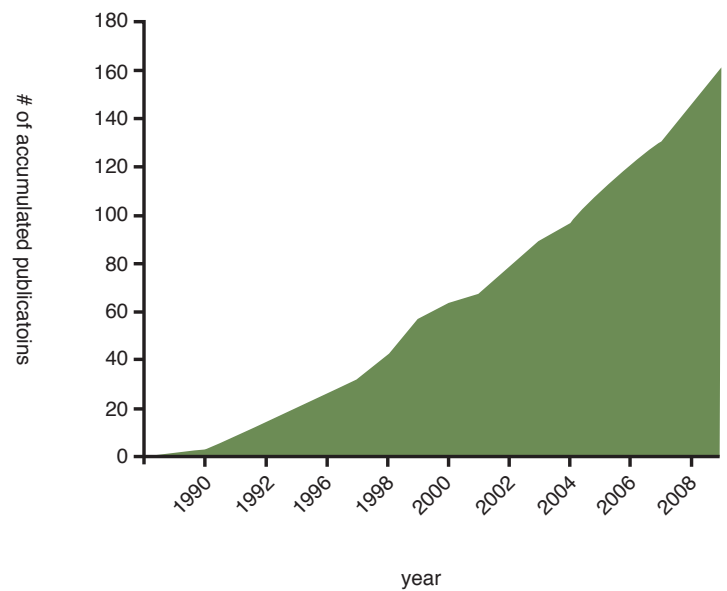


Figure 1. Total number of accumulated TGPP-related publications since the preserve's establishment.

2. History and Management

2.1 Osage, oil, and ranching history

The history of the land that would become the TGPP begins long before its purchase by The Nature Conservancy in 1989. The TGPP is located in Osage County, a place whose rich history has been undertaken by a number of authors. Several books have chronicled the land's rich Native American heritage and its history of oil and cattle booms. In this section we are indebted to Terry P. Wilson's The Underground Reservation: Osage Oil [173] and Luis F. Burns' A History of the Osage People [20] for background material on the history of the Osage people.

The preserve presently (and historically) falls within the domain of the Osage Nation. Linguistically, the Osage are of Dhegiha Siouan lineage and are thought to have originated in the Ohio River valley before migrating to the Ozarks of Missouri and Arkansas. In those wooded hills they maintained permanent villages but made periodic trips to the nearby prairies for hunting. During the 17th century, the Osage became actively involved in the fur trade with the French. Their strategic position on the Missouri River allowed them control over much of the fur industry as well as neighboring tribes.

The Louisiana Purchase in 1802 brought the Osage into the jurisdiction of the United States and with it, increasing intrusions by white settlers. A series of treaties with the American government forced the Osage to cede more and more land until 1825 when they were assigned a 50 mile by 125 mile reservation along the southern border of Kansas (Figure 2). At this time, the tribe was appointed its first in a series of Indian agents, primarily to help mediate conflicts with white settlers trespassing on Osage land. After the

Civil War, American westward expansion increased in earnest and along with it, conflicts with white settlers trying to stake homesteads on Osage land. In 1870, the Osage agreed to sell their Kansas reservation to the federal government for \$1.25 an acre. With funds from this sale and from previous land concessions, the Osage purchased a new reservation from the Cherokee in the Oklahoma Indian Territory and moved there in 1871. Bound by the Arkansas River on the west and the 96th meridian on the east, the new reservation encompassed almost 1.5 million acres of forest, prairie, and river bottoms (Figure 2).

From Pawhuska, the new capital of the Osage Nation, the Federal Indian Agents sought to promote an agrarian society amongst the Osage as the best means for acculturation within a changing world. Osage indifference to

farming, and lack of tillable land, never induced the Osage to whole heartedly adopt this new mode of life. Annuity payments from funds held in trust by the federal government from the Osages' previous land sales gave them financial security and little need to develop their land agriculturally. During the 1870s cattlemen started to allow their herds to illegally graze the lush natural pastures of the Osage Reservation. After continued prompting by Indian Agent Laban J. Miles, the Office of Indian Affairs remedied the problem by approving the first cattle leases in 1882. Most of these early leases encompassed the land that would become the TGPP [21].

In succeeding years, pressures internal and external to the tribe pushed for individual ownership of tribal lands. The Osage were initially exempt from the 1887 Dawes Severalty Act, which

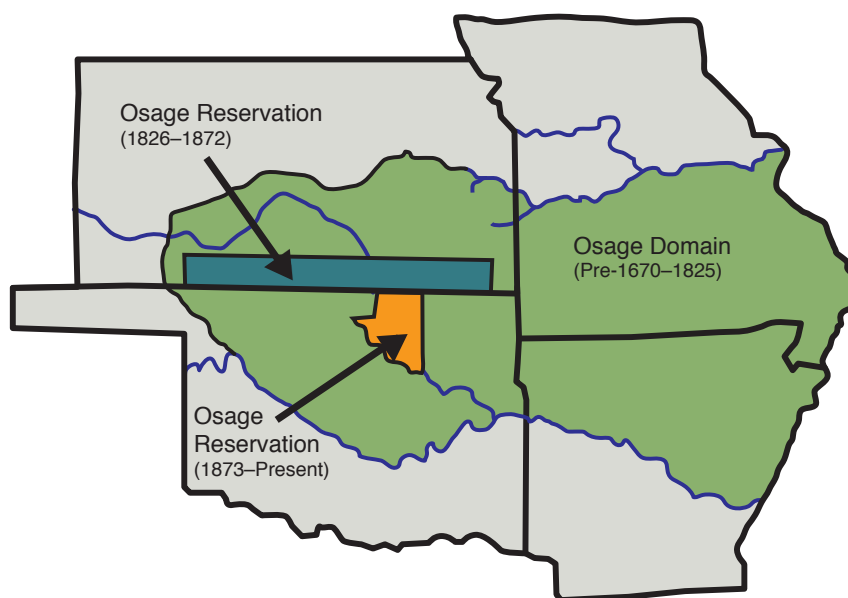


Figure 2. Osage lands from prehistoric times to the present. Map modified from reference #20.

mandated the allotment of tribal lands to individual tribal members within Oklahoma Territory. Most of the full-blood Osages opposed the partitioning of tribal lands, but several generations of intermarriage with white neighbors gave the mixed-blood members a numerical advantage and consequently a powerful lobby in determining the fate of Osage lands. In 1906, the pro-allotment faction won out and Congress applied the Dawes Act to the Osage Reservation, thus initiating the process of allotment to tribal members. In the end, 2,229 Osage

received allotments. In comparison with other tribes relocated to the Oklahoma Territory, the process of allotment was unique for the Osage in that Osage severalty did not include the subsurface mineral rights. Those rights remained collectively owned by the Osage Nation instead of being divided with the land as was the practice with other tribes in Oklahoma Territory.

In 1897 oil was discovered on the Osage Reservation, and though its potential resources were not fully tapped during the 1906 allotment, the Osage knew that significant amounts of

mineral resources awaited extraction. Eventually, the advent of the automobile, World War I, and the economic boom of the 1920s created huge demand for oil generating enormous revenues for the Osage. By the 1920s oil wells were being drilled throughout the reservation (Figure 3). In 1925, Osage earnings from oil royalties peaked, each headright (as determined by the 1906 allotment) earned \$13,200 that year. Families which held multiple headrights earned what would amount to a substantial fortune for the time. Ultimately, the Great Depression brought an end to the heyday of Osage oil revenues; brief resurgences in the oil economy increased during the oil shortages of the 1970s and most recently in the 2000s.

Concurrent with the expansion of the oil industry, the cattle industry thrived on Osage lands. During World War II, more cattle were shipped from the Osage prairies than anywhere else in the United States [152]. The region is still a major cattle production area today [89, 88].

In 1915, oilmen James A. Chapman and Horace G. Barnard began purchasing Osage land for cattle production, eventually growing their holdings to more than 100,000 acres, making it the largest ranch in Osage county during the 20th century [170]. After Chapman's death, the ranch was divided; the western side retained by the Chapmans and the eastern side by the Barnards. The Barnard Ranch eventually became the cornerstone property of the TGPP.



Figure 3. Modern day oil pumpjack at the TGPP.
Photo / Matt Allen

The path to establishing a preserve in the tallgrass prairie was a rocky one. Early efforts by the National Park Service to establish a national preserve in Osage County were not well received by most of the local populace [152]. During the 1980s the federal government came close to a deal that would have allowed the purchase of land within Osage County (including the Barnard Ranch), but this fell through in 1988 when fears over the fate of oil operations within the proposed national preserve and a dissolution of political will terminated the pending congressional legislation [152]. At this point, The Nature Conservancy began exploring the possibility of establishing a preserve in the tallgrass prairie. In 1989 they purchased the 29,000 acre Barnard Ranch and raised 15 million dollars in private funds for the project [152]. In succeeding years, additional land purchases and leases built the preserve's managed area to 39,100 acres, with an adjacent 5,950 acres protected by conservation deed restrictions. The Nature Conservancy is also pursuing conservation easements with ranchers in the surrounding area to preserve the intact nature of the Flint Hills landscape.

Though initially greeted with skepticism, The Nature Conservancy has been active in reaching out to its neighbors and collaborating with the Osage Tribe. The TGPP routinely provides equipment and helping hands to neighboring ranchers when they burn their pastures. As of 2009, The Nature Conservancy has helped burn 310,000 acres on neighboring lands and suppressed 80 wildfires.

2.2 Historical land use

Though little was formally recorded about the historical use and management of what is now TGPP land, it is relatively certain that the land has been actively managed with fire for at least the past few hundred years and probably much longer. Perhaps one of the earliest written accounts of fire management in the region comes from the expedition journals of naturalist Thomas Nuttall during his journey along the Arkansas and Verdigris rivers in Oklahoma. On September 10th, 1819 Nuttall “saw the smoke of Osage fires in all directions” [102]—though it is unclear from the context if his reference is to prairie fires or campfires. In contrast, accounts from American author Washington Irving’s 1832 hunting expedition [81], clearly describe prairie fires set by Osage hunters on several occasions. During Irving’s trip he directly observed or saw evidence of Osage burning on at least nine different occasions. On one occasion, his party inadvertently started their own grass fire when a campfire escaped its bounds. A few decades later in 1885, Indian Agent Miles lamented that the Osage prairies were “burned this autumn unutilized” for grazing (as quoted in [173]).

The Barnard Ranch primarily ran a cow-calf and yearling operation [64]. Their cattle management included prescribed fire on a four to five year rotation [64]. Additionally, the ranch aerially applied broadleaf herbicide on a four to five year rotation to suppress forbs and promote grass growth [64]. Portions of Cross Timbers forest on the preserve were clearly sprayed with herbicide at some point. Aerial spraying is continued on many lands neighboring the TGPP today.

2.3 Land stewardship under The Nature Conservancy

The primary ecological goal of the TGPP is to protect and maintain the indigenous biological diversity by restoring a functional grassland landscape [63, 64]. Managing for a patchy landscape (heterogeneity) is the central goal, thereby providing habitat for the complete array of native plants and animals. Grazing and fire were two of the primary ecological forces on the presettlement Great Plains, and their interaction created a heterogeneous shifting mosaic of landscape patches [55].

The TGPP bison herd was initiated in the fall of 1993 with the release of 300 animals on 5,000 acres. In 2008, the

herd reached its long-term target of 2,700 animals on 23,500 acres. The herd is managed with minimal inputs (no supplemental protein or energy, though mineral licks are provided). An annual fall roundup is conducted to maintain herd health (vaccinations to prevent bovine diseases and control parasites) and, since the historic large predators (wolves) were extirpated more than a century ago, to remove surplus animals to maintain an ecologically sustainable stocking rate.

Cattle are grazed on several areas of the TGPP outside of the bison unit. A local rancher leases approximately 12,000 acres, most of which is devoted to a promising cattle patch-burn study conducted in collaboration

with Oklahoma State University. This “conservation grazing” study is testing the wildlife and plant community responses, and cattle gains, in patch-burn versus completely burned pastures. The objective is to improve conservation benefits through creative cattle management that diversifies the landscape.

Fire is a major aspect of the TGPP management plan (Figure 4). In the fire-bison unit, randomly located prescribed burns are conducted to simulate the original fire frequency (3-year fire return interval) and seasonality (spring, summer and fall). Fire is also used in conjunction with all of the cattle grazed and ungrazed management units on the preserve. In total, approximately three dozen prescribed burns are conducted each year yielding approximately 15,000 burned acres. Since the preserve fire program began in 1991, over 500 prescribed burns have been conducted on 280,000 acres.

The bison herd has free-ranging access year-round to all points within the bison unit, allowing them complete access to an ever-shifting array of burn patches. The lush re-growth following a burn is very attractive to the bison, resulting in a fire-induced rotational grazing effect, which maintains a dynamic mosaic of landscape patches. The research and monitoring described in later sections shows this heterogeneous landscape is successfully supporting a broad array of biological diversity.



Figure 4. Prescribed fire during the early spring at the TGPP.
Photo / Matt Allen

3. Preserve Facilities

3.1 Tallgrass Prairie Ecological Research Station

The Tallgrass Prairie Ecological Research Station (TGPERS) building was dedicated on May 20, 2004. This multi-purpose building is located at the TGPP headquarters complex, and consists of 6,000 square feet of laboratories, offices, library/conference room, classrooms and restrooms (Figure 5) Additionally, the station is equipped with herbarium storage cabinets that contain approximately 1000 plant specimens (Figure 6). Other amenities include a small computer lab and wireless internet throughout the station. The station is dedicated to a three-fold mission of ecological research, education, and biodiversity conservation. It is a unique facility that provides opportunities for the study of tallgrass prairie associated ecosystems and for basic biological and ecological research on a wide range of taxa and processes. The station is open to scientists and students from throughout the world. It also serves as an environmental education facility for students, land managers, and the public.

The TGPERS is owned by The Nature Conservancy and jointly operated by The Nature Conservancy and The University of Tulsa. The TGPERS Facility Board is equally composed of members from The Nature Conservancy and University of Tulsa, and oversees the development of the station and sets station policies. A joint Nature Conservancy-University of Tulsa fundraising campaign raised \$2.2M from private sources to construct the station, re-model the Foreman's House (researcher housing—see section 3.2), and endow the operations of the facilities. Dr. Kerry L. Sublette, a professor of chemical engineering and geosciences and Sarkeys Chair of Environmental Engineering at the University of Tulsa, deserves special credit for having the vision, tenacity, and partnership skills to make the TGPERS a reality.



Figure 6. Herbarium cabinet at the TGPERS.
Photo / Matt Allen



Figure 5. TGPERS Ecological Research Station. a) exterior view; b) laboratory; c) conference room/library/computer lab; d) classroom. Photos / Matt Allen

3.2 Foreman's House

The historic Foreman's House is adjacent to the TGPERS and serves as housing for researchers at the TGPP (Figure 7). The Foreman's House has bunk beds to accommodate 18 people and has a fully equipped kitchen. Researchers interested in using either the Foreman's House or the TGPERS should contact the TGPP office as some fees apply.



Figure 7. Foreman's House at the TGPP.
Photo / Matt Allen

3.3 Public Facilities and Use

Approximately 20,000 visitors tour the TGPP each year. The headquarters has a gift shop/education center with a small museum that is staffed by a dedicated group of 100 volunteer docents. The gift shop/education center is generally open from late spring to early fall.

Adjacent to the headquarters is a picnic area and a self-guided hiking trail. The trail can be enjoyed as a one or three mile loop. An interpretive brochure for the trail is available at the kiosk in the trail parking lot.

