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Is Anthropogenic Habitat Change The Driving Force Of Rapid Evolution Of Southeastern U.S. Coastal Deer Populations?

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Is anthropogenic habitat change the driving force of rapid evolution of Southeastern US coastal deer populations?

BY

Nicole L. Storm

THESIS

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Abstract

Many factors, such as genetics, food availability and the exact food species, can affect the growth rate and asymptotic size of animals. Since the 1960's, the coastal areas and islands in Georgia, North Carolina, and South Carolina have become vacation destinations with large and lavish resort communities built to accommodate the large number of visitors to areas that were once called home by just a small number of residents. These developments brought with them non-native plants and improved soil quality for both native and non-native plants. During this same time period, the white-tailed deer (*Odocoileus virginianus*) native to the areas began to increase in size, as measured by skull size, which is a phenotypically stable character in mammals. The purpose of this project is to determine whether the increased size of deer is due to higher nutritional values of non-native plants and whether deer diets have shifted to include plants of higher nutritional content. Analysis proceeded by comparing the rumen contents of deer collected from the early 1970's to the late 1990's in comparable areas including developed, managed, and undeveloped habitats. The research showed that while the diet of deer has changed, the change is too minimal to have caused such a dramatic change in size. It is possible that the change has been caused macronutrients, such as calcium, phosphorus, and potassium.

Introduction

White-tailed deer (*Odocoileus virginianus*) are the most important big game species in North America. Deer are popular game animals due to their abundance, broad geographic range and ability to live in a broad variety of habitats (VerCauteren, 2003). Each fall more white-tailed deer are harvested than all other species of Cervidae combined (VerCauteren, 2003). White-tailed deer are an especially popular game species in the southeast and are considered the most important game species in South Carolina in terms of biomass harvested, effort expended and dollars spent (Ruth, 2003; Novak, 2003).

Anthropogenic effects have drastically affected this species over time. Population numbers increased when forests were removed and land was cleared for agricultural uses thus opening up more edge habitat beneficial to deer. As populations increased, deer became a more widespread staple in many diets and local population extinctions ensued due to overhunting. After World War II, there was a second increase in the local population density of deer, probably as a result of forest rejuvenation, enforcement of game laws, broad public support and successful reintroductions into many under-populated areas (Baker, 1984; McCabe and McCabe, 1984; Smith, 1991).

White-tailed deer look very similar, even across varied ecosystems, with the main difference being size differences with a cline of increasing size in North America from south to north. Taxonomists have divided the species into as many as 30 subspecies (VerCauteren, 2003). The main subspecies of white-tailed deer occurring in the southeast

is *Odocoileus virginianus virginianus* but there are five other subspecies within the Southeastern Coastal Plains region. Four of these subspecies are located on barrier islands (*O. v. taurinsulae*, Bull's Island, SC; *O. v. venatorius*, Hunting Island, SC; *O. v. hiltonensis*, Hilton Head Island, SC and *O. v. nigribarbis*, Blackbeard Island, GA) (Goldman and Kellogg, 1940; Novak, 2003) with the fifth located along the gulf coast of Georgia and Peninsular Florida (*O. v. seminolus*) (Purdue et al., 2000; Novak, 2003). In the subspecific description of the barrier island subspecies, small size, compared to mainland forms, is listed as a primary diagnostic characteristic.

White-tailed deer are an edge species, meaning second-growth forests, openings, and farmlands, often created due to logging, clearing, and agriculture are preferred habitat (McCabe and McCabe, 1984; Smith, 1991). Areas impacted by human endeavors provide the best habitat for deer because the fragmentation of large habitat patches into smaller patches creates a higher proportion of edge habitats. In addition, residential areas may provide supplemental forage as well as protection from predators, especially in cases where hunting is not allowed (VerCauteren, 2003). Unfortunately, in many of these urban and suburban areas, deer have become overabundant (Conover, 1997; Cromwell, et al., 1999) often due to either the increased forage or decreased mortality, or both. This overabundance of deer can create concerns over landscape destruction, deer-vehicle accidents and/or the potential spread of diseases (Conover, 1997; Cromwell, et al., 1999), such as Lyme disease (Cromwell, et al., 1999).

Large generalist herbivores, such as, ungulates, equines, and lagomorphs, generally eat a diet in which the nutritional content of the food eaten varies greatly

(Westoby, 1974; Belovsky, 1978; Vangilder, et al., 1982). Particular foods may be eaten preferentially at any given time based upon the digestibility, protein levels, or energy levels of the foods and the nutritional requirements of the individual (Seals et al., 1978; Ouellet et al., 2001; Page and Underwood, 2006). Many times, one food item is able to meet the nutritional energy requirement of the animal but it is unable to fulfill other nutritional requirements. For example calcium, potassium and phosphorus may not be at sufficient levels even in high caloric value foods. Therefore, over a season or longer time period, the animal must have a larger dietary breadth, that contains a large array of foods such that the diet is nutritionally adequate. Over shorter time frames, food intake is often restricted by gut capacity, turnover time in the digestive system, and food availability (Westoby, 1974, 1978; Vangilder, et al., 1982), thus one must always be aware of time scale when analyzing diets as the definition of an optimum diet is dependent on the time scale.

Areas along the southeastern coastal plains have transitioned in the recent years from primarily forests and wetlands to lavish resorts and residential areas. The local human population of many areas in the Southeastern United States coastal plain has grown considerably in a matter of fifty years. For example, Hilton Head Island, once a small community, has tripled its resident population from 1960 to 2000, introducing resorts and lavish residential neighborhoods with millions of tourist visits every year. This increased human population has led to an increase in human impacts and consequently to a change in the ecosystem in this area, in terms of both the landscape as well as the plant and animal communities (McCabe and McCabe, 1984; DeNicola, et al.,

2000). Many of these areas have proved to be very good habitat for edge species, such as white-tailed deer. The deer have easily adapted to utilize the new habitat and plants by foraging on residential lawns, golf courses, and resorts, eating a variety of both native and non-native species (DeNicola, et al., 2000).

The increased human population growth has also caused many barrier island communities to severely or completely eliminate hunting of deer on the island. This has caused white-tailed deer population control on the islands to depend on alligators, bobcats, and automobiles to keep the deer populations at an appropriate level (Tall Timbers Research Inc., 1992).