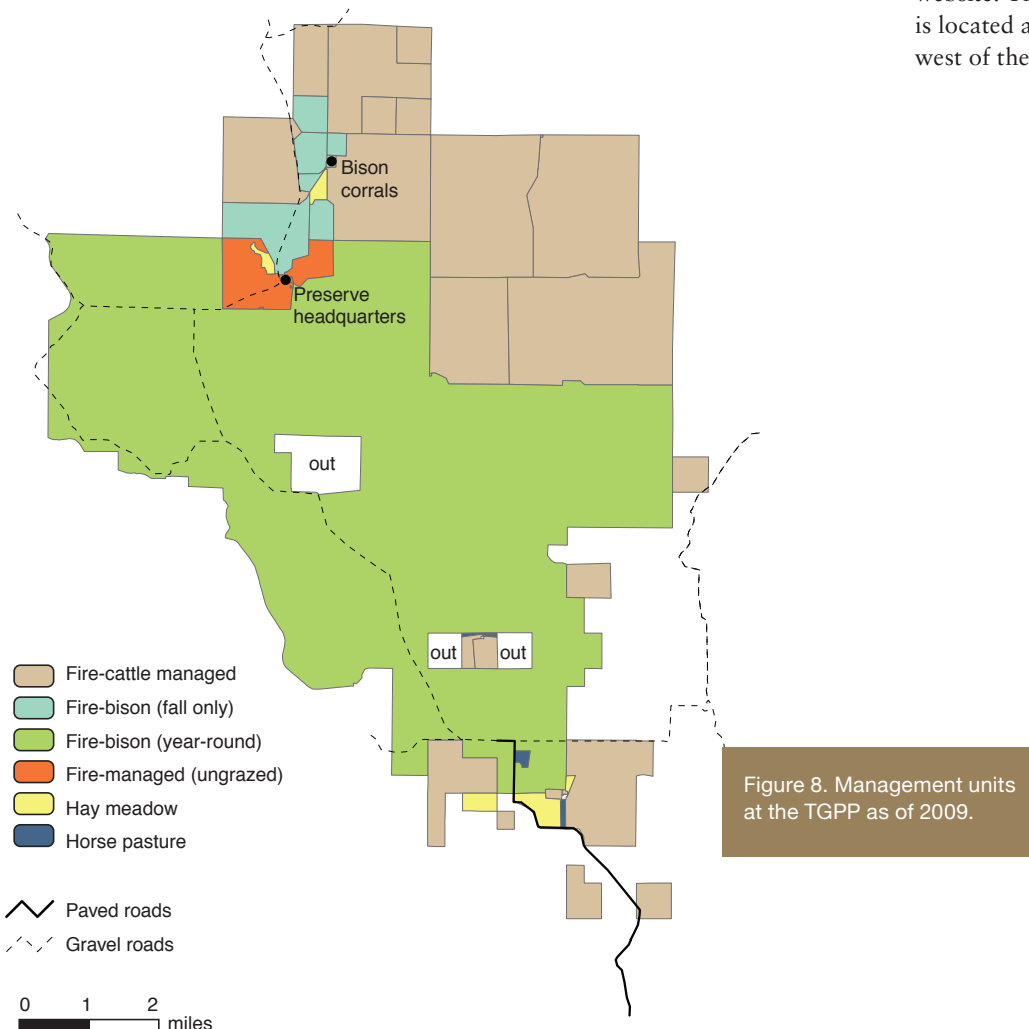
4. Site Description

The TGPP is located in Osage County of northeastern Oklahoma (36° 50' N, 96° 25' W) just north of the city of Pawhuska, the county seat. The preserve is a little over 15,800ha in area, making it the largest protected area of tallgrass prairie in North America. The southern two-thirds of the preserve is the bison unit (Figure 8). Bison are allowed free-ranging access to all portions of the preserve within this unit. The northern third of the preserve is leased for cattle grazing (Figure 8) as a part of ongoing research on cattle management and conservation. Approximately 10%

of the TGPP's area is forested, most of which is classified as Cross Timbers, though numerous riparian forests occur as well. The preserve encompasses all but the uppermost reaches of the Sand Creek drainage, the principal waterway running from northwest to southeast through the preserve. Several county roads bisect the preserve as well as numerous access roads, though most of those have restricted public access. Additionally, there are approximately 120 active oil wells on the preserve.

4.1 Climate

The TGPP is host to an Oklahoma Mesonet station (more information on the Oklahoma Mesonet may be found at www.mesonet.org [1]). These sophisticated weather stations monitor air temperature, relative humidity, barometric pressure, rainfall, solar radiation, soil temperature, and wind speed. All above ground measurements are recorded every five minutes and below ground measurements are recorded every fifteen minutes. All data are available through the Mesonet website. The preserve's Mesonet tower is located approximately a kilometer west of the preserve's headquarters.



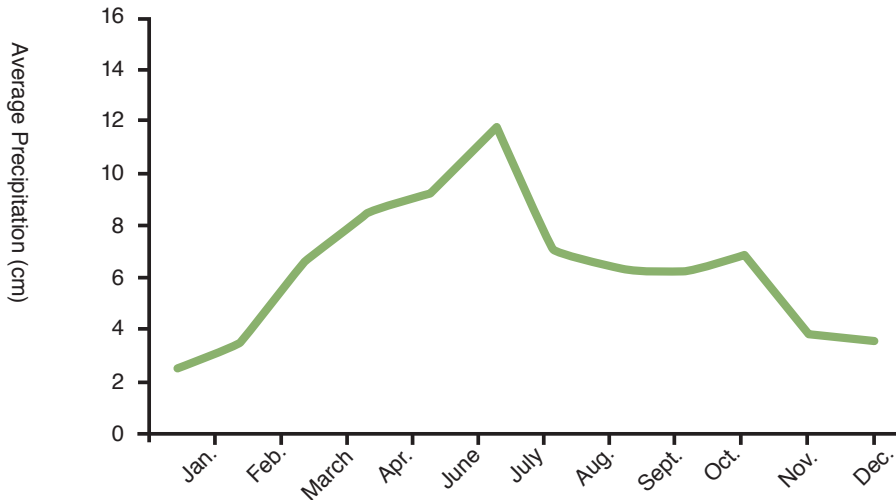


Figure 9. TGPP average monthly precipitation pattern from 1994–2008 as recorded by the Mesonet station.

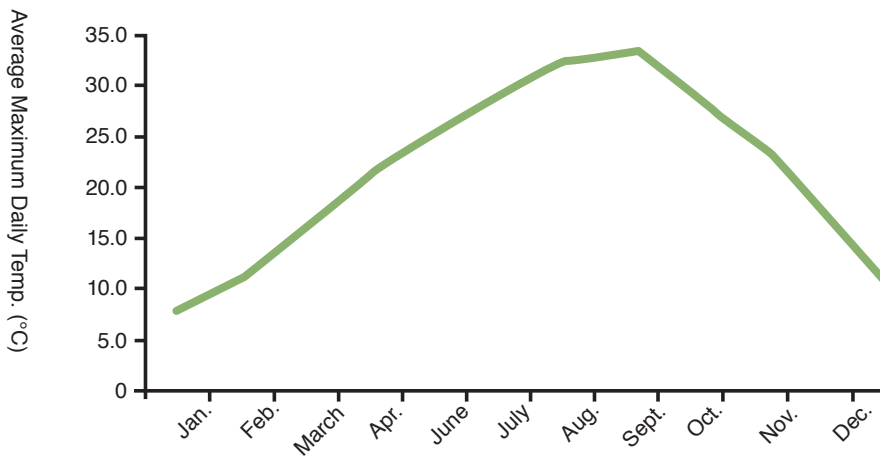


Figure 10. TGPP average maximum monthly temperature at the TGPP from 1994–2008 as recorded by the Mesonet station.

The climate of the preserve is classified as continental. Average annual precipitation at the preserve is 94cm. Most precipitation falls during the spring and, to a lesser extent, in the fall, (Figure 9) though substantial variation may occur between years. Temperatures at the preserve may range from below 0°C to above 38°C over the course of the year. July and August are usually the hottest months (Figure 10).

Severe weather is not uncommon at the preserve. In 2003, an F3 tornado uprooted trees and damaged fences in the southwest corner of the preserve. Some storms will produce torrential rains (on March 20, 2007 the preserve received 13cm in 24 hours) inducing flood conditions in many of the preserve’s drainages. Drought is also common in this region of the Great Plains. 1996, 2001, and 2006 are the driest years recorded by the Mesonet station, with only 75, 60, and 61cm of rainfall, respectively, during those years. In the winter, the TGPP may experience snowstorms or potentially more damaging, ice storms. In 2007 and 2008 severe ice storms damaged thousands of acres of forest in Oklahoma, though the TGPP’s forests were not much impacted by these events.

4.2 Topography

The topography of the Tallgrass Prairie Preserve consists of rolling hills, rocky flat-topped ridges, and long valleys. Steep slopes and prominent rock outcrops can be encountered along some of the preserve’s streams. Elevation within the preserve boundaries ranges from 253m to 366m (800–1200ft) above sea level [106].

4.3 Geology

The geology of the preserve was described in a guidebook by Suneson [162]. The geology of the preserve is relatively simple. Limestone, sandstone, and to a lesser extent shale are the predominant rock types found throughout the preserve (Figure 11). All of the rock layers in the preserve originate in the Pennsylvanian Period of the Paleozoic (323-290 million years old). The stratigraphy of rock layers at the preserve consists of repeating layers of shale, limestone, and sandstone. These rock layers owe their origin to the inland sea that once covered the North American midcontinent. Rising and falling sea levels are likely responsible for the cyclic repetition of rock layers found at the preserve. Rock outcrops of all the major strata can be observed throughout the preserve.

The limestone beds of the preserve contain abundant marine invertebrate fossils. Fossil animals encountered within the preserve include fusulinids, sponges, marine bryozoans, a variety of mollusks and echinoderms. Fossil plants include cryptozoan algae and some ferns. Cordova et al. is currently working on a sequence of phytoliths, carbon isotopes, and *Sporormiella* spores from a two thousand year sequence of paleosols at the TGPP in order to reconstruct vegetation composition and fire history, grassland-woodland changes, and large herbivore abundances, respectively.

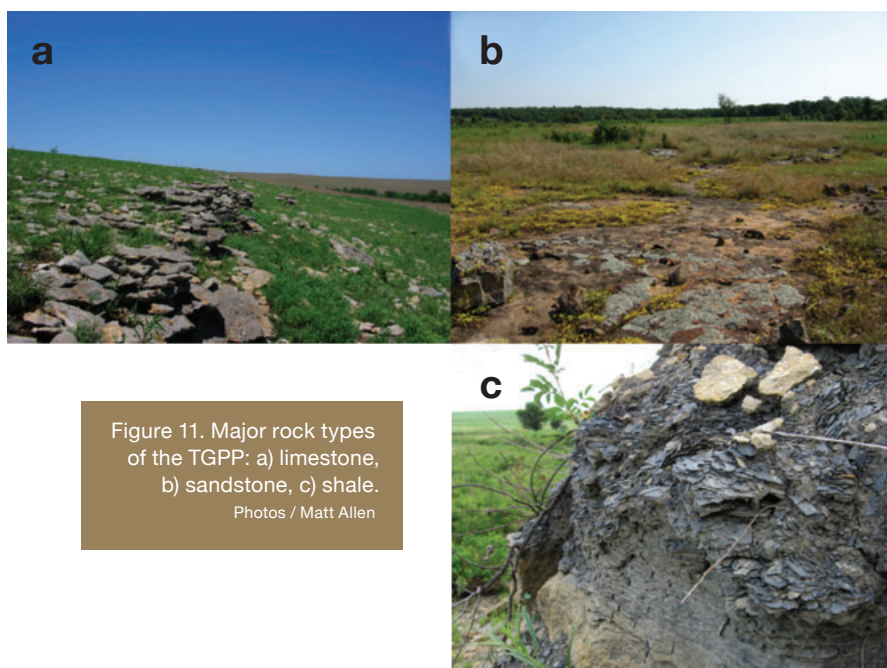


Figure 11. Major rock types of the TGPP: a) limestone, b) sandstone, c) shale.
Photos / Matt Allen



Figure 12. Grassland soil horizon at the TGPP.
Photo / Matt Allen

4.4 Soils

Given the underlying geology of the preserve, it is not surprising that the predominant soils of the preserve are either sandstone or limestone derived. According to the county soil survey [14] the Summit-Shidler complex is the main soil type encountered in the preserve's grasslands. These limestone derived soils range from being deep black-gray silty clay loams to shallow stony dark brown silty clay loams (Figure 12). The Niotaze-Darnell soil complex is primarily encountered in the forested portions of the preserve. They are derived from shale and sandstone and range from being moderately deep silty clays to shallow stony sandy loams. They are also characterized by low water capacity.

5. Plants

From the first flowers of spring, to the golden autumn grasses the TGPP is a botanically diverse and beautiful landscape (Figure 13). Within the boundaries of the preserve, one may encounter a variety of vegetation types including prairies, wetlands, woodlands, and forests. The vascular flora of the TGPP compiled by Palmer [106] includes 763 plant species in 411 genera and 109 families, making it richer than comparable prairie floras. Of that 763, 92 are non-native species. In the following sections we discuss the two dominant vegetation types of the TGPP: tallgrass prairie and Cross Timbers forest.



Figure 13. Prairie vista at the TGPP in early June.
Photo / Matt Allen

5.1 Tallgrass prairie

The TGPP protects a portion of the last vestiges of an ever diminishing landscape. Originally spanning portions of 14 states from Texas to Minnesota [135] (Figure 14), tallgrass prairie was one of North America’s magnificent presettlement ecosystems. Conversion to cropland, urban sprawl and other habitat losses reduced the tallgrass prairie to approximately 13% of its former distribution [136]. The 3.8 million acre Flint Hills of Oklahoma and Kansas comprise the only expansive, intact tallgrass prairie landscape remaining on the continent [136] (Figure 14). Its shallow rocky soils precluded it from widespread cultivation [89]. The TGPP is located in the southern end of the Flint Hills north of Pawhuska, Oklahoma (Figure 14).

As the name implies, the tallgrass prairie is dominated by tall warm-season grass species: big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), being the most characteristic. In general, the TGPP’s grasslands are consistent with most North American grassland floras having mostly broadly-distributed species and no endemics.

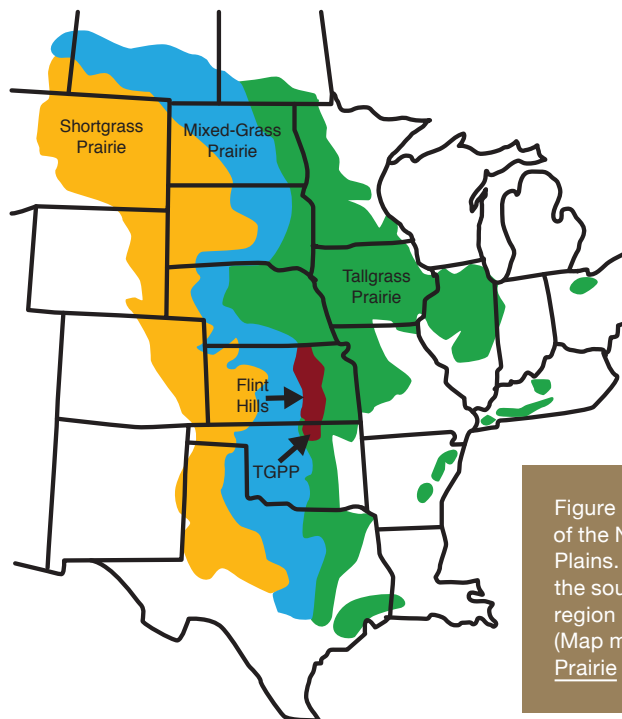


Figure 14. Locations of grasslands of the North American Great Plains. The TGPP is located at the southern end of the Flint Hills region (part of the tallgrass prairie). (Map modified from Tallgrass Prairie by John Madson, 1993).

5.11 Prairie biodiversity patterns

The tallgrass prairie is a dynamic system where vegetation and plant species composition is affected by a suite of variables. The variability and richness of the preserve makes it in many ways an exceptional place to evaluate questions regarding patterns of biodiversity. To better understand plant composition patterns across the preserve's changing landscape, Michael Palmer of Oklahoma State University established 10m by 10m permanent vegetation monitoring plots (informally referred to as VegMon) at every one kilometer intersection of the Universal Transverse Mercator grid. There are 276 VegMon plots at the preserve. Out of the 276, a random subset of 20 grassland plots are sampled each spring for plant species present and abundance estimated by percent cover. Using data from the VegMon plots Palmer et al. [107] determined that grassland species richness (number of species present) within the preserve is negatively correlated with soil calcium. In general, the more acidic the soil, the more species rich the area. Brokaw [15] noted that variation in species composition is also associated with the amount of organic matter (soil carbon) and phosphorous in the soil, though no causal relationship could be established.

Species richness may also change as a function of the heterogeneity of particular location. Palmer et al. [111, 108] developed the spectral variability hypothesis (SVH) to help predict locations of high plant species diversity. The SVH states that "species richness will be positively related to any objective measure of the variation in the spectral characteristics of a remotely sensed image" [111].

Using aerial photographs, Palmer et al. [108] assessed the spectral variability of the TGPP producing what essentially are maps of botanical uniqueness. Areas within the preserve that have high spectral variability include rock outcrops, forest edges, stream corridors, and areas of high relief; these are areas expected to contain unique botanical communities.

Other plant biodiversity studies at the TGPP include an analysis of communities emerging from prairie soil seed banks [109], a demonstration of artifacts in biodiversity statistics [110] and an evaluation of the species-area-time relationship [96].

5.12 Remote-sensing and grassland change

Aerial imagery is an important resource that can be utilized for monitoring land-use changes and estimating productivity of ecosystems. The studies discussed here incorporated imagery of the TGPP in work focused on understanding broad scale processes across the Great Plains.

Reed et al. [121] proposed a new method for assessing the onset of "greenness" across the North American grasslands by suggesting the establishment of threshold NDVI values to determine when the growing season begins. NDVI (normalized difference vegetation index) is a commonly used metric for assessing the vegetative condition of aerial imagery. Once threshold values

are surpassed Reed et al. [121] recommended continued vegetation monitoring by accumulating NDVI values throughout the growing season in order to more effectively monitor landscape change and compare productivity among years.

Tieszen et al. [166] measured NDVI in relation to C3 (cool-season grasses) and C4 (warm-season grasses) grass production and found that the Flint Hills region had the highest measures of NDVI as well as the earliest green-up of the 13 grassland cover classes assessed in their study. Tallgrass prairie primary productivity is primarily regulated by spring and summer precipitation [179]. At broader scales, long-term climate controls on grassland vegetation are primarily distinguished by the proportion of C3 versus C4 grass species present in the environment [128]. In particular, precipitation and average daily high temperatures in July best predict the percent of C4 species present in the environment [168].

Wylie et al. [178] took measurements of leaf area, biomass, and the fraction of photosynthetically absorbed light from plots within the preserve and generated a model using those variables and NDVI values computed from Landsat imagery to predict the biophysical parameters of those measured values across the whole preserve.

5.13 Fire and Management

Though seemingly wild and vast in appearance, the tallgrass prairie is in many ways a cultural landscape. In conjunction with climate and grazing animals (such as bison), people have been one of the primary factors in maintaining and managing the grassland landscape. The primary tool employed by people across history for tallgrass prairie management is fire. Native Americans burned the prairies for a variety of reasons, not least of which was to attract and concentrate game on the fresh growth available in recently burned patches thus facilitating hunting. In recent times, ranchers in the region continue the practice of burning the grasslands, albeit it in a different way and with the purpose of stimulating forage for cattle. The important differences in how fire is applied by ranchers today and how it was applied historically appear to be in the frequency of fire return intervals and the amount of heterogeneity generated in the landscape as a result of fire.

The common management practice throughout the Flint Hills region today consists of annual spring burning of all cattle pasturage followed by double stocking of cattle [153]. This practice creates a relatively uniform disturbance across the Flint Hills resulting in a homogeneous landscape [55]. Though an apparently economical management plan for cattle production [153], this practice depletes the natural environment by actively suppressing the inherent heterogeneity of the tallgrass prairie [55]. This loss of heterogeneity results in a loss of biodiversity.

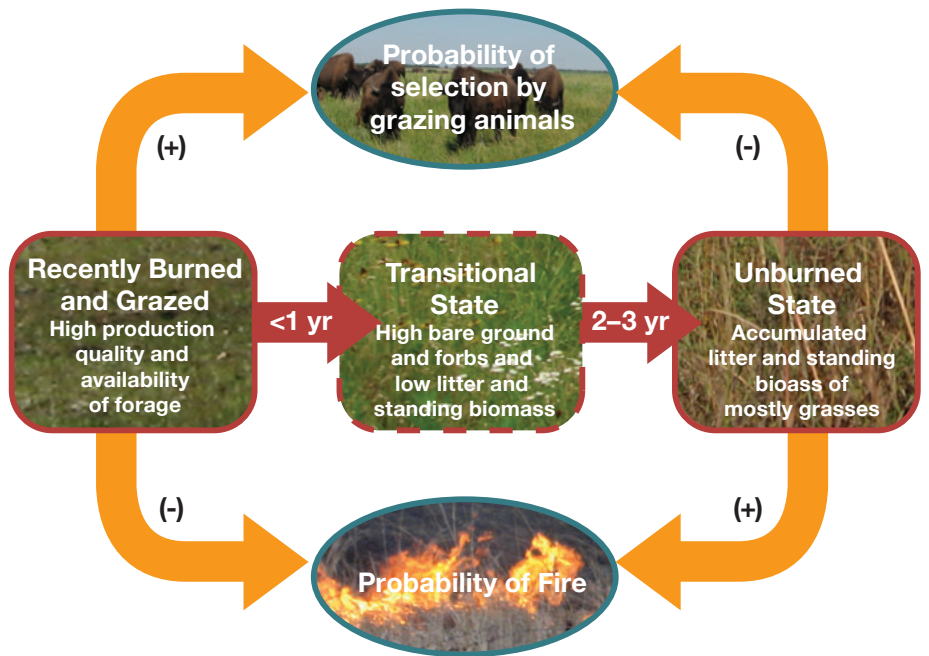


Figure 15. (Following reference #56) This conceptual model demonstrates the dynamics of a single patch within a shifting mosaic landscape. Fire and grazing (in ovals) represent the primary drivers while squares represent the ecosystem states within the patch as a function of time since disturbance. All states have the potential for fire or grazing, but may have higher or lower probabilities of this occurrence (orange arrows indicate positive (+) and negative (-) feedbacks) depending on plant community structure.

Tallgrass prairie vegetation varies in relation to soils, climate, grazing, time since fire, and season of fire [29], therefore the application of fire can be utilized to increase landscape variability. This idea encouraged Fuhlendorf and Engle [55] to argue for an alternative paradigm of rangeland management that seeks to actively increase grassland heterogeneity by basing management practices on evolutionary patterns of fire and grazing. Fire applied to a particular patch within an unburned landscape creates a grazing focal point as animals are attracted by the more palatable and nutritious regrowth [36] (Figure 15). This fire-grazing interaction

is taken advantage of at the TGPP through the discrete application of fire to create a spatially and temporally shifting mosaic of grassland patches with differing burn histories [63, 64] (Figure 15). This practice serves to increase landscape heterogeneity by increasing variability in vegetation structure, amount of litter accumulated, and plant species composition [56]. All of which may have positive implications for a variety of wildlife species (see wildlife chapters for further discussion). Other positive benefits include increased soil nitrogen availability under the fire-grazing interaction [2] and reduced spread of the exotic invasive *Lespedeza*

cuneata [56]. The Nature Conservancy's use of the fire-grazing interaction is an important component of their plan for capturing the full range of tallgrass prairie biodiversity and ensuring its conservation into the future at the TGPP. Fuhlendorf et al. [57] argue that the lessons learned at the TGPP have applications for ecosystems around the world that would be well served by restoring the evolutionary patterns of grazing and fire to increase landscape heterogeneity.

5.2 Cross Timbers

The Cross Timbers Forest is a long band of oak-dominated forest stretching from north Texas to southeastern Kansas [53]. Approximately 10% of the TGPP is forested, most of which is classified as Cross Timbers [64] (Figure 16). The Cross Timbers of the preserve is registered as a Research Natural Area by the Ancient Cross Timbers Consortium (more information may be found at <http://www.uark.edu/misc/xtimber>).

The dominant species of the Cross Timbers are post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*). Cross Timbers physiognomy consists of short stature trees in forest physiognomies ranging from dense oak thickets and closed canopy forest to open woodland and savanna-type environments; all of these are present at the TGPP. Trees within the Cross Timbers may be quite old; post oak can attain ages of 400+ years and blackjack 100+ years. Therrell and Stahle [163] developed a model based on the steep slopes and infertile soils where old trees are often found to predict the location of stands of ancient cross timbers in Osage County. After field testing the model they found that 74% of the locations predicted by the model to contain ancient forests did in fact have old trees. Within the preserve, most of the ancient stands of Cross Timbers are located along the eastern boundary.

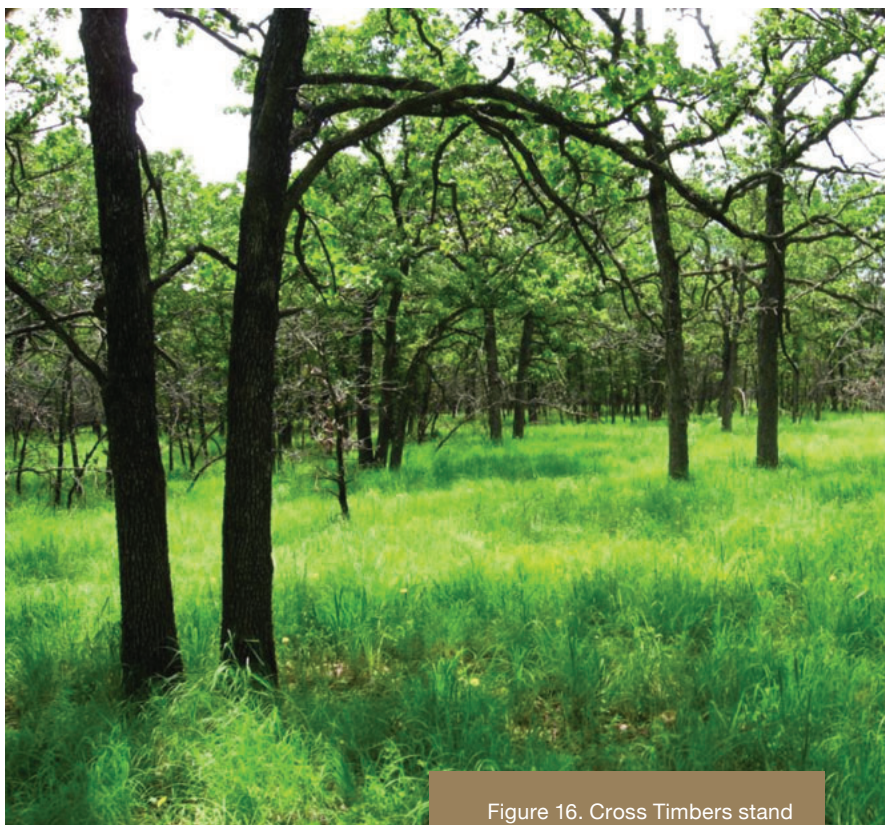


Figure 16. Cross Timbers stand on the eastern side of the TGPP.
Photo / Matt Allen

As stated above, the Cross Timbers are dominated by post oak and blackjack oak, and indeed, those are almost the only tree-species found in Cross Timbers-type stands. These two species often account for more than 95% of the trees in the forest [7, 147]. Arévalo [7] determined that within these stands, blackjack oak tends to be more distributed towards the forest edge and post oak in the forest interior, though the size-class distribution is not significantly different for edge and interior. Blackjack's edge preference is likely due to its higher drought tolerance [7]. In 1998, Arévalo and Palmer established a 4ha permanent plot within a Cross Timbers stand to monitor long-term forest dynamics. Data has yet to be published on the site, but a first resampling of the site in 2008 shows very little recruitment in the stand, slow growth rates, and a higher mortality rate for blackjack than post oak.

In 2003, a severe tornado struck a stand of Cross Timbers at the TGPP resulting in high levels of tree mortality. Shirakura et al. [147] assessed the damage and found that blackjack oak had a 12 times greater probability of mortality than post oak, resulting in a 53% loss of blackjack oak basal area as opposed to a 14.9% loss in basal area by post oak.

Fire is an important disturbance within the Cross Timbers, but fire-related mortality to Cross Timbers' oaks is generally low unless conditions and fuel permit a particularly intense fire [51]. Shirakura [146] collected post and blackjack oak cross-sections from trees killed by the aforementioned tornado in

order to assess the fire history of the site using fire scars in the tree-ring record (Figure 17). From 1947–2003, 29 fire events occurred at the site, giving a fire return interval of 1.35 years. Shirakura [146] determined that approximately 80% of those fires occurred during the dormant or very early growing season of the trees. Allen et al. is currently extending the fire history chronology of the preserve to the mid 1700s.

5.3 Plant Viruses

The presence and effects of viruses in non-cultivated plant species remains a scientific mystery. Approximately 77% of all known virus isolates come from cultivated species but only 6% are known from wild species [177]. Just as plants form mutually beneficial relationships with various bacteria and fungi, it seems likely that plants also



Figure 17. Post oak with multiple external fire scars.
Photo / Kiyoshi Sasaki

have important beneficial interactions with viruses, but this possibility is largely unexplored. In 2005, researchers from Oklahoma State University, the University of Oklahoma, and the Samuel Roberts Noble Foundation began collaboration on the EPSCoR funded Plant Virus Biodiversity and Ecology (PVBE) project to survey the biodiversity of plant viruses within the TGPP. This project was initiated to address two primary hypotheses: first, that there are many more viruses present in nature than are presently known and second, that most viruses do not produce obvious symptoms in their hosts [177]. Another, grander, purpose of the project was to help establish the discipline of plant virus ecology.

Since 2005, samples of most of the TGPP plant species have been collected for virus testing. Six species have received particular focus as a part of the virus project and have been collected annually in the areas around the VegMon plots at the TGPP (See section 5.11 for discussion of VegMon). Focal species are the forbs *Vernonia baldwinii* (ironweed), *Ambrosia psilostachya* (western ragweed), *Asclepias viridis* (antelope-horn milkweed), and *Ruellia humilis* (prairie petunia), and the grasses *Sorghastrum nutans* (indian grass), and *Panicum virgatum* (switchgrass).

The isolation of viruses from plants proved difficult and required the development of a new metagenomic method for virus extraction. Melcher et al. [98] using *Ambrosia psilostachya* specimens from the TGPP developed the virus-like particle-viral nucleic acid (VLP-VNA) method for virus extraction. The VLP-VNA approach resulted in solid evidence for at least four virus

species within *A. psilostachya*, none of which matched any previously known viruses. Muthukumar et al. [100] further applied the VLP-VNA technique on an additional 52 plant species and found 19% of them to contain RNA or DNA resembling those of viruses. Many plant specimens appeared to be infected by multiple virus species. Notably, Muthukumar et al. [100] found a new tymovirus species in six different plant species, including *Asclepias viridis* where it was particularly abundant. In the lab, Min et al. (in preparation) isolated this tymovirus and applied it to uninfected *Nicotiana benthamiana* (a tobacco relative that is the 'lab rat' of plant virology) and *A. viridis*. *N. benthamiana* developed typical viral infection symptoms while *A. viridis* remained asymptomatic, suggesting that it is either resistant to this virus or has some sort of special relationship with it. Results of these studies support the two primary hypotheses that there are many more viruses present in nature than previously known (approximately 100 putative viruses identified to date) and that often those viruses are asymptomatic.

In other PVBE work, Roossinck et al. [130] developed a double-stranded RNA method to identify signs of RNA viruses in plants. Not only did the method produce evidence supporting the hypotheses mentioned above, it was also able to find evidence of plant-associated viruses that were inaccessible to the VLP-VNA approach. Many of these viruses resemble fungal viruses in the Totiviridae and Partitiviridae families, a finding opening doors to the exploration of interactions between fungi, viruses, and plants.

Work on this project is ongoing; researchers are continuing to discover new viruses as their investigations on the role of viruses in the ecology of the TGPP progress. Spinoff projects continuing at the preserve include a survey of the bacterial endophytes of 10 plant species, a survey of the fungal endophytes (and the viruses of these endophytes) of *R. humilis* and *S. nutans*, and an investigation into the evolution and population dynamics of the newly discovered tymovirus. Given the large number of specimens collected over multiple years the potential exists for understanding the dynamics of virus populations over time and space within the preserve. The TGPP is certainly unique; few sites in the world have had the ecology of viruses so intensely investigated. Despite the volume of work accomplished, our knowledge of plant viruses within the preserve is still in its infancy; the discoveries made so far have raised new questions and fostered new collaborations among scientists which should ensure continued investigation into this subject in the coming years.

6. Mammals

At least 41 mammal species reside at the TGPP [117, 4] including its most emblematic species, the American bison. In the following section we summarize the large body of research conducted on TGPP bison and their effects on and responses to the tallgrass landscape. Additionally, we describe the few other studies that have focused on other mammal species found at the preserve.

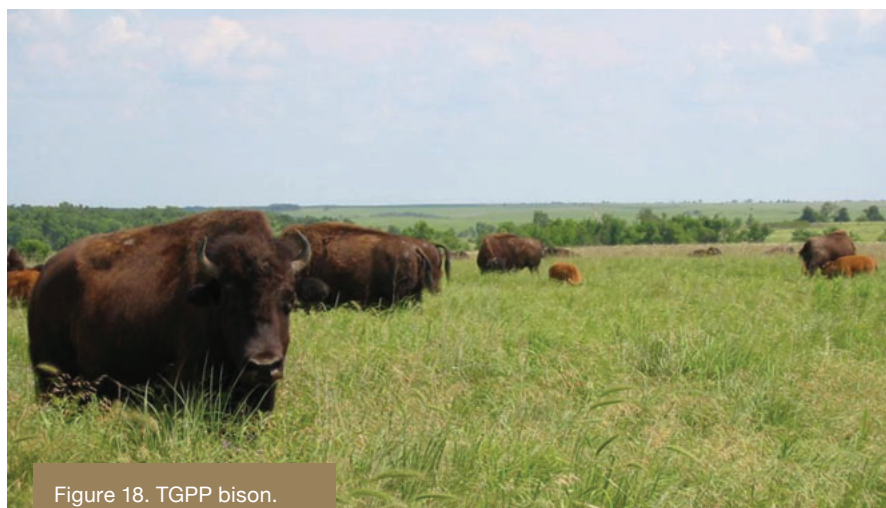


Figure 18. TGPP bison.
Photo / Bob Hamilton

6.1 American Bison

American bison (*Bison bison*) (Figure 18) are a hallmark of the North American Great Plains. Historically, these animals ranged in vast herds of perhaps millions of animals [139] throughout the prairies before nearing extinction during the latter part of the 19th century [73, 141]. Shaw and Lee [144] used accounts of early explorer and pioneer encounters with bison to show that for the first few decades of the 1800s the relative abundance of bison was lower in the tallgrass prairie region than in the rest of the Great Plains. Eventually bison disappeared

from the region by the 1830s [144]. The most stable bison populations, by those early accounts, existed farther west in the mixed grass region where conditions were buffered longer from European and American activities as well as Native American migration [144].