Novak (2003) found that deer collected from Hilton Head Island exhibited a significantly larger skull size when compared to deer collected on either Sapelo or St. Catherine's Island. The deer on Hilton Head in the early 2000's exhibited a mean skull size indistinguishable from deer populations living on either the upper or lower coastal plains of South Carolina (Novak 2003). Hilton Head Island is a highly developed resort community, while Sapelo and St. Catherine's Islands are relatively undeveloped areas. St. Catherine's Island is closed off from the general public, except for the beach areas which have general access. Sapelo Island is only reachable by ferry and is a national estuarine reserve. The residents of Hilton Head Island have increased the number of residential horticultural plantings as well as their subsequent irrigation, and fertilization. These changes have immensely improved the forage quality on Hilton Head Island compared to other less developed barrier islands (Caudell and Warren, 1997). It is believed that the smaller mass and structural size of barrier island deer may be due to the

poorer forage quality of the islands compared to mainland areas (Tall Timbers Research Inc., 1992). The barrier islands represent smaller, more fragmented and slightly more isolated habitats compared to areas in the lower coastal plains (Tall Timbers Research Inc., 1992). Barrier islands are also expected to support smaller, more rapidly evolving populations whose dynamics are influenced by colonization and extinction processes to a greater degree (Novak, 2003).

The potential mechanism of increased skull size found in developed areas in the southeastern United States coastal plains has not been fully investigated. To date, no study has focused on the changing patterns of food resources found in developed compared to undeveloped areas. To explore the possibility that anthropogenic processes are responsible for the skull size increase, I sought to determine: 1) whether white-tailed deer had changed their foraging habits from the 1970's to the late 1990's by looking at studies of rumen contents; 2) whether deer in developed areas were foraging on different plants or plant types compared to deer in undeveloped areas and; 3) whether the deer in developed areas were eating plants with a higher energy content compared to deer in undeveloped areas. This information could be potentially useful in selecting horticultural plants, irrigation regimes, and fertilizers that include more native plants and horticultural techniques that more closely resemble natural barrier island habitat to reducing the size of both individuals and populations of deer. This could lower the severity of deer-vehicle accidents, the potential for deer to cause landscape destruction, and even impact the potential spread of deer-borne human diseases.

Methods

Six published rumen content studies were examined for this study. In all, 839 deer rumens were collected and their contents recorded. The studies encompassed seventeen sites over thirty-three years. The sites include Kiawah Island (west and east end) (Jordan, 1998), Blackbeard Island (Vansant III, 1973), Cumberland Island (north and south end) (Warren et al., 1990), Eastern Northern Carolina Pocosin (Sossman, 1973), Broad River Management Area, Enoree Management Area, Parson Mountain Management Area, Forks-Key Bridge Management Area, Clemson Management Area, Chauga Management Area, Francis Marion Management Area, Belmont Plantation, private farmland in Calhoun County, South Carolina (Connelly, 1971), Leaf River, and Tallahala, Mississippi (Mitchell, 1980).

The dates of the data collected were used to determine whether the sites were development or undeveloped. This allowed the sites to then be separated into developed, managed, and undeveloped areas. Developed areas were defined as land with major improvements and changes. Managed areas were any areas that were managed for timber or wildlife species, besides white-tailed deer. Undeveloped areas were defined as land with minimal improvements and changes. Of these seventeen areas six areas were considered developed, five area were categorized as managed, and the remaining six were considered undeveloped.

The data was separated into seasons. For the studies that contained months rather than seasons, the months were categorized into seasons and the mean percentage plant

usage was used to determine a seasonal average (Spring: March-May; Summer: June-August; Fall: September-November; Winter: December-February).

Some of the data were eliminated before any of the analyses were completed. When more than one species was present for a genus, the species were condensed down to the genus level, except in the case of mast. The variance in caloric value of mast among species will not necessarily be greater than the variance among trees within a species (Vansant, 1976). Plant material that was indentified without a genus, such as unidentified browse, was eliminated from the analyses, since a caloric value could not be assigned. Also, animal matter was eliminated from the analyses due to the low percentage in most studies and most of the animal matter consumed is likely accidental consumption (Connelly, 1971). Lastly, data from studies containing less than five rumens per study location were eliminated due to the limited sample size and possible age and/or sex bias in mean diets.

The caloric values of plants were retrieved from published and unpublished information from previous studies. All of the caloric values were estimated as gross energy (GE) calories per 1 gram of plant material (cal/gm) estimated using a Parr bomb calorimeter. When more than one GE values were available for a plant species, the average value was used. Plants were categorized into eight groups: graminoid, sedge, agricultural products, fungi, trees and shrubs, forbs and herbs, and vines. The plants were divided into these groups using information found on the Plant Database, provided by the United States Department of Agriculture - Natural Resources Conservation Service.

Once grouped, the caloric averages were calculated for each group.

Study Sites

The Clemson Management Area was not used due to a sample size smaller than five rumens.

Kiawah Island (West and East end)

Kiawah Island is a barrier island located off the coast of South Carolina. The island is approximately 3,200-ha and 1.6 km in width. The island is oriented in an east-west direction. The west end and the east end have different habitats with the majority of development on the west end. The development on Kiawah Island began in 1974 and increased to over 1,500 permanent residents in 1998. Thousands of tourists visit during the year (Jordan, 1988). Homes and landscaped yards replaced the maritime forests and marshes which once covered the area. The deer on Kiawah have adapted to the development and are often seen feeding on landscaped yards and residential areas (Jordan, 1988). Jordan (1998) completed this study on Kiawah Island. The island was divided into the west end and the east end. On the west end of Kiawah Island, 33 rumens were collected and 17 rumens were collected on the east end. The study took place from winter 1997 to winter 1998 (Jordan, 1998).

Blackbeard Island

Blackbeard Island is located in McIntosh County, Georgia. It covers 2273.6 ha, including 843.4 ha of salt marsh and 852.3 ha of forest and dunes. The remaining area is

fresh and brackish ponds, brackish marsh, and fields (U.S. Fish and Wildlife Service 1962). The soils on the island are poorly developed and infertile and the topography is characterized by a series of steep, narrow, northeasterly oriented sand ridges separated by wet depressions. There are two man-made freshwater ponds on the island. Flag Pond is 218.5 hectares and North Pond covers 31.6 hectares. The ponds were created by dikes constructed across the salt marsh perpendicular to sand ridges. The marsh behind the dikes collected rainwater and eventually formed freshwater ponds. The study on Blackbeard Island consisted of 150 rumens. The study took place in August 1974, October - December 1974, March and April 1975, June 1975, October - December 1975, and March 1976 (Vansant, 1976).

Cumberland Island (North and South sides)

Cumberland Island is a barrier island located off the coast of Georgia. It is 25 km long by 1 to 9 km wide and is separated from the mainland by 1 to 3 km of open water from the Cumberland River and Sound (Hillestad et al., 1975). The island is bordered on the west by the intercoastal waterway and extensive salt marsh, and on the east by the Atlantic Ocean. In 1972, the island was declared a National Seashore and has since been managed by National Park Service. This study took place in March 1986, June 1986, August - September 1986, November 1986, January 1987, March 1987, June 1987, August - September 1987, November 1987, and January 1988. The island was divided into the north and south side with 135 rumens collected on the north side and 124 rumens collected from the south side (Warren et al. 1990).

Eastern Northern Carolina Pocosin

The Eastern Northern Carolina Pocosin study was conducted in Craven, Pamlico, and Beaufort Counties, North Carolina. The area encompasses approximately 10,521 hectares that had been harvested, site prepared, and replanted with loblolly pine eight years previous to the study. The site preparation was accomplished by mechanical removal of organic material (slash) with tractors equipped with combinations of KG blades, root rakes, discs, and bedding plows. The area was adjacent to several agricultural fields. The study consisted of 128 rumen samples and took place from fall 1971 to summer 1973 (Sossman, 1973).

Broad River Management Area

The Broad River management area is owned by the United States Forest Service and managed by private timber companies. It is located in Madison County, Georgia. The area is composed of 44,110.7 hectares with only a few tenant farms. In addition, there are some food plots maintained by the South Carolina Wildlife Resources Department. The study consisted of 11 deer rumen. It took place in fall 1966 and 1969 and was completed by Connelly (1971).

Enoree Game Management Area

Connelly (1971) also completed a study at Enoree game management area from fall 1971 to spring of 1973. The study consisted of 22 rumens from deer of all ages and both sexes. The Enoree game management area is owned by the United States Forest Service and private companies and was also managed for timber production. The area

stretches across Newberry, Laurens, and Union Counties, SC and consists of 44,110.7 hectares with very little farming except for a few tenant farms. There were some food plots but these were primarily for turkey management.

Parsons Mountain Game Management Area

The Parsons Mountain game management area is composed of 20,234.2 hectares and is located in Abbeville and McCormick Counties. Private land owners and timber companies owned 20,000 acres and the remaining acreage is owned by the United States Forest Service. Approximately 10 percent of the land was farmed, producing mainly corn and soybeans. The remainder was managed timber production. The study took place in fall 1967 and 1969, five rumens were used. This study was also completed by Connelly (1971).

Forks-Key Bridge Game Management

The study that took place at Forks-Key Bridge game management area and consisted of 25 rumens collected in the fall of 1965, 1967, 1968, 1969, spring 1967 and 1968, summer 1967, and winter 1968. The area consists of 14,163.9 hectares and is located in Edgefield and McCormick Counties, SC. The United States Forest Service owns approximately 65 percent and the remaining is owned by private land owners and timber companies. There was some farming practiced but the area was primarily used for timber production. Food plots located there are winter wheat. The study was completed by Connelly (1971).

Chauga Game Management Area

The Chauga game management area study consisted of nine rumens and took place from fall 1965 to fall 1969. The area was approximately 31,970.1 hectares and was located in Oconee County, GA. The area is owned by the United States Forest Service (74,000 acres), Georgia Power and Light Company (4,000 acres), and private individuals (1,000 acres). There was practically no farming done there (Connelly, 1971).

Francis Marion Game Management Area

The Francis Marion game management area study consisted of 27 rumens and took place in fall 1965 and 1969. The area consisted of 24,281.1 hectares and is owned by the United States Forest Service in Charleston and Berkeley Counties, SC. The area was managed for timber production and some food plots were also maintained (Connelly, 1971).

Belmont Plantation

The Belmont Plantation consisted of approximately 2,306.7 hectares and was located in Hampton County, SC. Farming was practiced here and the main crop was corn. Farms surrounding this area planted soybean as the main crop. The study consisted of 41 rumens. Ten of the rumens were recovered in fall 1969 and 1970 and another 31 rumens were recovered at an unknown time (Connelly, 1971).

Private Farm Land in Calhoun County

Between fall 1968 and summer 1969, 34 rumens were collected on private farm

lands in Calhoun County, SC. The main crops were soybean and cotton (Connelly, 1971).

Leaf River and Tallahala Wildlife Management Areas

The Leaf River Wildlife Management Area and the Tallahala Wildlife Management Area were used in Mitchell's (1980) study. The Leaf River Wildlife Management Area is located in DeSoto National Forest in southeast Mississippi. The area is 17,800 hectares of longleaf and slash pine-dominated forest stands typical of the coastal plains of the Southeastern United States. This study took place from August 1977 to July 1978. The Tallahala Wildlife Management Area and four adjoining ranges were studied within the Bienville National Forest of central Mississippi. The area is 12,100 hectares. The habitat is typical of loblolly-shortleaf pine and mixed hardwood forests. The study took place from November 1976 to October 1977. In the Leaf River and the Tallahala studies 75 rumens were collected and examined (Mitchell, 1980).

Results

The top 10 plants represented 93.6% of the total food eaten by deer on the east end of Kiawah Island, 90.0% of the food eaten by deer on the west end of Kiawah Island, 67.5% of the food eaten on Blackbeard Island, 82.3% of the food eaten on the north side of Cumberland Island, 84.6% of food eaten on the south side of Cumberland Island, 80.4% of food eaten in the Eastern Northern Carolina Pocosin, 80.5% of food eaten at Leaf River, 85.0% of food eaten at Tallahala, 81.2% of food eaten at Francis Marion Management Area, 99.2% of food eaten at Chauga Management Area, 99.9% of food eaten at Broad River Management Area, 68.5% of food eaten at Belmont Plantation, 96.3% of food eaten at Enoree Management Area, 91.7% of food eaten at Forks-Key Bridge Management Area, 87.6% of food eaten on private farmland in Calhoun County, and 99.9% of food eaten at Parson Mountain Management Area. Thus the top 10 food types eaten in each area makes up the majority of the deer diets (67.5% to 99.9%) in each area.