In October of 1993, The Nature Conservancy introduced 300 bison to a 1,960ha unit in the TGPP [62, 63]. By

the spring of 2008 the herd had grown to its target size of a summer herd of approximately 2,700 animals occupying 9,500ha [64]. The bison herd has access to the entire unit and is allowed to freely interact with the randomly selected burn patches within the unit. The Nature Conservancy has been utilizing bison for native grassland restoration since 1978 and as of early 2009 has plains bison on nine native grassland preserves in North and South Dakota, Iowa, Nebraska, Colorado, Kansas, and Oklahoma. Eight of these herds are owned and managed by The Nature Conservancy and one herd is owned

by Kansas State University. All are year-round resident herds. These nine herds total 5,643 head (over-wintering count) on 44,440ha of native rangeland.

The Nature Conservancy historically considered bison to be an ecological restoration tool, but increasingly it and other conservation entities are considering bison as a species conservation target. Since the late 1990s, these organizations have been actively involved in research on the genetic integrity of most large state and federal bison herds. These projects are particularly concerned with the potential long-term impact of cattle genes holding over from crossbreeding efforts in the late 1800s. All Nature Conservancy bison herds, along with several additional conservation herds, are currently involved in a bison genetics research project led by Dr. James Derr and Dr. Natalie Halbert of Texas A&M University. This project documented the cattle introgression status of the bison herds, looking at both the mitochondrial and nuclear DNA components. The entire TGPP bison herd was sampled from 2004-2009. The project finished in September of 2009 and several publications are anticipated. Continued and expanded investigation is certainly warranted in the interests of maintaining the integrity of this iconic and ecological important species.

Since the establishment of the herd, TGPP managers periodically introduced bison from other populations to enhance the genetic diversity of the bison population. In one such event, the Wichita Mountains National Wildlife Refuge donated 43 bison calves to the TGPP. Monitoring these introduced calves Coppedge et al. [28] found that other bison were initially more aggressive to the “orphan” calves

than to any of the resident bison. Over time, aggressive interactions decreased with no apparent long-term effect on the calves' health.

Bison are the largest animal in North America and consequently have a large impact on their environment. Coppedge and Shaw [35] found that horning and rubbing behavior in the TGPP resulted in severe damage or death to 4% of woody plants with moderate to light damage to an additional 25%. Bison showed strong preference for saplings of black willow (*Salix nigra*) making use of approximately 60% of the available saplings within the study area while killing 17% outright. The most common trees in the preserve, post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*), were significantly underutilized. Coppedge and Shaw concluded that bison rubbing and horning behavior may have historically had a strong effect on the distribution of woody vegetation in North American grasslands. Crockett and Engle [44] speculate that the burning of bison fecal pats may change the distribution of soil resources. Their analysis revealed that bison fecal pats produce up to 74,340kJ of heat per square meter (depending on season of burn), an amount significantly higher than most woody fuels. These small hot fires may create fine scale heterogeneity in soil properties across the prairie landscape.

Another study by Coppedge and Shaw [38] found that TGPP bison wallowing also has an important effect on the landscape. Adult bulls and cows exhibited the greatest propensity for wallowing. Wallowing appeared to primarily be a grooming and comfort behavior and was not found to be an aggressive action as witnessed in other

bison populations (perhaps due to the skewed sex ratio of the herd). Bison preferred to form new wallows on areas where spring or fall burns had occurred and on areas of moderate (4–7%) slope. Throughout the prairie landscape many depressions exist that had conventionally been assumed to be relict bison wallows. Coppedge et al. [30] showed that bison made no use of these pre-existing depressions. Soil analyses by Coppedge et al. [30] of active wallows and pre-existing soil depressions revealed that soil depressions usually occurred in soils of significantly greater bulk density, salt, and clay content, suggesting an origin due to the pedologic processes of clay pan formation rather than historic bison wallowing activity.

de la Fuente et al. [46] found that TGPP bison are naturally infected with *Anaplasma marginale*, a tick born pathogen that causes anaplasmosis (anemia and wasting) in cattle. Bison appeared to be primarily carriers of the pathogen, rarely exhibiting symptoms themselves. Disease transmission between bison and cattle is a concern for The Nature Conservancy, so the TGPP herd is given vaccinations during the herd's annual round-up.

A study by Rosas et al. [133] reported on the high diversity of seeds dispersed in bison hair (Figure 19) and feces. They found seeds from 76 plant species in the hair of TGPP bison. They also found significant differences in seed species composition among bison age-sex classes with bulls carrying more seeds of plants associated with bare areas, juveniles more seeds of plants from wetland plants, and cows more seeds of wetland shrubs, perhaps in relation to differences among these classes in terms of wallowing and foraging habits. Rosas



Figure 19. Bison with numerous cocklebur (*Xanthium strumarium*) caught in its hair.

Photo / Michael Palmer

et al. also discovered seeds from at least 70 species in bison dung. Surprisingly, only 53% of the total number of seeds and 39% of the diversity came from graminoids, indicating that bison are consuming significant amounts of forb fruits. This result is somewhat in contrast with earlier results by Coppedge et al. [32] where histological analysis of fecal samples revealed graminoids as the overwhelmingly preferred forage, constituting some 98% of their diet across all seasons. Clearly, more research is needed to clarify bison foraging preferences.

Bison grazing patterns are one of the better studied aspects of bison ecology at the TGPP. Tieszen [165] showed that the most nutritious forage is available during early green-up in the spring, when nitrogen is most available in the system. A study by Maichak et al. [93] on daily patterns of TGPP bison activity showed that bison forage primarily during the day, but may reduce activity when high ambient temperatures induce thermoregulatory stress. Most studies of grazing preferences highlight the importance of graminoids for bison.

For example, Coppedge et al. [32] showed that sedges are favored in the spring and winter comprising 17% of the bison's diet. Sedge consumption, however, differs amongst bison social groups during this time as bull groups seem to continue to emphasize maximizing intake rates while mixed groups of cows focus on forage nutrition by selecting the more nutritious sedges [37]. Analysis of carbon isotopes in bison hair by Rosas et al. [132] supported this result showing that bison bulls tend to consume more C4 grasses than



Figure 20. Bison grazing a recently burned patch in the spring at the TGPP.
Photo /Matt Allen

cows or juveniles. These differences in foraging patterns amongst bison genders and groups may have important consequences on vegetation composition and structure, particularly since the TGPP herd is female skewed [132]. As of yet, this has not been specifically assessed. Hoppe et al. [72] also used carbon isotopes to assess the amount $\delta^{13}\text{C}$ assimilated in bison tooth enamel in relation to the proportion of C4 grasses available in the environment. They found a strong correlation of $\delta^{13}\text{C}$ and the abundance of C4 grasses, suggesting these techniques might be further extended in the reconstruction of grassland C3/C4 ratios from fossilized bison teeth. In related work, Hoppe [71] found that oxygen isotope ratios in bison enamel correlated well with local surface waters and precipitation, again suggesting a useful application in the reconstruction of paleoclimates.

The aspect of bison ecology that has received the most attention at the TGPP is the interaction of grazing with fire. Bison preferentially graze areas burned recently [36, 10] (Figure 20). Coppedge and Shaw [36] found that in relation to availability, summer burns are particularly attractive for bison as they provide a new round of regrowth in a landscape where most vegetation is reaching maturity and therefore less nutritious. Biondini et al. [10] compared the TGPP herd with bison populations in more northern latitudes and found that TGPP bison exhibit increased choice for burned sites in the dormant season, likely because of the persistent fall and winter regrowth possible in these lower climes. Wallace and Crosthwaite [169] showed that the size of the area burned has a non-significant effect on bison grazing intensity; though

smaller patches do tend to be slightly more intensely grazed. The amount of area burned has little effect on the amount of weight gained by bison calves and yearlings, though the timing and amount of precipitation is important for bison weight gain [42]. Craine et al. [42] found that for every 100mm of precipitation in mid-summer bison calves and yearlings were 9.7–17.3kg lighter presumably because of higher stem production (hypothetically resulting in lower nutritional quality, though more research is needed on this point). Conversely, for every additional 100mm of precipitation in late-summer bison were 6.4–15.3kg heavier.

The process of bison grazing as it relates to fire is central to The Nature Conservancy's management of the TGPP. Through grazing and fire preserve managers seek to create a spatiotemporally shifting mosaic of burned and grazed areas on the prairie landscape [63, 64] thus restoring the historical processes responsible for the maintenance of this grassland system [55]. The utility of the fire-grazing interaction for increasing the heterogeneity and diversity of grasslands is one of the primary ideas exported by the TGPP and was proposed by Fuhlendorf and Engle [55] as a paradigm for the management of rangelands throughout the Great Plains.

6.2 Other studies of mammals

The preserve hosts a few regionally uncommon mammal species. Payne and Caire [115] captured 10 cotton mice (*Peromyscus gossypinus*) representing a new northwestern extension to their distribution. Thies et al. [164] captured 12 individuals of eastern harvest mice (*Reithrodontomys humilis*), establishing a new western extension to their range.

Though never visually confirmed, Payne [114] reported evidence of at least one mountain lion (*Felix concolor*) to have been present within the preserve.

Payne and Caire [116] compared the diversity of small mammal species in the preserve's various habitat types. They found that grasslands were the richest with 13 species encountered. All other habitats contained 6–9 species and represented a subset of those found in the grasslands.

An epidemiological survey by Nisbett et al. [101] found four small mammal species at the TGPP serologically positive for antibodies of the Sin Nombre virus. This virus is the primary agent of hantavirus pulmonary syndrome in humans.

Smith-Patten et al. [150] found 18 mammal species in their study of roadkill rates for different mammals. They also found that unpaved roads (such as those on the preserve) tended to have lower numbers of roadkill than paved roads. Several species (i.e.—armadillo, opossum, striped skunk, and raccoon) showed distinct mortality peaks during the season coincident with dispersal activities during their reproductive cycles.

Maichak and Schuler [92] tested a new technique for estimating wildlife population size from road counts. Instead of taking field measurements of visible area, they used a viewshed analysis extension in Arcview GIS to calculate visible area and determine an optimal driving route. They tested this technique on the preserve's bison and determined that 99% of bison group locations occurred within the viewshed. Their population estimates were not significantly different from the true bison population number.

7. Birds

The TGPP provides important habitat for many declining grassland bird species. Its conservation value for birds is confirmed by the presence of a large breeding population of the rare Henslow's Sparrow (*Ammodramus henslowii*) [167, 125]. Additionally, other regionally uncommon species such as the Common Poorwill (*Phalaenoptilus nuttalli*) and Short-eared Owl (*Asio flammeus*) have nested within the preserve [59, 13]. As of 2009, 210 bird species comprise the TGPP bird checklist [3] giving it the highest observed bird species richness of any Nature Conservancy preserve in Oklahoma [3]. Regionally, this diversity is increasingly threatened due to loss or conversion of grasslands and/or management practices that provide unsuitable grassland bird habitat [174]. These changes appear to be inducing precipitous population declines in many grassland bird species within the Flint Hills causing uncertainty as to whether enough grassland habitat remains to maintain viable grassland bird populations [174]. Consequently, the habitat requirements and responses of grassland birds to various management regimes is an area of considerable attention by TGPP researchers.

7.1 Henslow's Sparrow

As mentioned above, Henslow's sparrow (*Ammodramus henslowii*) is a rare grassland bird that is currently classified as "near threatened" on the IUCN Red List [11]. From 1992–1996, Reinking et al. [126, 127] documented the existence of a breeding population of hundreds to thousands of Henslow's Sparrow on the TGPP making it one of the largest known populations of Henslow's Sparrow in North America. From a sample of 24 nests found during their

study, they observed that Henslow's Sparrow always nest in areas of tall dead standing grass (usually areas more than 2 years post burn); 45% of those nests were successful in fledging at least one young. Herkert et al. [69] found that the daily risk of nest predation for Henslow's Sparrow decreases with the size of the prairie fragment, suggesting that larger fragments are needed for species viability. For the TGPP they found that Henslow's Sparrows experience approximately a 4% daily chance of being depredated and a 9% daily chance of having their nest parasitized by the brood parasite Brown-headed Cowbird (*Molothrus ater*). Due to the secrecy and rarity of Henslow's Sparrow, its range, population dynamics, and basic biology are not yet clearly understood [122]. The particular habitat requirements Henslow's Sparrows have for nesting are generally not found in the annually burned Flint Hills, explaining the rarity of this species. The spatially and temporally heterogeneous burning program employed at the TGPP provides the necessary vegetation structure for Henslow's Sparrows to nest (See section 7.3 for further discussion on burning and birds).

7.2 Greater Prairie-Chicken

Historically common in the southern plains [9], the Greater Prairie-Chicken (*Tympanuchus cupido*) (Figure 21) is presently listed as vulnerable on the IUCN Redlist [12]. Habitat loss, woody invasion in grasslands, poor grazing management, and herbicide and insecticide use have all contributed to Greater Prairie-Chicken decline [9]. Greater Prairie-Chicken mostly use unburned areas with standing cover for foraging and nesting, but they also require areas of short-stature grass

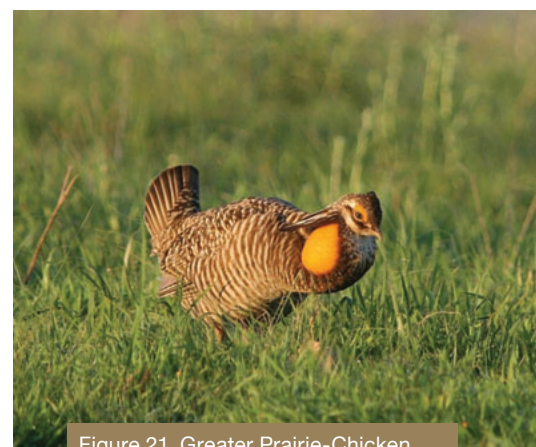


Figure 21. Greater Prairie-Chicken.
Photo / Dan L. Reinking

(often resulting from fire) for lekking [172]. A four year study by Wiedenfeld et al. [172] determined the success of a nest to fledge at least one young ranged from 11% to 31% depending on year with a 24% average over the whole study period. Patten et al. [112] found that Greater Prairie-Chicken only established leks on areas less than 200m from unburned prairie; a spatial arrangement which may be largely unavailable with the common fire practices used in the Flint Hills today (for more discussion on fire and birds see section 7.3). Threats to the Greater Prairie-Chicken population are still increasing. Due to the propensity of these birds to avoid vertical structures [118] (thought to be a behavioral adaptation to avoid predation by perching predators), the continued expansion and pressure for wind energy development in this region constitutes a threat for Greater Prairie-Chickens since these windfarms are often built in prime Greater Prairie-Chicken habitat [9, 119, 118]. Nature Conservancy staff survey the preserve's Greater Prairie-Chicken population each spring. All leks are

located and mapped and the number of birds on each lek is determined by flush counts. Since 1991, the TGPP population has ranged from 56 to 126 birds on the lekking sites [65].

7.3 Grassland birds in a dynamic landscape

As described by With et al. [174], changes in the North American grasslands resulting from fragmentation, development, or environmentally detrimental management techniques have resulted in severe consequences for the viability of grassland bird populations. The challenges grassland birds face in the changing grassland landscape is reflected in TGPP research. Most ornithological research at the TGPP has focused on how birds and bird communities respond to various environmental stimuli.

Brood parasitism by the Brown-headed Cowbird is one factor reducing nest success in the Flint Hills region. Herkert et al. [69] found a strong positive relationship between the rate of brood parasitism and the regional Brown-headed Cowbird abundance, though the effect may be reduced for some species (i.e., Eastern Meadowlark (*Sturnella magna*)) depending on grassland area. After surveying across the Flint Hills region Jensen and Cully [86] found that as latitude increases so does Brown-headed Cowbird abundance and, not surprisingly, so also the rate of brood parasitism. Nests surveyed in the northern range of the Flint Hills were 80–90% parasitized while only 5% of nests in the TGPP (southern Flint Hills) were parasitized. Reasons for higher cowbird abundance in the northern Flint Hills remain unclear. In general, nests located close to wooded edges have higher

nest parasitism rates [85] and also those within intensively grazed pastures [113, 120]. Nests located in pastures managed with the patch-burn method show reduced rates of brood parasitism [31].

Much of the tallgrass prairie pasturage within the Flint Hills region is burned annually and double-stocked with cattle [153] resulting in uniform intense grazing across the landscape. Though fire is important within the tallgrass prairie landscape, the homogenizing effect of this particular management regime has deleterious effects for grassland birds [123, 124]. Rohrbaugh et al. [129] found more nests of Eastern Meadowlark, Grasshopper Sparrow (*Ammodramus savannarum*), and Dickcissel (*Spiza americana*) in burned and grazed areas than in undisturbed areas, but their nesting success was lower in the disturbed areas. Similarly, Hendricks and Reinking [68] found lower nest predation in areas left unburned. As explained by Shochat et al. [148] the propensity for grassland, ground nesting species to nest in burned areas constitutes an ecological trap where the cues birds use for selecting appropriate habitat are decoupled from the actual suitability of that habitat. Using data from the TGPP and surrounding areas Shochat et al. [148] explain that this ecological trap likely arises from the annual spring burning practice. Areas managed with annual fire and intensive grazing had high arthropod abundances making them attractive to birds, but also low cover and much higher reptile nest predator abundances. Predation accounted for 77.5%

of the 1327 nest failures observed in their study. Across the Flint Hills native hay meadows often serve as the only ungrazed grassland habitat available for birds where they might experience a higher chance of nest success [120].