The developed areas had a range of 68.5% to 99.9% of the total diet represented in the top 10 food types eaten in each area. Undeveloped areas had a range of 67.5% to 99.2% and managed areas had a range of 80.4% to 99.9% of the total diet made up by the top 10 food types eaten in each area.

When analyzing the percentage of plant types eaten across the three habitat types, it is obvious that the food plants eaten are different. In the undeveloped areas trees and shrubs were the most widely eaten plant type out of the eight and were consumed as a

majority (50.9%). The same was true for managed areas (68.6%). The developed area had very different results. Trees and shrubs (26.7%) were the second most eaten plant type and followed vines (34.9%) as the most widely eaten plant type (Figure 1).

The diversity of the diets eaten by deer across developed, undeveloped, and managed areas is depicted in Figure 2.

The dietary overlap between managed and developed areas was lower because the managed areas are highly populated with trees and shrubs for tree harvest. The pairwise overlap in diets between developed and undeveloped and developed and managed is illustrated in Figure 3.

Developed areas showed a change in diet (Figure 4). Pre-1970 agricultural products (20.3%), forbs-herbs (6.2%)), fungi (.4%), graminoid (5.1%), trees-shrubs (40.2%), and vines (27.7%) made of the diets. Post 1970 looked very different. The diet consisted of graminoid (22.2%), mast (48.4%), trees-shrubs (15.3%), and vines (14.1%).

For most of the plant groups there was little difference in caloric value. Mast (5158.4 Cal/g) was the highest value followed by sedge (4756 Cal/g), trees and shrubs (4745.9 Cal/g), agricultural products (4731 Cal/g), and vines (4663.9 Cal/g) (Figure 5). Even though mast has the highest caloric value, it is eaten at low levels within the diets as mast is mostly available during the fall but the data were analyzed over all seasons. In addition, only four studies separated out the mast from leaves and stems. There are no error bars (95% confidence interval) for fungi or sedges because only one caloric value was available for each.

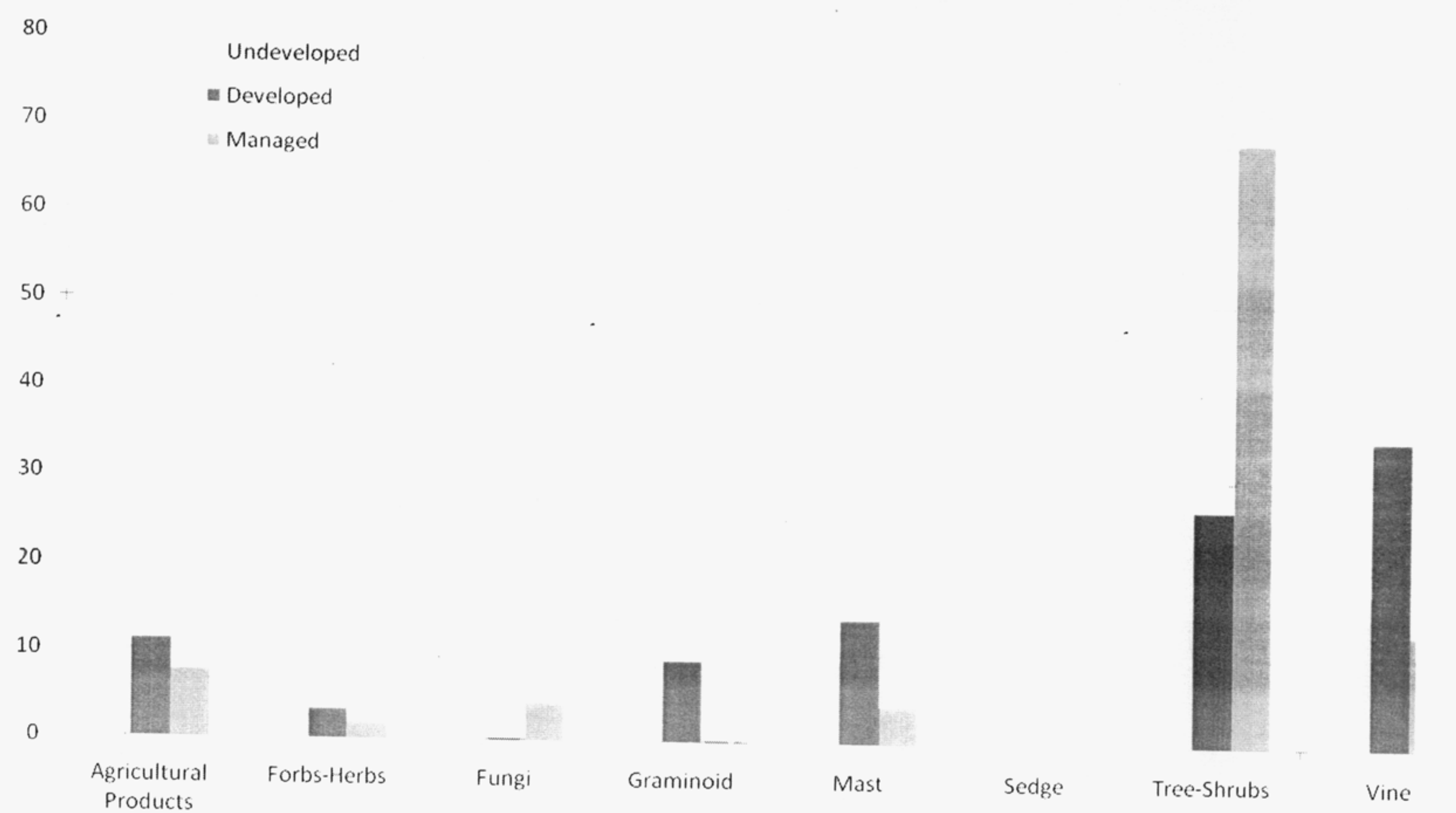

Figure 1: Percentage of plant types across the three categories (developed, managed, and undeveloped).