In light of the apparent unsuitability of the present regional management practices for grassland birds, several studies have assessed grassland bird response to patch-burning. Churchwell et al. [24] noted that pastures managed with patch-burning yielded lower rates of nest parasitism and predation for Dickcissel than pastures managed with the traditional system. Coppedge et al. [31] determined that these positive effects of patch-burning hold at the community level as well with patch-burned pastures having higher grassland bird richness and diversity. Coppedge et al. [31] also found that Henslow's Sparrow was entirely absent from traditionally managed pastures, but was found in patch-burned pastures. Fuhlendorf et al. [58] explain that the structurally and compositionally diverse vegetation arising from the patch-burn method provides the broad range of habitat needed for grassland bird species to succeed. Notably, this method provides the range of habitat needed for the Greater Prairie-Chicken which, as described above, uses unburned areas for nesting and recently burned areas with low grass stature for lekking [172, 112]. Traditional management is focused towards generating habitat homogeneity, and as a result poor habitat for grassland birds.

7.4 Other studies of avian ecology

Artificial nests are often used in studies of nest predation, but their utility in accurately estimating nest predation had gone unevaluated in grassland environments subjected to burning. Hendricks and Reinking [68] compared artificial and real nest predation rates in burned and unburned environments and found no significant difference (though artificial nests generally had lower predation rates) between the two nest types. They also observed no clear trend for the predation rate of nests placed in burned and unburned pastures.

Coppedge et al. [39] used artificial nests to assess how egg size and nest olfactory attributes affect nest predation. They found no difference in predation rates for nests baited with house sparrow (*Passer domesticus*) feathers (an olfactory cue) than nests left unbaited. In contrast, egg size was an important factor in the rate of nest predation in grasslands. Nests baited with small house sparrow eggs suffered up 75% loss while eggs baited with larger quail or chicken eggs had only 5% cumulative losses. In a rare instance, Coppedge [27] discovered an artificial nest parasitized by at least one Brown-headed Cowbird.

Wolfe [175] noted several instances of female nest competition or nest sharing in the Eastern Meadowlark. This in some instances resulted in the ejection of the eggs of one female.

Shochat et al. [149] examined the effects of different management (burned or unburned) along roadsides on all species of birds found nesting there. They observed an increase in nest success in burned areas. This higher success was probably due to the greater arthropod density and biomass they found along the burned roadsides. Nest success, however, varied greatly depending on nesting habit; ground nesting birds suffered approximately 90% nest failure while shrub and tree nesting birds experienced 50-70% failure.

Frey et al. [54] measured nest success as a function of topographic position for Grasshopper Sparrow, Dickcissel, and Eastern Meadowlark. They found topography to be at most only indirectly related to nest success. Nest success was positively related to increasing vertical vegetation structure, which might in part be mediated by the productivity of the particular slope.

Long et al. [90] examined the orientation of Grasshopper Sparrow and Meadowlark nest openings in relation to prevailing wind direction. Both species of birds are ground nesters and construct dome-shaped nests. The nest openings were usually oriented facing the northeast, while the prevailing winds during the study were from the south-southeast. Possible reasons for constructing the nests in this way included improved thermoregulatory capacity of the nest, better aerodynamic configuration, and solar radiation avoidance.

Schook et al. [137] studied the spatial patterns of song sharing in Dickcissel across the Flint Hills region. In their study they found that individual males tend to sing the same song elements both within and between years. At local scales, songs were similar and predictably declined with greater distance. At scales surpassing 10km, song sharing was either low or absent. The Dickcissel song is characterized by two elements, the dick and cissel elements. Interestingly, those song elements differed in the spatial scale of sharing observed; i.e., one element might be shared at a broader scale depending on the site.

8. Reptiles, Amphibians and Fish

The TGPP is host to 56 reptiles and amphibian species [5]. Surprisingly, no studies have been conducted at the TGPP involving reptiles or amphibians.

A few studies have been conducted on fish at the TGPP. The assemblage of fish species at the TGPP is representative of both the Ozark and Ouachita uplands as well as the Osage Plains [157]. However, within a given stream, fish species assemblages may vary as a function of stream order, habitat, and number and/or kinds of predatory fish [155]. In total, Stewart et al. [157] documented the presence of 23 fish species on the preserve. In general, water quality within the preserve's streams is high [8], as indicated by nitrogen and phosphorous limitations within the streams [94].

The principal waterway of the TGPP is Sand Creek, with its main tributary being Wild Hog Creek. In most years, the flow in these streams is intermittent, though pools may be found year-round up and down the drainages. The higher reaches of these streams typically exhibit more variability, with greater fluctuations in flow, temperature and conductivity [156]. Spranza and Stanley [156] examined the growth, condition,

and reproductive strategies of fish in both the higher and lower basins of Wild Hog Creek, and found that though water conditions were more stressful in the upper reaches of the stream, fish condition and growth was higher than in the more stable lower basins. They speculated that, in this case, water condition was not a limiting variable, and that higher primary productivity in the upper basins due to increased sunlight from a lack of shade trees and a noted lack of predatory fish may allow for increased fish vigor in the upper reaches. Though the upper and lower basins were separated by less than a kilometer, Spranza and Stanley [156] observed distinct reproductive strategies between the two basins. The upper basin fish employed a "bet-hedging" reproductive cycle where multiple cohorts of juvenile fish were observed during the study period, likely to cope with the higher variability of the upper basin environment. In contrast, the stable conditions present in the lower basin allowed the fish to make a single reproductive investment producing one large cohort.

9. Invertebrates

Prairies are great repositories of invertebrate diversity and the TGPP is no exception. Fay [52] captured 379 invertebrate taxa representing seven different orders. Arenz [6] encountered 74 butterfly species (Figure 22), 18 of which are believed to be dependent on remnant prairies. Smith-Patten et al. [151] found 55 species of *Odonata* (dragonflies) in the TGPP area. Hunt and Stanley [79] reported greater richness and abundances of hyporheic invertebrates in the TGPP's Wild Hog Creek than all the other Oklahoma prairie streams surveyed in their study. Bass [8] found 134 aquatic macroinvertebrate taxa in the drainages of Sand Creek, many of which are species relatively intolerant to pollution. Of this diversity of taxa, only two have received specific attention at the TGPP: termites and the prairie mole cricket.

9.1 Subterranean Termites

Brown et al. [19, 17] examined populations of four different termite species to reevaluate diagnostic morphological characteristics used in taxonomic identification. From their analyses they identified nine characteristics useful for distinguishing between species. They also used genetic analysis for independent verification and found that these characters resulted in 100% accuracy in the segregation of two termite species, *Reticulitermes tibialis* and *R. hageni*, but provided less than 90% accuracy in segregating *R. flavipes* from *R. virginicus* which appeared to show some degree of interspecific overlap in their physical characteristics.

A separate study by Brown et al. [18] estimated termite colony size and foraging territory in the TGPP. In this study they color-dyed termites from three colonies by feeding them differently colored papers and thereby allowing them to conduct mark-recapture techniques. Though their results varied, foraging population estimates ranged from approximately 10,000 individuals to 180,000 individuals per colony indicating these are relatively small colonies compared with those found in other environments such as urban and industrial areas. Foraging area ranged from 9m² to 92.3m² [18]. They also found that at least 2.6–4.46% of

the foraging populations were soldier termites and that these soldiers tended to occupy the more central portion of the foraging area. The higher concentration of soldiers in this central indicates that the primary queen may also be centrally located. This is because a primary role of the soldiers is to protect the founding queen and thus preserve the colonies' reproductive potential.

Several additional subterranean termite studies are ongoing at the TGPP. These studies address the impact of termites on plant and soil factors within the tallgrass prairie.



Figure 22. Butterfly on *Echinacea pallida*.
Photo / Matt Allen



Figure 23. Prairie mole cricket.

Photo / Dan Howard

9.2 Prairie Mole Cricket

The largest of North American crickets, the prairie mole cricket (*Gryllotalpa major*) (Figure 23) is one of the few endemics of the southern tallgrass prairie and is probably the single best studied invertebrate at the TGPP. It is also potentially threatened, with remaining populations known to only a few tallgrass prairie remnants. Presently the species is listed as “data deficient” by the International Union for Conservation of Nature [82] indicating a need for future research on the conservation status of this species.

Research on prairie mole crickets at the TGPP has primarily focused on male prairie mole cricket calling and lekking behaviors. Howard and Hill [74] assessed the cricket’s song characteristics in relation to morphological characteristics of and found a negative relationship between body length and the dominant frequency of the song and a positive relationship between body length and the number of syllables per chirp. In other words, larger male crickets produced lower frequency songs, with more syllables. Notably, larger crickets did not produce louder songs. The role

of these factors in attracting females is unknown. Howard and Hill [77] also assessed cricket hearing in relation to their spatial arrangement and found that males usually constructed burrows out of hearing distance of the higher harmonics of their neighbors’ calls, suggesting that the highest harmonic overtones probably do not contribute significantly to male-male spacing. It is possible that female prairie mole crickets are able to use harmonic content of the calls to gauge distance and thus assess proximity to a particular male. The grass height and biomass at a lek site are also correlated with the spatial distributions of lekking males, who are spaced further apart when the grass is taller and biomass is greater. This spacing presumably helps minimize female confusion as to the call source in thicker vegetation [76]. Additionally, the crickets modify the construction of their burrows in heavier vegetation, presumably to enhance the acoustic signature of their call [76]. Prairie mole crickets seem to construct their calling chambers in areas of a particular post-burn age. Howard and Hill [75] found that 60% of male crickets at the TGPP were in areas that had been burned less than 11 months and 90% in areas that had been burned less than 20 months previously, suggesting that these species depend on periodic fires to provide appropriate lek sites. Finally, even though soil characteristics are an important predictor of whether habitat is suitable for prairie mole cricket burrow construction, Hill et al. [70] found no differences in soil microhabitat attributes that would explain the aggregation of advertising males in lek areas.

9.3 Other studies of invertebrates

Fay [52] compared the invertebrate diversity of management units within The Nature Conservancy’s TGPP and Niobrara Valley Preserve in northern Nebraska. At both sites, invertebrate diversity was highest in heterogeneously managed bison units and lowest in cattle grazed units. At the TGPP insect diversity was highest in the burn patches, but at the Niobrara Valley Preserve, invertebrate diversity was low in burned patches, likely because grazing pressure was much more intense at the Niobrara Valley Preserve.

DeRennaux and Palmer are developing a collection of leafhopper and planthopper specimens found at the preserve. These invertebrates feed on the phloem of plants and so might potentially be an important vector for plant viruses (see Section 5.3).

Howard and Hall (in preparation) describe the population structure, habitat preferences and movement patterns of a newly discovered population of American burying beetles (*Nicrophorus americanus*) located at the TGPP during a preserve-wide survey conducted in July 2009. 415 beetles were captured over 16 days, with the largest numbers of these critically endangered beetles located in savannah and grassland areas along the Sand Creek watershed. Few beetles were captured in dense forest stands. Individuals dispersed an average of 809 meters/day.

10. Oil and Brine Remediation

Given the preserve's long oil-production history, it is not surprising that a number of petroleum spills have occurred at the preserve. Most spills at the TGPP result from leaks due to aging infrastructure. Pumping oil at the TGPP also brings up underground saltwater brine, usually at a ratio of 10–15 parts brine and one part oil [160]. The brine-oil mixture is pumped into tanks where the two liquids are separated so that the brine can be disposed of by reinjecting it into the rock strata. The risk of brine spill occurrence is generally higher due to corrosion caused by saline water in steel pipes and tanks [181]. Most of the spill sites at the TGPP are relatively small in area, around a few hundred square meters, though some are larger. Some brine scars at the TGPP have been present for decades and can be seen in aerial photographs from as far back as the 1930s [161].

Both brine and petroleum spills result in ecological problems. Increases in soil salinity from the spilled brine can result in an osmotic imbalance causing vegetation death within impacted areas (as seen in [67]) because plant roots can no longer withdraw water from the soil. The excess sodium ion in the brine also causes a loss of soil structure due to dispersal and tight packing of clay particles. Petroleum adversely affects soil nutrient cycling and structure, reducing plant productivity and viability [159]. Subsequent loss of vegetation increases erosion thereby elevating the probability of contaminants being transported elsewhere.

10.1 Bioremediation of oil spills

Since the mid-1990s, University of Tulsa researchers have been actively investigating oil sites at the TGPP in order to develop new cost-effective remediation techniques. The primary technique investigated at the TGPP is in situ “landfarming” which includes tillage and fertilization in order to improve soil structure and fertility. Undisturbed tallgrass prairie soils naturally have high levels of denitrifying microbes, indicating only a small amount of fertilization is needed to stimulation bioremediation [48]. Duncan et al. [50] assessed bioavailability of petrochemicals using semipermeable membrane devices and solid phase microextraction fibres, both of which accumulated petroleum hydrocarbons, indicating they are a good tool for determining the amount of petroleum hydrocarbons biologically available for degradation.

In oil spill sites, many soil microbes are capable of digesting petroleum hydrocarbons, but may require some fertilization to promote growth and initiate the degradation process [48]. Duncan et al. [48] determined that nitrous oxide emissions from soils may be a good measure of the amount of nitrogen fertilizer needed for a particular spill site. The first year of bioremediation is generally when most petroleum degradation occurs as all the easily metabolized hydrocarbons are used up [49]. Duncan

et al. [49] observed a significant peak in methane production during the first year of remediation, indicating it is an important part of hydrocarbon degradation. Sublette et al. [159] found that six years after an oil spill, very little petroleum hydrocarbons remained in bioremediated sites, though some residual contamination of unidentified methylene chloride extractable material did occur. In addition, Sublette et al. [159] observed no acute toxicity remaining in sunflowers within the remediated spill-zone; seed set and germination for *Helianthus maximiliani* were not



significantly different from individuals in control areas. Sublette et al. [159] monitored soil ecosystem recovery utilizing a number of ecological indicators. They found that nematode community structure was the most sensitive measure of the contaminated soil's recovery. Though recovery of the soil ecosystem may be accelerated by a fertilizer amendment, differences in soil chemistry, bacterial populations, nematode populations, and plant community composition persist for several years even after petroleum hydrocarbons have been reduced to a negligible level [47].

10.2 Brine remediation

Brine remediation has also been a target of University of Tulsa researchers; several studies have focused on methods of reducing soil salinity following a spill. Brine cannot be biodegraded, so effective remediation of brine spill sites must focus on transporting the salts out of the root zone. A study by Harris et al. [67] resulted in the recommendation a two-step landfarming process for brine remediation. In their study they first tilled native prairie hay into the soil at the spill site to improve soil porosity

(Figure 24), which resulted in enhanced drainage of salts out of the root-zone. Additionally, the hay served as an added seed source for the contaminated site. In sites that are heavily contaminated with brine and where tilling proves insufficient, they recommended the installation of a sub-surface drainage system to facilitate salt drainage from the soil. Over time, the microbial community structure of remediated brine spill sites approached pre-spill levels [160].

10.3 Spill prevention

Though the above techniques are relatively cost-efficient and easy to implement in the remediation of brine and oil spill sites, they do nothing to predict or prevent the actual occurrence of a spill. Jager et al. [83] developed models to help predict the spatial distribution of brine spills in landscapes with varying densities of oil wells. These models may be extrapolated to help identify sensitive areas of the landscape. Zambrano et al. [181] utilized probabilistic reliability modeling to identify spill risks during oil production. Their models identified corrosion as the largest cause of failure for oil-pumping machinery and storage equipment. Within a given time horizon, these models generated failure probabilities for the various pieces of oil equipment, indicating which items would be most likely to fail and cause a spill.



Figure 24. Soil tillage is an effective measure to improve soil structure and enhance brine drainage in contaminated sites.

Photo / Kerry Sublette

11. Conclusion

Twenty years of research at the TGPP has produced a significant body of research yielding important insights for both basic and applied science. This body of work demonstrates not only the value of the TGPP as a scientific and educational resource but also its importance as a protector of tallgrass prairie biodiversity. From the biochemistry of plant viruses to landscape-scale processes involving fire and grazing, research at the TGPP is increasing our understanding of biological processes within the tallgrass prairie landscape. The results of these inquiries will continue to inspire new ideas for both scientists and land-managers alike.

Despite the volume of work accomplished so far, there is certainly opportunity for new and expanded work at the TGPP. The unique status of the TGPP as the largest protected area of tallgrass prairie in North America affords an opportunity for understanding the tallgrass prairie ecosystem that may be found nowhere else. Additionally, the preserve presents the opportunity to understand the flora and fauna of the tallgrass prairie in the

context of a management program that emphasizes landscape heterogeneity through the manipulation of fire and grazing. Though much work has been accomplished on this front, much remains to be understood. By way of example, the preserve's reptiles and amphibians have yet to be studied at the TGPP in any context. Additionally, very few species at the TGPP have been subject to direct study. Certainly much can be learned from species-specific responses and interactions within the TGPP's ecosystems. Long-term studies will continue to help understand the dynamics of the tallgrass prairie and will facilitate better preparation for an always unknown future.