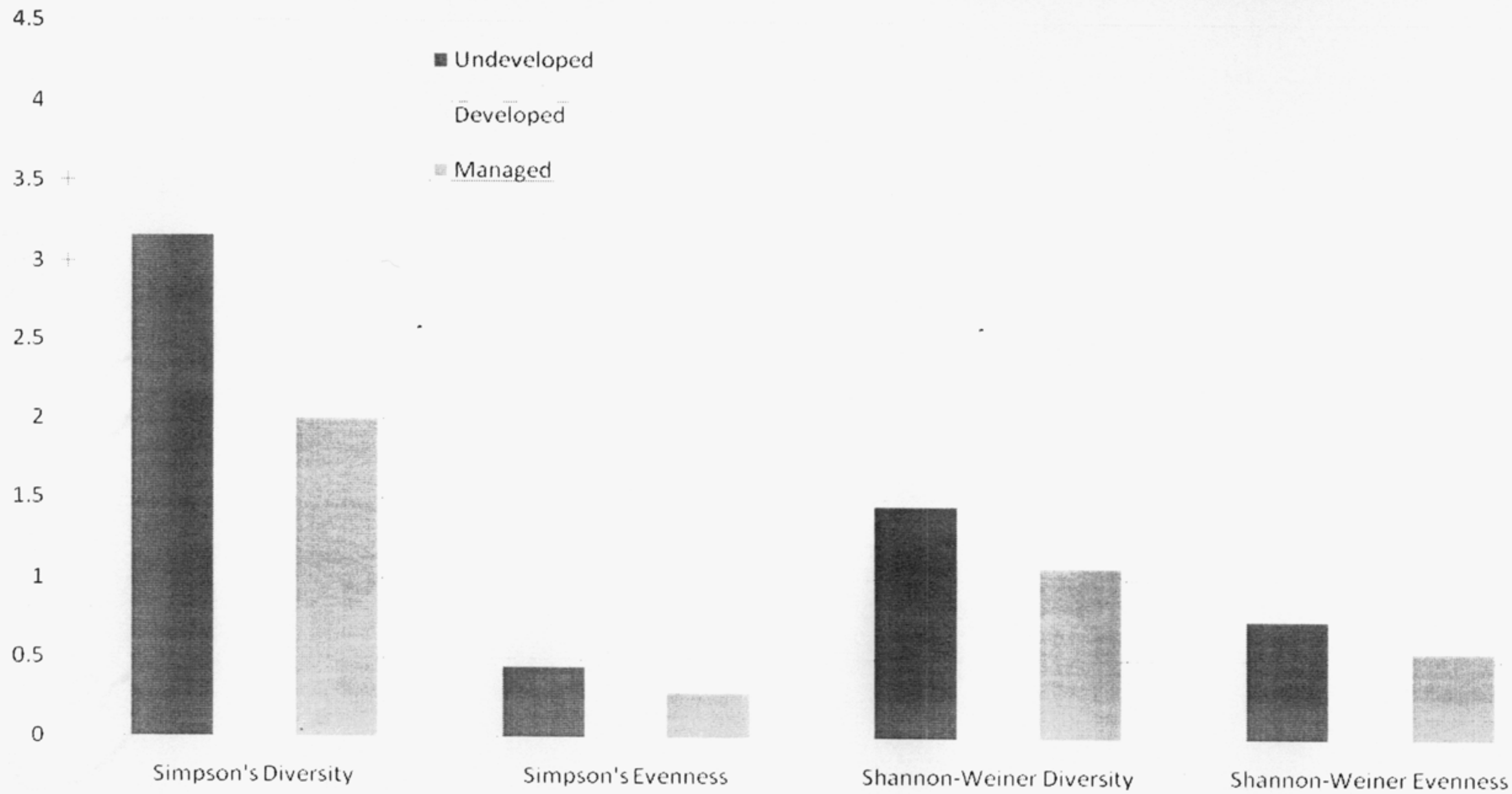

Figure 2: Simpson's Diversity, Simpson's Evenness, Shannon-Weiner Diversity, and Shannon-Weiner for deer diets in developed, managed, and undeveloped area.