It is the authors' hope that this document has not only acquainted the reader with the work that has been so far accomplished at the TGPP, but that it will inform them of the possibilities inherent in continued work at the TGPP. Our hope and expectation is that research at the TGPP will be even more productive over the next two decades as researchers continue to explore and investigate the diversity of the tallgrass prairie.

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Soil from three lysimeters (one contaminated with oil (O), one contaminated with oil and fertilized (OF), and one control (C)) was evaluated for long term effects of contamination and bioremediation. The OF lysimeter showed a higher level of bioremediation with lower levels of petroleum hydrocarbons and a more fully restored ecosystem. Five years

post contamination treated lysimeters (O and OF) still differed from the C lysimeter in terms of soil properties and communities.

48. **Duncan, K., E. Jennings, S. Hettenbach, W. Potter, K. Sublette, G. Subramaniam, and R. Narasimhan.** 1998. *Nitrogen cycling and nitric oxide emissions in oil-impacted prairie soils.* *Bioremediation Journal* 1:195–208.

Application of fertilizer to an oil contaminated site at the TGPP resulted in higher levels of microbial nitrogen metabolism and cycling and evaluation of soil nitrous oxide emissions indicated their utility as a measure of the amount of fertilizer needed to stimulate bioremediation. Excessive fertilizer application can have deleterious effects on bioremediation, and reduce overall remediation efficiency.

49. **Duncan, K., R. Kolhatkar, G. Subramaniam, R. Narasimhan, E. Jennings, S. Hettenbach, A. Brown, C. McComas, W. Potter, and K. Sublette.** 1999. *Microbial dynamics of oil-impacted prairie soil.* *Applied Biochemistry and Biotechnology* 77–79:421–434.

This study evaluated levels of soil microbial activity during two years post oil contamination. Overtime the rate of petroleum hydrocarbon decreased, with most of the easily digestible petroleum hydrocarbons degraded during the first year. Methane formation was clearly stimulated during the first year, suggesting it is an important component of hydrocarbon degradation.

50. **Duncan, K. E., M. Carey, J. B. Wells, and R. P. Lanno.** 1999. Assessing the bioavailability of petrochemicals in soils using chemical and biological measures in Proceedings of the 6th International Petroleum Environmental Conference.

Semipermeable membrane devices (SPMD) and solid phase microextraction fibres were evaluated in terms of their ability to assess the bioavailability of petroleum hydrocarbons. The SPMDs were shown to accumulate petroleum hydrocarbons.

51. **Engle, D. M., T. G. Bidwell, and R. E. Masters.** 1996. *Restoring cross timbers ecosystems with fire.* Pages 190–199 in Transactions of the 61st North American Wildlife and Nature Resources Conference.

Evaluation of Cross Timbers stands revealed that oaks rarely suffer significant scorch or mortality from prescribed fire unless conditions permit an unusually intense fire.

52. **Fay, P. A.** 2003. *Insect diversity in two burned and grazed grasslands.* *Environmental Entomology* 32:1099–1104.

Study of insect diversity at The Nature Conservancy's Niobrara Valley Preserve and the TGPP yielded 379 taxa representing seven different orders for the TGPP. Within each preserve, insect diversity was highest in units managed heterogeneously with fire and bison grazing.

53. **Francaviglia, R. V.** 2000. *The cast iron forest: A natural and cultural history of the North American Cross Timbers.* University of Texas Press. Austin, Texas, USA.

54. **Frey, C. M., W. E. Jensen, and K. A. With.** 2008. *Topographic patterns of nest placement and habitat quality for grassland birds in tallgrass prairie.* *American Midland Naturalist* 160:220–234.

This study observed no direct effect of topography on nest success. Topography may, however, mediate vegetation structure which was correlated with nest success.

55. **Fuhlendorf, S. D. and D. M. Engle.** 2001. *Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns.* *Bioscience* 51:625–632.

Here, the authors propose a new paradigm for rangeland management that seeks to enhance the inherent heterogeneity of the grassland environment through the heterogeneous application of fire, produces a shifting mosaic of patches within the landscape that differ in burning and grazing history.

56. **Fuhlendorf, S. D. and D. M. Engle.** 2004. *Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie.* *Journal of Applied Ecology* 41:604–614.

Though data for this study was not collected at the TGPP, a very similar study is ongoing at the preserve and so bears inclusion here. In this study, patch-burning generated substantially more variation in vegetation structure, litter, and plant species composition than traditional management. Additionally, patch-burning reduced spread of the invasive *Lespedeza cuneata*.

57. **Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton.** 2009. *Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing.* *Conservation Biology* 23:588–598.

Pyric herbivory (or the interaction of grazing with fire) is presented here as a model for restoration of the evolutionary processes that shaped grassland environments. Using TGPP data, they show that pyric herbivory effectively increases grassland heterogeneity and provides the necessary variability for the persistence of biological diversity.

58. **Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie.** 2006. *Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing.* *Ecological Applications* 16:1706–1716.

The structurally and compositionally diverse vegetation arising from the fire-grazing interaction under the patch-burn management method creates the necessary landscape heterogeneity for grassland bird success.

59. **Glass, C. R., P. Hendricks, M. Phillips, and T. L. Waltman.** 1994. *Common Poorwills nesting in Osage County, Oklahoma.* *Bulletin of the Oklahoma Ornithological Society* 27:12–13.

This brief note documents the rare occurrence of Common Poorwills (*Phalaenoptilus nuttallii*) breeding at the TGPP. Their usual breeding range in the state is farther west.

60. **Glenn, S. M., M. L. Francis, and I. H. Butler.** 1994. *Vegetation mapping of the Tallgrass Prairie Preserve using LANDSAT thematic mapper imagery.* Unpublished report. Part I of the Final Report to The Nature Conservancy. Oklahoma Natural Heritage Inventory, Pawhuska OK.

This report describes the application of landsat imagery to classify vegetation types within the TGPP. Analysis revealed 18 distinct community types within the TGPP.

61. **Hall, S. A.** 1999. *Pollen influx at the Tallgrass Prairie Preserve, Osage County, Oklahoma.* *Texas Journal of Science* 51:317–322.

This study assessed the pollen rain of the TGPP. Like other tallgrass prairie locations, the rain was characteristically dominated by a high amount of *Ambrosia* pollen.

62. **Hamilton, R. G.** 1993. *The Nature Conservancy bison herd report.* Pages 415–422 in Proceedings of the North American Public Bison Herds Symposium, LaCrosse, Wisconsin.

This report briefly describes the status and management of The Nature Conservancy's bison herds during the early 1990s. At the time of this publication, the Conservancy maintained 410 bison on three preserves in North Dakota, South Dakota and Nebraska. The TGPP had not yet been stocked with its bison herd.

63. **Hamilton, R. G.** 1996. *Using fire and bison to restore a functional tallgrass prairie landscape*. Pages 208–214 in Transactions of the 61st North American Wildlife and Natural Resources Conference.

This article explains the TGPP's management plan for increasing and maintaining biological diversity by reinstating the historical processes of grazing and fire to the tallgrass prairie landscape.

64. **Hamilton, R. G.** 2007. *Restoring heterogeneity on the Tallgrass Prairie Preserve: Applying the fire-grazing interaction model*. Pages 163–169 in Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems, Tall Timbers Research Station, Tallahassee, Florida, USA.

This updated explanation of the TGPP's management program describes the successes of heterogeneity-based management (i.e., patch burn) for bison, cattle, and biodiversity.

65. **Hamilton, R. G.** 2009. *Tallgrass Prairie Preserve Greater Prairie Chicken counts*. Unpublished data.

66. **Harrell, W. C.** 2004. *Importance of heterogeneity in a grassland ecosystem*. Ph.D. dissertation. Oklahoma State University, Stillwater, Oklahoma.

This Ph.D. dissertation evaluates the effects of landscape heterogeneity on grassland bird communities and plant composition and diversity in tallgrass prairie.

67. **Harris, T. M., J. B. Tapp, and K. L. Sublette.** 2005. *Remediation of oilfield brine-impacted soil using a subsurface drainage system*. Environmental Geosciences 12:101–113.

Brine contamination of a prairie site was remediated through the mobilization salts by tilling hay into the soil to improve soil structure and drainage. Additionally, a sub-surface drainage system was installed to further facilitate drainage of salts from the site.

68. **Hendricks, P. and D. L. Reinking.** 1994. *Investigator visitation and predation rates on bird nests in burned and unburned tallgrass prairie in Oklahoma—An experimental study*. Southwestern Naturalist 39:196–200.

Comparison of burned and unburned areas of tallgrass prairie revealed that nest depredation was lower in areas left unburned.

69. **Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson.** 2003. *Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States*. Conservation Biology 17:587–594.

Grassland breeding bird success was examined in relation to prairie fragment size. Determined that chance of nest depredation declined with prairie fragment size for Grasshopper Sparrows, Dickcissels, Eastern Meadowlarks, and Henslow's Sparrow (though nonsignificantly).

70. **Hill, P. S. M., J. P. H. H. Deere, J. Fancher, D. R. Howard, and J. B. Tapp.** 2009. *Burrow aggregation of prairie mole cricket (*Gryllotalpa major saussure*: Orthoptera: Gryllotalpidae) males is not based on soil microhabitat constraints at lek sites in Oklahoma*. Journal of the Kansas Entomological Society In Press.

Analysis of soil samples from transects running across lek sites revealed commonalities and differences in soil attributes among sites where prairie mole crickets construct their burrows. However, none of these variations in soil microhabitats from on or off lek sites could be used to predict aggregation of male calling chambers within the larger lek.

71. **Hoppe, K. A.** 2006. *Correlation between the oxygen isotope ratio of North American bison teeth and local waters: Implication for paleoclimatic reconstructions*. Earth and Planetary Science Letters 244:408–417.

Oxygen isotopes in bison tooth enamel correlated well with local water and surface precipitation, implying that fossil bison teeth might be useful in the reconstruction of historical precipitation patterns.

72. **Hoppe, K. A., A. Paytan, and P. Chamberlain.** 2006. *Reconstructing grassland vegetation and paleotemperatures using*

carbon isotope ratios of bison tooth enamel. Geology 34:649–652.

Examination of the relationship between carbon isotope ratios and the proportion of C3 versus C4 grasses available in the environment revealed a strong correlation. This again suggests an application whereby fossil bison teeth might be used to reconstruct grassland vegetation.

73. **Hornaday, W. T.** 1989. *The extermination of the American bison, with a sketch of its discovery and life history*. Smithsonian Institution, Washington, D.C., USA.

74. **Howard, D. R. and P. S. M. Hill.** 2006. *Morphology and call song characteristics in *Gryllotalpa major* S. (Orthoptera: Gryllotalpidae)*. The Journal of Orthopteran Research 15:53–57.

Examination of the relationships between body and song characteristics revealed a negative relationship between body length and the dominant frequency of the song and a positive relationship between body length and the number of syllables per chirp. Larger crickets did not necessarily produce louder songs.

75. **Howard, D. R. and P. S. M. Hill.** 2007. *The effect of fire on spatial distributions of male mating aggregations in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae) at The Nature Conservancy's Tallgrass Prairie Preserve in Oklahoma: Evidence of a fire-dependent species*. Journal of the Kansas Entomological Society 80:51–64.

The spatial distribution of prairie mole crickets were related to the distribution of recently burned patches. Analysis revealed that 60% of male crickets at the TGPP were in areas that had been burned less than 11 months previous and 90% in areas that had been burned less than 20 months previous, suggesting that this species is dependent on fire to provide appropriate lek sites.

76. **Howard, D. R. and P. S. M. Hill.** 2009. *Grassland botanical structure influences lek spatial organization in *Gryllotalpa major* S. (Orthoptera: Gryllotalpidae)*. American Midland Naturalist 161:206–218.

Grass height and biomass affect the spatial arrangements of lekking prairie mole cricket males. Greater vegetation height and biomass causes crickets to space themselves further apart, presumably to avoid female confusion as to the source of the call in the thicker vegetation. Additionally, crickets

modify the construction of their burrows in heavier vegetation, likely to enhance the acoustic signature of their call.

77. **Howard, D. R., A. C. Mason, and P. S. M. Hill.** 2008. *Hearing and spatial behavior in Gryllotalpa major Saussure (Orthoptera: Gryllotalpidae).* Journal of Experimental Biology 211:3613–3618.

Assessment of prairie mole cricket hearing in relation to their spatial arrangement revealed that males usually construct burrows out of hearing distance of the higher harmonics of their neighbors' calls, suggesting that the higher harmonics are not important factors in determining male-male spacing. Female crickets may be able to use the higher harmonics of the call to assess proximity to a particular male.

78. **Hunt, G. W.** 1999. *The ecology of hyporheic invertebrates in Oklahoma and Arkansas streams.* Ph.D. dissertation. Oklahoma State University, Stillwater, Oklahoma.

This Ph.D. dissertation has four components related to the ecology of hyporheic invertebrates including: factors influencing hyporheic fauna composition, spatial and temporal distribution of hyporheic invertebrates, effects of point source effluent on hyporheic communities, and an assessment of hyporheic sampling procedures.

79. **Hunt, G. W. and E. H. Stanley.** 2003. *Environmental factors influencing the composition and distribution of the hyporheic fauna in Oklahoma streams: Variation across ecoregions.* Archiv Fur Hydrobiologie 158:1–23.

In comparison with other areas of Oklahoma, Wild Hog Creek at the TGPP had greater richness and abundance of hyporheic fauna than all other prairie streams assessed.

80. **Hussain, M.** 1994. *The structure of plant microcommunities emerging from soil seed banks.* Ph.D. dissertation. Oklahoma State University, Stillwater, Oklahoma.

This Ph.D. dissertation contains four components evaluating effects of disturbance on and structure of plant microcommunities

81. **Irving, W., editors G. C. Wells and J. B. Thoburn.** 1926. *A Tour on the Prairies.* Harlow Publishing Company, Oklahoma City, USA.

82. **IUCN.** 2000. *Gryllotalpa major.* 2008 IUCN Red List of Threatened Species.

83. **Jager, H. I., R. A. Efrogmson, K. L. Sublette, and T. L. Ashwood.** 2005. *Un-natural landscapes in ecology: generating the spatial distribution of brine spills.* Environmetrics 16:687–698.

Models based on the spatial arrangements of brine spills at the TGPP were generated to help identify areas of the landscape that might be particularly susceptible to spills.

84. **Jensen, W. E.** 2003. *Spatial variation in brown-headed cowbird (Molothrus ater) abundance and brood parasitism in the Flint Hills tallgrass prairie.* Ph.D. Kansas State University, Manhattan, Kansas.

This Ph.D. dissertation focuses on the spatial patterns of brood parasitism by Brown-headed Cowbirds in the grassland bird community of the Flint Hills region of Kansas and Oklahoma.

85. **Jensen, W. E. and J. F. Cully.** 2005. *Density-dependent habitat selection by brown-headed cowbirds (Molothrus ater) in tallgrass prairie.* Oecologia 142:136–149.

Grassland bird nests located closer to wooded edges have higher brood-parasitism by Brown-headed Cowbirds than nests located in the prairie interior, but only in regions of low cowbird abundance.

86. **Jensen, W. E. and J. F. Cully.** 2005. *Geographic variation in Brown-headed Cowbird (Molothrus ater) parasitism on Dickcissels (Spiza americana) in great plains tallgrass prairie.* Auk 122:648–660.

For reasons not clearly understood, Brown-headed Cowbirds are more abundant in the northern Flint hills than in the southern Flint Hills and consequently have much higher parasitism rates in the northern part of the region.

87. **Kerby, J.** 2002. *Patch-level foraging behavior of bison and cattle on tallgrass prairie.* M.S. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis evaluates both bison and cattle grazing behaviors in heterogeneously managed landscapes.

88. **Kindscher, K. and N. Scott.** 1997. *Land ownership and tenure of the largest land parcels in the Flint Hills of Kansas,* USA. Natural Areas Journal 17:131–135.

89. **Kollmorgen, W. M. and D. S. Simo-nett.** 1965. *Grazing operations in the Flint Hills-Bluestem Pastures of Chase County, Kansas.* Annals of the Association of American Geographers 55:260–290.

90. **Long, A. M., W. E. Jensen, and K. A. With.** 2009. *Orientation of Grasshopper Sparrow and Eastern Meadowlark nests in relation to wind direction.* Condor 111:395–399.

Nest openings were generally oriented to the northeast, opposite prevailing winds.

91. **Maichak, E. J.** 2002. *Behavioral differences of bison (Bos bison bison) and effects of seasonal ambient temperature on a tallgrass prairie.* M.S. Thesis. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis evaluates seasonal changes in bison behavior.

92. **Maichak, E. J. and K. L. Schuler.** 2004. *Applicability of viewshed analysis to wildlife population estimation.* American Midland Naturalist 152:277–285.