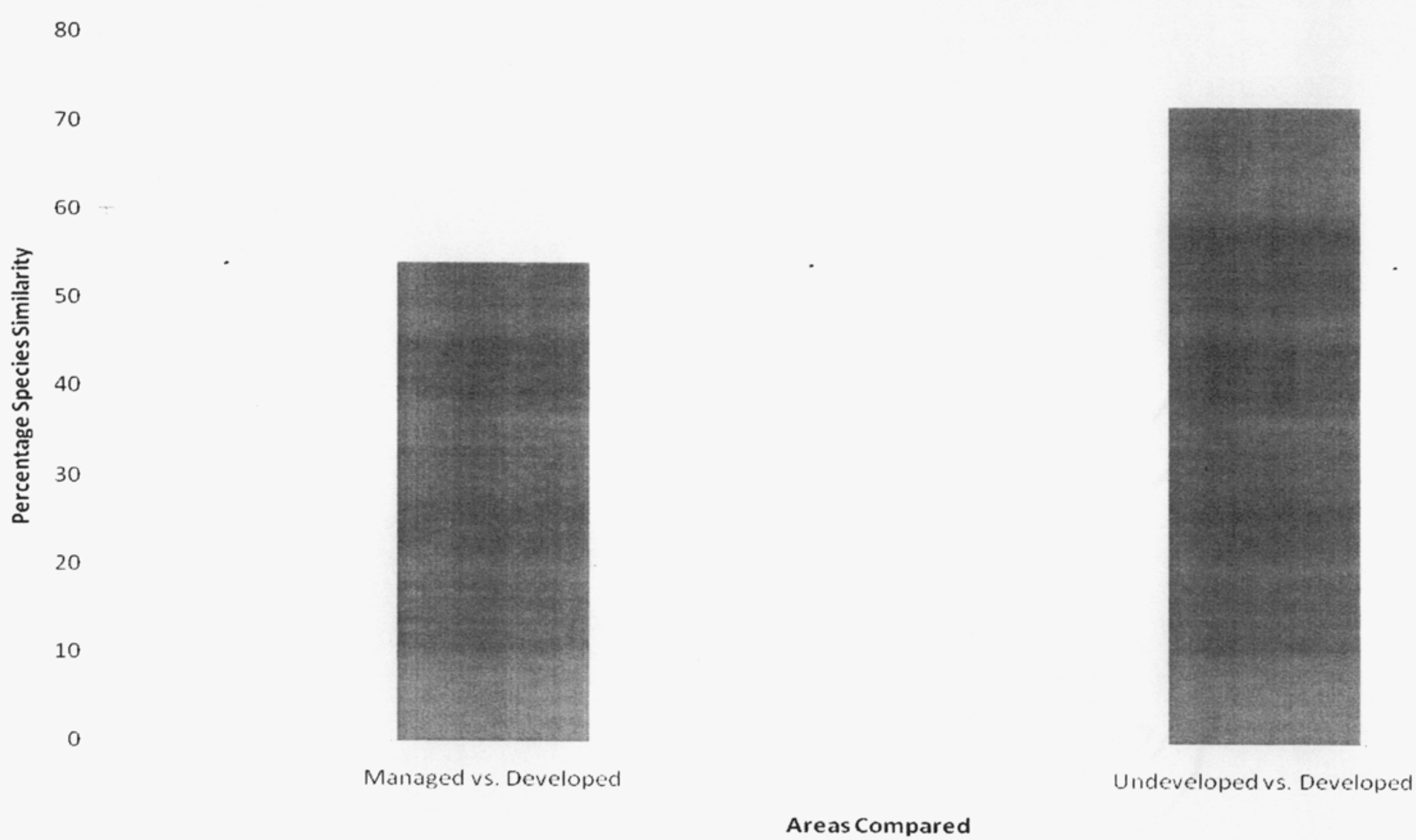

Figure 3: Percentage of species similarity of deer diets among the three focal populations.

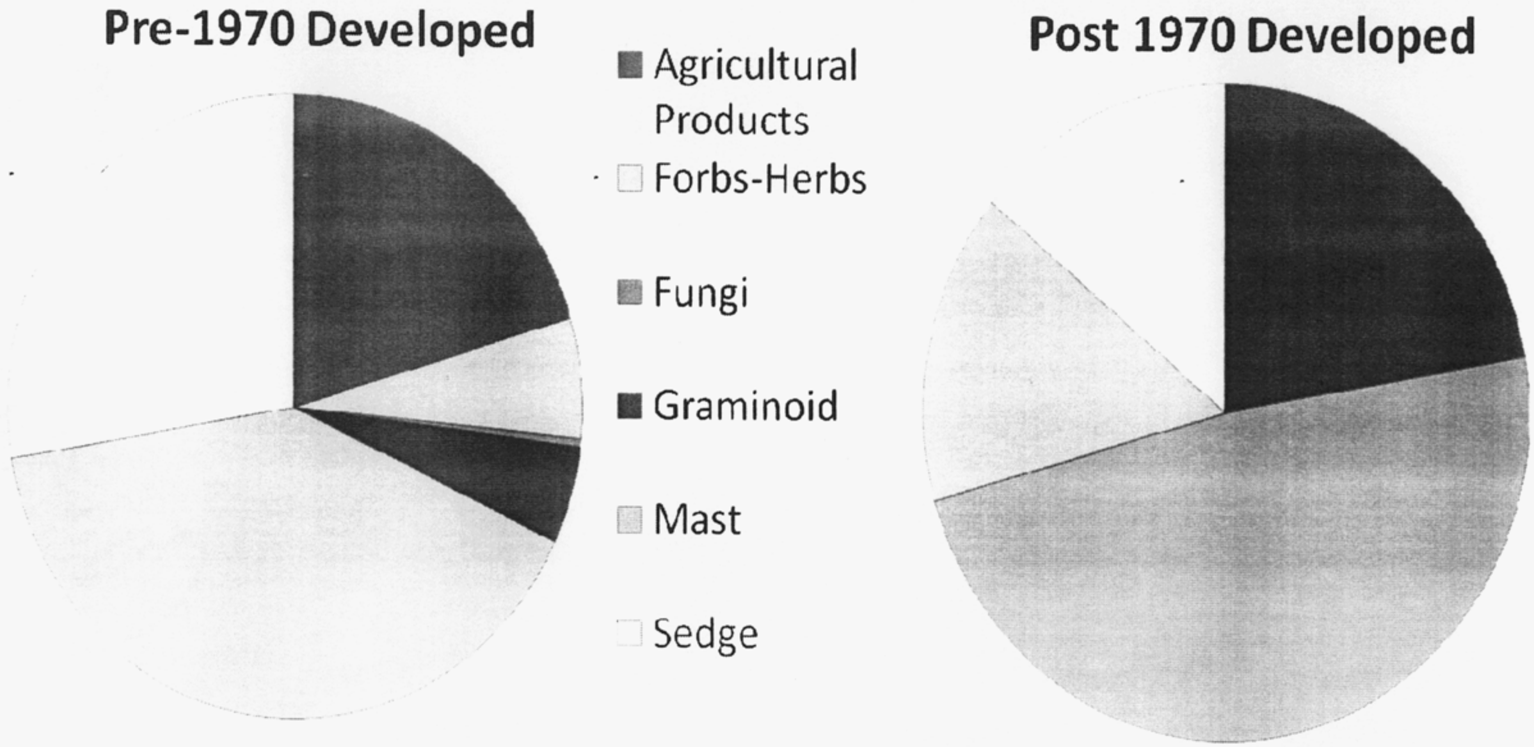

Figure 4: Percentage of plant groups for pre-1970 and post 1970 developed areas.

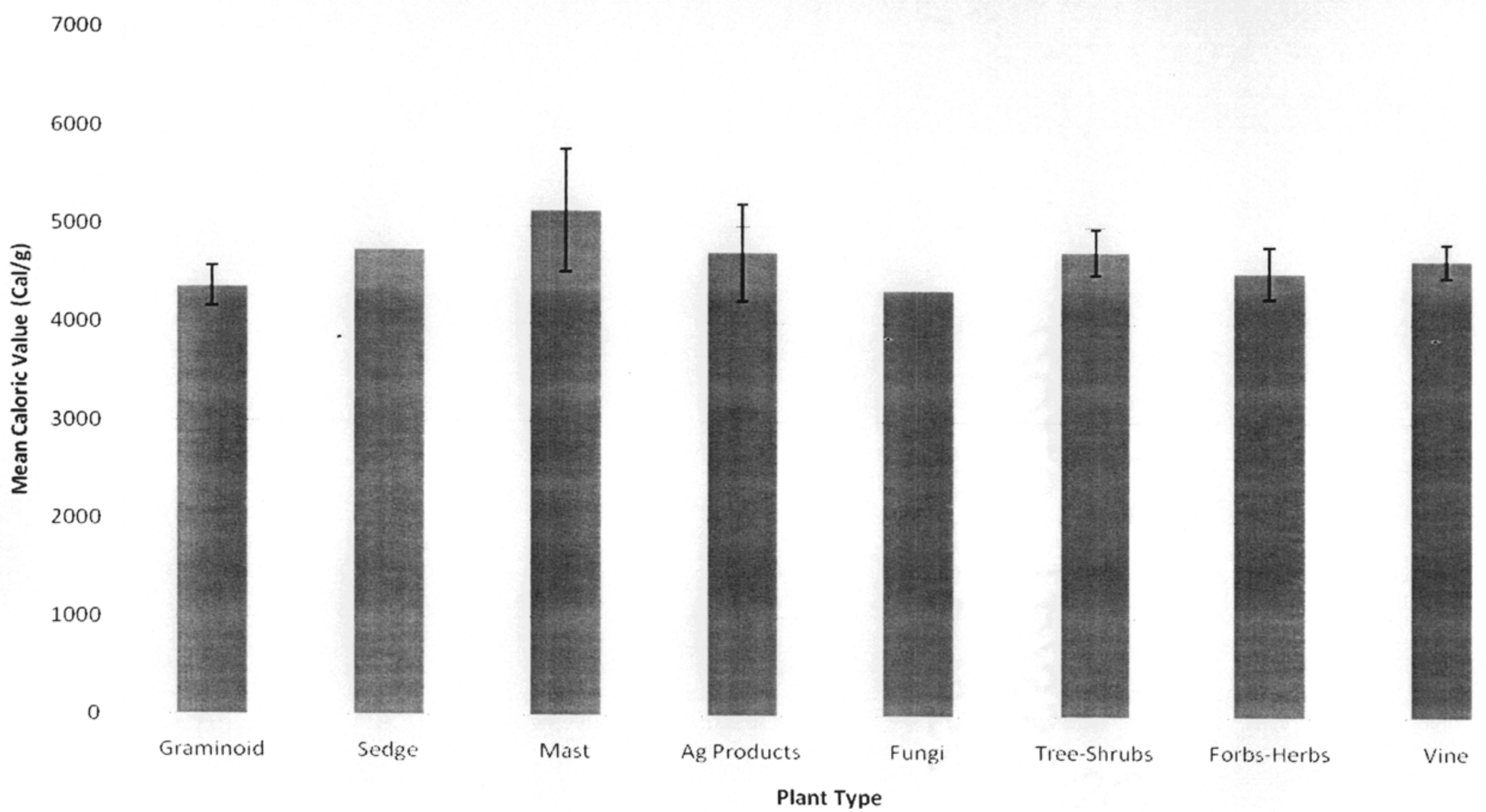

Figure 5: Caloric value (Cal/g) of each plant type.

The caloric value between diets showed statically significance (Figure 6) (t_{10}=2.04, p= 0.068 between undeveloped and developed; t_9=3.16, p=0.012 between developed and managed). The caloric difference between diets was low (117.9 Cal/g between undeveloped and developed; 150.0 Cal/g between developed and managed).

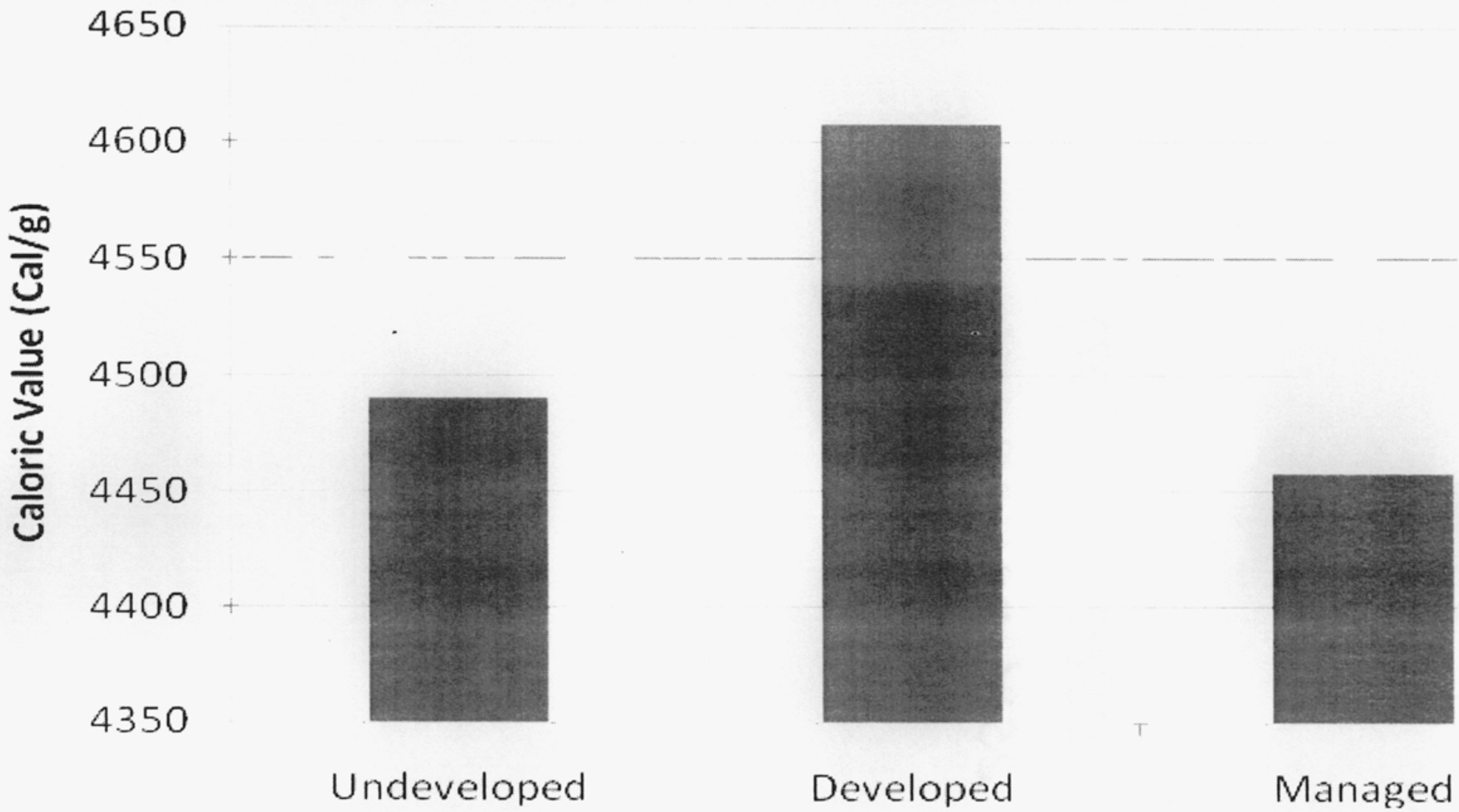

Figure 6: Total caloric value (Cal/g) for each diet (undeveloped, developed, and managed).