Viewshed Analysis in ARCGIS was used to calculate visible area for an optimal census route for estimating bison population size at the TGPP. This technique worked well, the resulting route intercepting enough of the landscape to provide a reasonably close estimate of the true bison population size.

93. **Maichak, E. J., K. L. Schuler, and M. E. Payton.** 2004. *Daily and seasonal behavior of bison on an Oklahoma tallgrass prairie.* The Prairie Naturalist 36:103–118.

Analysis of daily patterns of TGPP bison activity showed that bison forage primarily during the day, but may reduce activity when high ambient temperatures induce thermoregulatory stress.

94. **Mallet Jr., W. M.** 1998. *Controls of nutrient concentrations in a prairie stream.* M.S. Thesis. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis evaluated factors controlling concentrations of mineral nutrients within the Wild Hog Creek watershed.

95. **Mannel, S.** 1999. *Biophysical characterization of the tallgrass prairie in Oklahoma: Grassland canopy parameters and their relationships to satellite derived NDVI*. Landscape Ecology Diploma Thesis. University of Potsdam, Germany.

This master's thesis developed models of grassland biophysical parameters from Landsat imagery and was able to identify differences in grassland status at the TGPP (i.e., burned, grazed, etc.).

96. **McGlenn, D. J. and M. W. Palmer.** 2009. *Modeling the sampling effect in the species-time-area relationship*. Ecology 90:836–846.

A model to evaluate rarefaction in the species-time-area relationship (STAR) was compared to an empirically derived STAR from plant diversity data collected at the TGPP. This model generated a number of STARs that varied depending on the available species pool or replacement rate of individuals. These varying outcomes did not permit rejection of rarefaction as a structuring effect in the STAR derived from TGPP data.

97. **Mehta, C. S.** 2004. *Study of ecological indicators in bioremediation and restoration of crude oil contaminated soil*. Ph.D. dissertation. The University of Tulsa, Tulsa, OK.

This Ph.D. dissertation evaluates the bioremediation of several oil contaminated spill sites at the TGPP using analysis of soil bacterial and nematode populations as well as soil chemistry.

98. **Melcher, U., V. Muthukumar, G. B. Wiley, B. E. Min, M. W. Palmer, J. Verchot-Lubicz, A. Ali, R. S. Nelson, B. A. Roe, V. Thapa, and M. L. Pierce.** 2008. *Evidence for novel viruses by analysis of nucleic acids in virus-like particle fractions from Ambrosia psilostachya*. Journal of Virological Methods 152:49–55.

Ambrosia psilostachya specimens from the TGPP were used to develop the virus-like particle-viral nucleic acid (VLP-VNA) method for virus extraction. The VLP-VNA approach resulted in solid evidence for at least four virus species within *A. psilostachya*, none of which matched any previously known viruses.

99. **Muthukumar, V.** 2008. *Metagenomics for the identification of plant viruses in the Tallgrass Prairie Preserve*. M.S. thesis. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis describes a metagenomic technique used to discover novel viruses from non-cultivated plants. At least nine different viruses were found via this technique.

100. **Muthukumar, V., U. Melcher, M. Pierce, G. B. Wiley, B. A. Roe, M. W. Palmer, V. Thapa, A. Ali, and T. Ding.** 2009. *Non-cultivated plants of the Tallgrass Prairie Preserve of northeastern Oklahoma frequently contain virus-like sequences in particulate fractions*. Virus Research 141:169–173.

The application of the VLP-VNA technique to 52 plant species determined that 10 of them contained RNA or DNA resembling those of viruses. Many plant specimens appeared to be infected by multiple virus species. Also a new tymovirus species was found in six different plant species, including *Asclepias viridis* where it was particularly abundant.

101. **Nisbett, R. A., W. Caire, M. D. Stuart, G. M. Caddell, J. M. Crutcher, and C. H. Calisher.** 2001. *Serologic survey of Oklahoma rodents: Evidence for the presence of Hantavirus and an Arenavirus*. Proceedings of the Oklahoma Academy of Sciences 81:53–66.

Four small mammal species at the TGPP were found to be serologically positive for antibodies of the Sin Nombre virus. This virus is the primary agent of hantavirus pulmonary syndrome in humans.

102. **Nuttall, T., editor.** 1980. *A journal of travels into the Arkansas Territory during the year 1819*. University of Oklahoma Press, Norman, Oklahoma, USA.

103. **Oklahoma Natural Heritage Inventory.** 1993. *Species inventory for significant species at the Tallgrass Prairie Preserve*. Unpublished report. Part II of the Final Report to the Nature Conservancy, Pawhuska, OK.

This report includes preliminary inventories of the aquatic invertebrate, fish, birds, and mammals of the TGPP.

104. **Palmer, M. W.** 1993. *Vascular plant diversity in Oklahoma*. Water Resources Research A—124:1–32.

This report contains an early version of the flora of the TGPP.

105. **Palmer, M. W.** 2002. *Scale detection using semivariograms and autocorrelograms*. Pages 129–144 in S. E. Gergel and M. G. Turner, editors. Learning Landscape

Ecology: A Practical Guide to Concepts and techniques. Springer, New York City, New York, USA.

Teaching tools for describing spatial variation and how to create and interpret semivariograms and autocorrelograms are explained in this educational chapter. Utilizes TGPP data in examples.

106. **Palmer, M. W.** 2007. *The vascular flora of the Tallgrass Prairie Preserve, Osage County, Oklahoma*. Castanea 72:235–246.

The TGPP's flora includes 763 species of which 92 are non-native. 411 genera and 109 families are represented at the TGPP.

107. **Palmer, M. W., J. R. Arévalo, M. D. Cobo, and P. G. Earls.** 2003. *Species richness and soil reaction in a northeastern Oklahoma landscape*. Folia Geobotanica 38:381–389.

Species richness is significantly negatively correlated with soil calcium in the tallgrass prairie. In woodlands, richness is weakly positively correlated with soil calcium.

108. **Palmer, M. W., P. G. Earls, B. W. Hoagland, P. S. White, and T. M. Wohlgemuth.** 2002. *Quantitative tools for perfecting species lists*. Environmetrics 13:121–137.

Three methods are suggested for perfecting species lists for a given area. These include using existing species list to predict what might also occur in an area, searching unique areas that might harbor uncommon species, and using spectral variability measures from aerial imagery to determine which areas may be particularly unique, thereby giving a map of locations to search.

109. **Palmer, M. W. and M. Hussain.** 1997. *The unimodal species richness-biomass relationship in plant communities emerging from soil seed banks*. Proceedings of the Oklahoma Academy of Sciences 77:17–26.

Germination of soil seedbank samples from various habitats in the TGPP yielded an unimodal peak in the species richness and biomass relationship. This suggests that soil seedbank samples may be useful for examining relationships between richness and biomass.

110. **Palmer, M. W., D. J. McGlenn, and J. D. Fridley.** 2008. *Artifacts and artificions in biodiversity research*. Folia Geobotanica 43:245–257.

Reviews issues in the use or interpretation of biodiversity statistics. Problems covered are: the use of taxonomic ratios, standardizing richness by dividing by area, and rarefaction (or the sampling effect).

111. **Palmer, M. W., T. M. Wohlgemuth, P. G. Earls, J. R. Arévalo, and S. D. Thompson.** 2000. *Opportunities for long-term ecological research at the Tallgrass Prairie Preserve in Cooperation in Long Term Ecological Research in Central and Eastern Europe: Proceedings of the ILTER Regional Workshop*. Oregon State University, Corvallis, OR, Budapest, Hungary.

This brief document describes research opportunities at the TGPP. It also lists the availability of long-term datasets on tallgrass prairie and crosstimbers vegetation at the TGPP.

112. **Patten, M. A., E. Schochat, D. H. Wolfe, and S. K. Sherrod.** 2007. *Lekking and nesting response of the Greater Prairie-chicken to burning of tallgrass prairie*. Pages 149-155 in Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems, Tall Timbers Research Station, Tallahassee, Florida, USA.

Greater Prairie-Chicken were more likely to establish leks on burned areas or areas of low stature grass less than 200m from unburned prairie. Unburned prairie was utilized for nesting.

113. **Patten, M. A., E. Shochat, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod.** 2006. *Habitat edge, land management, and rates of brood parasitism in tallgrass prairie*. *Ecological Applications* 16:687-695.

Edge effects, i.e., trees, substantially increase brood parasitism rates for five tallgrass prairie passerine species. Areas grazed by cattle also had higher rates of brood parasitism.

114. **Payne, T.** 1992. *Mammals of the Tallgrass Prairie Preserve*. M.S. thesis. University of Central Oklahoma, Edmond, OK.

This master's thesis contains an early list of mammal species occurring at the TGPP.

115. **Payne, T. and W. Caire.** 1992. *Occurrence of the Cotton Mouse, Peromyscus gossypinus, in Northcentral Oklahoma*. Proceedings of the Oklahoma Academy of Sciences 72:67.

10 Cotton Mice were captured at the TGPP representing a new northwest extension to the distribution of this species.

116. **Payne, T. and W. Caire.** 1999. Species diversity of small mammals in the Tallgrass Prairie Preserve, Osage County, Oklahoma. Proceedings of the Oklahoma Academy of Sciences 79:51-59.

Comparison of small mammal diversity in the TGPP's various habitat types determined grasslands to be richest, containing 13 species. All other habitats contained 6-9 species and represented a subset of those found in the grasslands.

117. **Payne, T., S. Stevens, and W. Caire.** 2001. *Annotated checklist of the mammals of the Tallgrass Prairie Preserve, Osage County, Oklahoma*. Proceedings of the Oklahoma Academy of Sciences 81:41-51.

Early checklist of the mammal species present at the TGPP. This list includes 39 species.

118. **Pruett, C. L., M. A. Patten, and D. H. Wolfe.** 2009. *Avoidance behavior by prairie grouse: implications for development of wind energy*. *Conservation Biology* 23:1253-1259.

Power lines and other vertical structures proved to be a significant physical deterrent for Greater Prairie-Chickens. Prairie chickens generally did not approach power lines, maintaining a buffer of at least 100m.

119. **Pruett, C. L., M. A. Patten, and D. H. Wolfe.** 2009. *It's not easy being green: Wind energy and a declining grassland bird*. *Bioscience* 59:257-262.

Wind energy development poses a threat for the Lesser Prairie-Chicken as wind farms are generally placed in areas of prime prairie-chicken habitat. These birds have a behavioral adaptation to avoid any vertical structure and so will naturally not utilize areas with windmills.

120. **Rahmig, C. J., W. E. Jensen, and K. A. With.** 2009. *Grassland bird responses to land management in the largest remaining tallgrass prairie*. *Conservation Biology* 23:420-432.

Grassland bird responses to grazing, fire, and haying on traditionally used and Conservation Reserve Program (CRP) lands were compared across the Flint Hills region. CRP fields had less diverse bird communities,

overall. Nest success was highest for two species (Dickcissel and Grasshopper Sparrow) in one of two study years.

121. **Reed, B. C., T. R. Loveland, and L. L. Tieszen.** 1996. *An approach for using AVHRR data to monitor U.S. Great Plains grasslands*. *Geocarto International* 11:13-22.

A new method for assessing the onset of "greenness" across North American grasslands by establishing threshold Normalized Difference Vegetation Index values to determine when the growing season begins is proposed here. Once threshold values are surpassed, vegetation monitoring should be continued by accumulating NDVI values throughout the growing season in order to effectively monitor landscape change and compare productivity between years.

122. **Reinking, D. L.** 2002. *Rare, little-known, and declining North American breeders. A closer look: Henslow's Sparrow*. *Birding* 34:146-153.

Provides a description of the Henslow's Sparrow's natural history and conservation concerns.

123. **Reinking, D. L.** 2005. *Fire regimes and avian responses in the central tallgrass prairie*. *Studies in Avian Biology* 30:116-126.

Review article describing avian responses to fire in the tallgrass prairie. Primarily discusses the deleterious effects of the current Flint Hills management paradigm of annual burning and intense grazing for grassland bird species. Argues for more heterogeneous management to promote grassland bird viability.

124. **Reinking, D. L.** 2006. *Fire in the tallgrass prairie: Finding the right balance of burning for birds*. *Birding* 37:32-38.

This review article describes the importance for heterogeneous applications of fire to promote grassland bird viability.

125. **Reinking, D. L. and D. P. Hendricks.** 1993. *Occurrence and nesting of Henslow's Sparrow in Oklahoma*. *Bulletin of the Oklahoma Ornithological Society* 26:33-44.

This article represents the first documentation of a seemingly large population of Henslow's Sparrow nesting at the TGPP.

126. **Reinking, D. L., D. H. Wiedenfeld, D. H. Wolfe, and R. W. Rohrbaugh Jr.** 2000. *Distribution, habitat use, and nesting success of Henslow's Sparrow in Oklahoma*. The Prairie Naturalist 32:219–232.

Assessment of Henslow's Sparrow habitat requirements determined that tgrassland habitat of at least two years post-burn is required for nesting. The success of 24 nests was monitored, 10 of which were successful, the rest were either depredated or parasitized by Brown-headed Cowbirds.

127. **Reinking, D. L., D. H. Wolfe, and S. K. Sherrod.** 2009. *Nest monitoring, point counts, and habitat of tallgrass prairie breeding birds of Northeastern Oklahoma, 1992–2996*. Publications of the Oklahoma Biological Survey In Press.

Summarizes nest success, nest height, clutch size, and other metrics related to tallgrass prairie nesting birds at the TGPP and nearby ranches from a 5 year study of over 2700 nests belonging to over 40 species.

128. **Ricotta, C., B. C. Reed, and L. T. Tieszen.** 2003. *The role of C-3 and C-4 grasses to interannual variability in remotely sensed ecosystem performance over the US Great Plains*. International Journal of Remote Sensing 24:4421–4431.

At broader scales, long-term climate controls on North American Great Plains vegetation is primarily distinguished by the proportion of C3 versus C4 grass species present in the environment.

129. **Rohrbaugh Jr., R. W., D. L. Reinking, D. H. Wolfe, and S. K. Sherrod.** 1999. *Effects of prescribed burning and grazing on nesting and reproductive success of three grassland passerine species in tallgrass prairie*. Studies in Avian Biology 19:165–170.

The grassland birds Eastern Meadowlark, Grasshopper Sparrow, and Dickcissel were found to nest more frequently in burned and grazed areas than in undisturbed areas, but their nesting success was lower in the disturbed areas.

130. **Roossinck, M. J., S. Prasenjit, G. B. Wiley, J. Quan, J. D. White, H. Lai, F. Chavarría, G. Shen, and B. A. Roe.** 2009. *Ecogenomics: Using massively parallel pyrosequencing to understand virus ecology*. Molecular Ecology In Press.

New plant viruses were identified using a new technique to isolate double-stranded RNA. This technique was applied to numerous specimens yielding potentially thousands of new plant viruses.

131. **Rosas, C. A.** 2003. *Some aspects of bison ecology and behavior in a tallgrass prairie*. Ph.D. dissertation. Oklahoma State University, Stillwater, Oklahoma.

This Ph.D. dissertation examines four aspects of bison ecology: seed dispersal by bison, behavior in comparison to cattle, herd sex ratios and their impact on prairie vegetation, and bison productivity on tallgrass prairie as opposed to other vegetation types.

132. **Rosas, C. A., D. M. Engle, and J. H. Shaw.** 2005. *Potential ecological impact of diet selectivity and bison herd composition*. Great Plains Research 15:3–13.

Bison cows and juveniles consume less C4 grasses than bulls. Since the TGPP herd is female skewed, this could potentially result in vegetation changes.

133. **Rosas, C. A., D. M. Engle, J. H. Shaw, and M. W. Palmer.** 2008. *Seed dispersal by Bison bison in a tallgrass prairie*. Journal of Vegetation Science 19:769–778.

Seeds from 76 plant species were found in the hair of TGPP bison. Significant differences in species composition of seeds occurred among bison age-sex classes. Bulls carried more seeds of plants associated with bare areas, juveniles more seeds of plants from wetland plants, and cows more seeds of wetland shrubs. Also reported seeds from at least 70 species in bison dung. Surprisingly, only 53% of the total number of seeds and 39% of the diversity came from graminoids, indicating that bison are consuming significant amounts of forb fruits.

134. **Ryburn, A. K.** 2003. *Taxonomic investigations of Oklahoma flora*. Ph.D. dissertation. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis includes work on the population biology of the pale purple coneflower (*Echinacea pallida*) at the TGPP. Population numbers of *E. pallida* fluctuated between years, though slightly increased over time.

135. **Samson, F. and F. Knopf.** 1994. *Prairie conservation in North America*. Bioscience 44:418–421.

136. **Samson, F. B., F. L. Knopf, and W. R. Ostlie.** 2004. *Great Plains ecosystems: Past, present, and future*. Wildlife Society Bulletin 32:6–15.

137. **Schook, D. M., M. D. Collins, W. E. Jensen, P. J. Williams, N. E. Bader, and T. H. Parker.** 2008. Geographic patterns of song similarity in the Dickcissel (*Spiza americana*). Auk 125:953–964.

Individual males had similar songs both in and between years. Song sharing evident at local scales, but decreasing at broader scales. At scales greater than 10km, no or little song sharing observed. Sharing of song phrases occurred at different scales.

138. **Schuler, K. L.** 2002. *Seasonal variation in bison distribution and group behavior on Oklahoma tallgrass prairie*. M.S. thesis. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis contains two components, an evaluation of bison as a keystone species in the tallgrass prairie and an analysis of bison group behavior. The applicability of the keystone species concept to bison may be suspect in the heterogeneously managed TGPP landscape where bison-related effects are transient. Bison behaviors differed significantly between genders and age classes in terms of grazing, rumination, and movement.

139. **Shaw, J. H.** 1995. *How many bison originally populated western rangelands?* Rangelands 17:148–150.

Estimates of pre-EuroAmerican settlement bison population size on the Great Plains are reviewed based on three methods: direct observation, number of bison killed, and carrying capacity. Given the error associated with any of these methods the true population could have ranged from millions to tens of millions of bison.

140. **Shaw, J. H.** 1998. *Bison ecology—What we do and do not know*. Pages 113–120 in International Symposium on Bison Ecology and Management in North America, Montana State University, Bozeman, Montana.

An evaluation of the status of bison research as well as recommendations for continued research are highlighted in this article. It emphasizes understanding the historical context of bison populations and their multi-scale effects.

141. **Shaw, J. H.** 1999. *American bison*. Pages 342–343 in D. E. Wilson and S. Ruff, editors. *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press, Washington, D.C., USA.

Short encyclopedic article on the basic biology and history of the American bison.

142. **Shaw, J. H.** 1999. *Bison ecology—What we do and do not know*. Pages 33–36 in *Bison World*.

An evaluation of the status of bison research as well as recommendations for continued research are highlighted in this article. It emphasizes understanding the historical context of bison populations and their multi-scale effects.

143. **Shaw, J. H. and M. Lee.** 1995. *Ecological interpretation of historical accounts of bison and fire on the southern plains with emphasis on tallgrass prairie*. Unpublished report. Final Report to The Nature Conservancy. Oklahoma State University.

Early accounts from expeditions on the Southern Great Plains were analyzed to infer historic population sizes of bison, elk, and pronghorn antelope and also to document prairie fire events.

144. **Shaw, J. H. and M. Lee.** 1997. *Relative abundance of bison, elk, and pronghorn on the Southern Plains, 1806-1857*. *Plains Anthropologist* 42:263–172.

Early travelers' accounts were used to estimate relative abundances of bison, elk, and pronghorn in the Southern Plains. Bison populations were most stabled in the mixed-grass prairie region, but appeared to be mostly absent from the tallgrass prairie region by the early 1830s. Elk abundances were highest early on in the tallgrass prairie; pronghorn were most abundant in the short and mixed-grass prairie regions.

145. **Shaw, J. H. and M. Meagher.** 1999. *Bison*. Pages 447–466 in S. Demarais and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice-Hall, Upper Saddle River, New Jersey, USA.

This textbook chapter describes the basic biology of bison, reviews bison research, and provides management recommendations for this species' management.

146. **Shirakura, F.** 2006. *Tornado damage and fire history in the Cross Timbers of the Tallgrass Prairie Preserve, Oklahoma*. M.S. Thesis. Oklahoma State University, United States—Oklahoma.

This master's thesis has two components, the analysis of tree damage and mortality resulting from a tornado passing through a Cross Timbers stand at the TGPP and also an assessment of the wildfire history of the tornado-impacted site.

147. **Shirakura, F., K. Sasaki, J. R. Arévalo, and M. W. Palmer.** 2006. *Tornado damage of Quercus stellata and Quercus marilandica in the cross timbers, Oklahoma, USA*. *Journal of Vegetation Science* 17:347-352.

Assessment of a tornado-damaged Cross Timbers stand determined that blackjack oak had a 12 times greater probability of mortality than post oak, resulting in a 53% loss of blackjack oak basal area as opposed to a 14.9% loss in basal area by post oak.

148. **Shochat, E., M. A. Patten, D. W. Morris, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod.** 2005. *Ecological traps in isodars: Effects of tallgrass prairie management on bird nest success*. *Oikos* 111:159–169.

The common management program in the Flint Hills region of annual burning coupled with double stocked cattle produces an ecological trap for grassland birds since it seemingly increases opportunity for nest predation.

149. **Shochat, E., D. H. Wolfe, M. A. Patten, D. L. Reinking, and S. K. Sherrod.** 2005. *Tallgrass prairie management and bird nest success along roadsides*. *Biological Conservation* 121:399–407.

Different management (burned or unburned) along roadsides had a strong effect on birds nesting there. In general, nest success increased in burned areas. Higher success was probably due to the greater arthropod density and biomass found along the burned roadsides. Nest success varied greatly depending on nesting habit; ground nesting birds suffered approximately 90% nest failure while shrub and tree nesting birds experienced only 50–70% failure.

150. **Smith-Patten, B. D. and M. A. Patten.** 2008. *Diversity, seasonality, and context of mammalian roadkills in the southern great plains*. *Environmental Management* 41:844–852.

18 mammal species were evaluated in terms of probability of colliding with an automobile. Unpaved roads (such as those on the TGPP) tended to have lower numbers of roadkill than paved roads. Several species (i.e.-armadillo, opossum, striped skunk, and raccoon) showed distinct mortality peaks during the season coincident with dispersal activities during their reproductive cycles.

151. **Smith-Patten, B. D., M. A. Patten, M. J. Dreiling, and J. Fisher.** 2007. *Phenology and new county records of Odonta of Northeastern Oklahoma*. *Publications of the Oklahoma Biological Survey* 8:1-13.

55 species of Odonta (dragonflies) were observed in the TGPP area.

152. **Smith, A.** 1996. *Big Bluestem: Journey into the tall grass*. Council Oak Books, Tulsa, OK.

153. **Smith, E. F. and C. E. Owensby.** 1978. *Intensive-early stocking and season-long stocking of Kansas Flint Hills range*. *Journal of Range Management* 31:14–17.

154. **Smith, M. P.** 2008. *Subterranean termites of the Oklahoma tallgrass prairie preserve Cross Timbers*. M.S. thesis. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis has two main components, the development of criteria for termite species identification and the characterization of termite colonies at the TGPP.

155. **Spranza, J. J.** 1998. *Spatial and temporal differences in assemblages, condition factors, and growth rates of warmwater stream fishes in Northcentral Oklahoma*. M.S. thesis. Oklahoma State University, Stillwater, Oklahoma.

This master's thesis contains two components, a study of mechanisms structure fish assemblages and a study of spatial and temporal variation in fish growth rates and condition factors.

156. **Spranza, J. J. and E. H. Stanley.** 2000. *Condition, growth, and reproductive styles of fishes exposed to different environmental regimes in a prairie drainage.* Environmental Biology of Fishes 59:99–109.

Stressful water conditions in the upper basins of Wild Hog Creek were offset by higher primary productivity for resident fish populations. This allowed faster growth for fish in the upper basins. Upper basin fish also differed in terms of their reproductive strategy; they produced multiple cohorts of offspring during the breeding season as opposed to lower basin fish that produced a single cohort.

157. **Stewart, J. G., F. P. Gelwick, W. J. Matthews, and C. M. Taylor.** 1999. *An annotated checklist of the fishes of the Tallgrass Prairie Preserve, Osage County, Oklahoma.* Proceedings of the Oklahoma Academy of Sciences 79:13–17.

23 fish species are present at the TGPP.

158. **Sublette, K., E. Jennings, C. Mehta, K. Duncan, J. Brokaw, T. Todd, and G. Thoma.** 2007. *Monitoring soil ecosystem recovery following bioremediation of a terrestrial crude oil spill with and without a fertilizer amendment.* Soil and Sediment Contamination: An International Journal 16:181–208.

Several ecological indicators were used to monitor and identify the status of soil at an oil spill site at the TGPP. Nematode community structure was most sensitive and proved to be the best and lowest cost method for evaluating the remediation of a spill site.

159. **Sublette, K. L., R. Kolhatkar, K. Pim, A. Kolhatkar, K. E. Duncan, B. Miller, R. Fogg, P. Rider, A. Stepp, M. Carey, T. Todd, and A. Cross.** 2002. *Long-term impacts of a crude oil spill on a pristine soil ecosystem.* Pages 979–1011 in Proceedings of the 25th Arctic and Marine Oilspill Program Technical Seminar, Calgary, Alberta, Canada.

A long term study (six years) of an remediated oil spill site yielded very little residual petroleum contamination, though the contamination did appear to have disrupted the

nitrogen cycle at the site. Additionally, there appeared to be no acute toxicity remaining in the plants at the site, seed set and germination for sunflowers was not significantly different from those in uncontaminated sites.

160. **Sublette, K. L., A. Moralwar, L. Ford, K. Duncan, G. Thoma, and J. Brokaw.** 2005. *Remediation of a spill of crude oil and brine without gypsum.* Environmental Geosciences 12:115–125.

This article provides a full description of the remediation method used by University of Tulsa researchers for oil and brine spill sites at the TGPP. The method combines soil tillage with fertilization to improve soil structure and promote microbial degradation of petroleum hydrocarbons.

161. **Sublette, K. L., J. B. Tapp, J. B. Fisher, E. Jennings, K. Duncan, G. Thoma, J. Brokaw, and T. Todd.** 2007. *Lessons learned in remediation and restoration in the Oklahoma prairie: A review.* Applied Geochemistry 22:2225–2239.

This review synthesizes all the brine and oil remediation research conducted at the TGPP, it includes the methods for remediation and monitoring of spill sites.

162. **Suneson, N. H.** 2000. *The geology of the Tallgrass Prairie Preserve, Osage County, Oklahoma.* Oklahoma Geological Survey, Norman, OK.

This general guide to the geology of the TGPP includes a discussion of the landforms, geology, mineral resources, and fossils of the preserve. It also includes a description of a driving-route where one can see most of the geologic features characteristic of the TGPP.

163. **Therrell, M. D. and D. W. Stahle.** 1998. *A predictive model to locate ancient forests in the Cross Timbers of Osage County, Oklahoma.* Journal of Biogeography 25:847–854.

In this study, they generated a model based on steep slopes and infertile soils to locate ancient Cross Timbers. 74% of the locations predicted by the model did contain ancient stands of Cross Timbers.

164. **Thies, M., T. L. Payne, and W. Caire.** 1993. *The Eastern Harvest Mouse, Reithrodontomys humilis, in Northcentral Oklahoma.* Proceedings of the Oklahoma Academy of Sciences 73:79–80.

12 individuals of Eastern Harvest Mice were captured, establishing a new western extension to their distribution.

165. **Tieszen, L. L.** 1998. *Stable isotopic determination of seasonal dietary patterns in bison at four preserves across the Great Plains.* Pages 130–140 in International Symposium on Bison Ecology and Management in North America, Montana State University, Bozeman, Montana.

Evaluation of bison dietary patterns determined that the most nutritious vegetation is available during the early spring when nitrogen is most available in the grassland system.

166. **Tieszen, L. L., B. C. Reed, N. B. Bliss, B. K. Wylie, and D. D. DeJong.** 1997. *NDVI, C-3 and C-4 production, and distributions in great plains grassland land cover classes.* Ecological Applications 7:59–78.

Used C3 and C4 grass distributions to assess performance and production of Great Plains grasslands. The Flint Hills regions had the highest measures of NDVI (a proxy for productivity) and the earliest green-up in the spring.

167. **Verser, D. W.** 1990. *Henslow's Sparrow in Northeast Oklahoma.* Bulletin of the Oklahoma Ornithological Society 23:9–13.

This Early account documents the presence of Henslow's Sparrow at the TGPP.

168. **von Fischer, J. C., L. L. Tieszen, and D. S. Schimel.** 2008. *Climate controls on C3 vs. C4 productivity in North American grasslands from carbon isotope composition of soil organic matter.* Global Change Biology 14:1141–1155.

Assessment of climate controls on C3 and C4 abundance and productivity determined that precipitation and average daily high temperatures in July best predicts the percent of C4 species present in the environment.

169. **Wallace, L. L. and K. A. Crosthwaite.** 2005. *The effect of fire spatial scale on Bison grazing intensity*. *Landscape Ecology* 20:337–349.

The size of the area burned has a non-significant impact on bison grazing intensity; though smaller patches do tend to be slightly more intensely grazed.

170. **Warehime, L.** 2000. *History of Ranching the Osage*. W. W. Publishing, Tulsa, OK, USA.

171. **Wethington, M. K.** 1994. A spatial and temporal analysis of forest and grassland changes at the Tallgrass Prairie Preserve. M.S. Thesis. Oklahoma State University, Stillwater, OK.

This master's thesis assessed changes in forest cover at the TGPP between 1937 and 1984. While overall forest area decreased, tree density in xeric forests increased substantially.

172. **Wiedenfeld, D. H., D. H. Wolfe, and S. K. Sherrod.** 2002. *A study of factors affecting nesting success and mortality of Greater Prairie Chickens in Northeastern Oklahoma 1997–2000*. Unpublished report. George Miskisch Sutton Avian Research Center.

Conducted over four years, this study determined the success of a Greater Prairie-Chicken nest to fledge at least one young ranged from 11% to 31% depending on year with a 24% average over the whole study period.

173. **Wilson, T. P.** 1985. *The Underground Reservation: Osage Oil*. University of Nebraska Press, Lincoln, USA and London, UK.

174. **With, K. A., A. W. King, and W. E. Jensen.** 2008. *Remaining large grasslands may not be sufficient to prevent grassland bird declines*. *Biological Conservation* 141:3152–3167.

Loss and fragmentation of habitat has possibly left insufficient habitat for grassland bird population viability in the Flint Hills region. Grasshopper Sparrow, Eastern Meadowlark,

and Dickcissel continue to decline in the region, possibly as a result from an extinction debt owed from over a century of habitat loss.

175. **Wolfe, D. H.** 1996. *Nest competition in Eastern Meadowlarks*. *Bulletin of the Oklahoma Ornithological Society* 29:6–7.

This brief note documents several instances of female nest competition or nest sharing by Eastern Meadowlarks observed at the TGPP. This competition in some instances resulted in the ejection of the eggs of one female.

176. **Wong, C. Y.** 2005. *Consequences analysis of oil production fluids spills and risk index generation of tallgrass prairie preserve with GIS*. Ph.D. dissertation. University of Arkansas, United States—Arkansas.

This Ph.D. dissertation's main focus was the utilization of models to generate risk ranked maps for the prediction of areas within the TGPP likely to suffer significant ecological or economic damage due to an accidental brine or oil spill.

177. **Wren, J. D., M. J. Roossinck, R. S. Nelson, K. Scheets, M. W. Palmer, and U. Melcher.** 2006. *Plant virus biodiversity and ecology*. *Public Library of Science Biology* 4:e80.

Describes the purpose and research objectives of the Plant Virus Biodiversity and Ecology project at the TGPP. Primary hypotheses were: first, that there are many more viruses present in nature than are presently known and second, that most viruses do not produce obvious symptoms in their hosts.

178. **Wylie, B. K., D. J. Meyer, L. L. Tieszen, and S. Mannel.** 2002. *Satellite mapping of surface biophysical parameters at the biome scale over the North American grasslands—A case study*. *Remote Sensing of Environment* 79:266–278.

Measurements were taken of leaf area, biomass, and the fraction of photosynthetically absorbed light from plots within the TGPP and used to generate a model using those variables and NDVI values computed from Landsat imagery to predict the biophysical parameters across the whole preserve.

179. **Yang, L. M., B. K. Wylie, L. L. Tieszen, and B. C. Reed.** 1998. *An analysis of relationships among climate forcing and time-integrated NDVI of grasslands over the US northern and central Great Plains*. *Remote Sensing of Environment* 65:25–37.

Analysis of the relationship between grassland productivity and broad-scale climate patterns determined that for the tallgrass prairie, productivity is primarily regulated by spring and summer precipitation.

180. **Yates, R. G.** 2000. *Transportation of brine components and revegetation of a brine spill site in the Tallgrass Prairie Preserve*. Ph.D. The University of Tulsa, Tulsa, Oklahoma.

This Ph.D. dissertation evaluated the recovery of a brine-impacted site at the TGPP. Over the course of the study, salt were mobilized out of the site allowing for at least partial revegetation of the site, though not with climax tallgrass prairie species.

181. **Zambrano, L., K. Sublette, K. Duncan, and G. Thoma.** 2007. *Probabilistic reliability modeling for oil exploration & production (E&P) facilities in the tallgrass prairie preserve*. *Risk Analysis* 27:1323–1333.

A risk model for oil exploration infrastructure failure determined that mechanical components servicing brine were most likely to fail due to elevated rates of corrosion because of the high salt content.

182. **Zambrano, L. C.** 2007. *Development of decision algorithms for resource allocation in exploration and production facilities*. Ph.D. University of Arkansas, Fayetteville, Arkansas.

This Ph.D. dissertation uses risk based decision models to evaluate failure probabilities for oil-field equipment deployed at the TGPP.

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