Discussion

The managed areas had a large amount of trees and shrubs (68.6%) consumed as the majority of these areas were managed for tree production that will be used for timber or pulp production. Vines (13.0%) are the second most heavily foraged group in the managed areas. There is also a high amount of agricultural products (7.8%) found within the rumens. Many of these managed areas had small tenant farmers within their borders or were bordered by agricultural lands.

In undeveloped areas, the top group of plants was trees and shrubs (50.9%), followed by vines (17.4%), fungi (10.5%), and mast (9.5%). This diet is considered the white-tailed deer's natural diet since at the time the original study took place the area had minimal development or management of the habitat.

The diets of deer from developed areas have a much more even dispersion among the food groups. Vines (34.9%) are the most consumed plants followed by trees and shrubs (26.7%), mast (14.1%), agricultural products (11.2%), and graminoid (9.3%).

The overall diet diversity differs between the three areas (undeveloped, managed and developed). The developed areas have the greatest diversity followed by undeveloped areas and then managed areas. The diversity is greatest in the developed areas due to the native and non-native plants that are present. The managed areas have the lowest amount of diversity because these areas are managed for certain plant groups, therefore for fewer plant groups are available. This shows that deer select a variety of food types and when more food types are present the deer will select from all available

food items.

Dietary overlap is higher between the developed and undeveloped areas than between managed and developed areas. This shows that the deer in developed and undeveloped areas are eating the same type of foods. The reason for this is that both developed and undeveloped areas contain many of the same plant groups. The dietary overlap between developed and managed areas is lower due to the low variety of plant groups available.

The differences show that white-tailed deer while generalist feeders over the year, are selective foragers over shorter time frames and within nutritional categories. That is, deer consume plants that have a wide variety of nutritional content, from very high to low energy, varied degrees of protein, fiber, vitamins, and minerals. When given the opportunity, deer select forages with the highest value of all of these essentials within categories. Therefore, deer can be identified as being selective generalist foragers.

An example of this behavior has been demonstrated by Koerth and Stuth (1991). Deer were given a limited number of forage choices, in this case nine species. There was very little spatial variation among the plants. If deer were generalists, all of the plants should have been eaten at an even rate. Instead, each animal appeared to avoid some plant species while eating others. When the preferred plants were devoured, the less palatable plants were eaten. This supports the theory that deer are both selective and generalists. This study shows that deer are selective feeders and attempt to obtain a nutrient optimizing diet (Nudds, 1980).

For deer that live in developed areas, the number of native plants available is

much lower compared to undeveloped areas. Resorts and private land owners often prefer non-native plants because these species are normally greener and lusher than the native plants of the barrier islands and are readily available from nurseries. Therefore, deer are forced to change their normal diet and forage on non-native plants. Many of these non-native plants have a higher caloric value than those naturally found on barrier islands. Eventually deer develop a preference towards these non-native plants and actively seek them out (Tall Timbers Research Inc., 1992).

In addition, many of the non-native plants are not adapted to the specific climate or soil type found on the barrier islands. Therefore, the plants usually require more water, additional nutrients and a more intensive degree of management. The deer may be seeking the nutrients that result from the additional fertilizers and other additives as well as preferring the more succulent vegetation, especially during periods of drought.

Environment plasticity is likely a large component of the change in the deer phenotype. Steffensen et al. (2008) states paleoclimate data reveal that populations that experience a sudden major change in the environment, such as precipitation and temperature, can experience a change in phenotype. In this situation, the sudden change in the environment was a change in available nutrition caused by anthropogenic effects. Thus both the rate and magnitude of the change are important.

It has been proposed that, after a change in the environment, developmental plasticity can cause a relatively rapid change toward a more adaptive phenotype. This can augment change due to natural selection if the change results in increased fitness and has a heritable genetic basis. This process may develop as persistent feedback loop

within the altered environment and lead to more rapid evolutionary changed compared to that expected from natural selection alone (Baldwin, 1896; Morgan, 1896; Osborn, 1897; Osborn and Poulton, 1897; Lande, 2009).

In cases of small or isolated populations, rapid phenotypic adaptations may be necessary to prevent extinction of modern species when subjected to anthropogenic effects, including global warming. This is especially true in species with long generation lengths such as large bodied vertebrates and perennial plants, when natural barriers or artificial habitat destruction and fragmentation restrict opportunities for dispersal and change in geographical range (Peters & Lovejoy, 1994; Lovejoy, 2005; Parmesan, 2006; Gienapp et al., 2008; Lande, 2009). The deer on many of the barrier islands can move from the island to the mainland but very little emigration can actually be detected (Tall Timbers Research Inc., 1992). Deer populations in these coastal areas are relatively dense and increasing (Ruth, 2003) and thus the opportunity for effective dispersal and gene flow is likely limited as empty home ranges would be rare. Thus changes in skull size (Novak, 2003) or body size (Novak, Pers. Comm.) are likely due to rapid evolution as a result of phenotypic plasticity and genetic assimilation (Lande, 2009).

The data from this study indicate that deer diets have changed over the recent past but that this change does not result in a necessarily higher energy diet. Thus, although diet change may be ultimately responsible for structural size changes in white-tailed deer, increased energy from the diet change does not appear to be the mechanistic explanation for this change. Data concerning nutrient structure (i.e. proportions of carbohydrates, proteins and lipids), digestibility and micronutrient and mineral concentrations may

actually be more important than gross caloric value in providing the physiological latitude to allow increased structural size of deer. Unfortunately, such data is not available for deer in these areas so this hypothesis, though logically consistent, is not currently testable. A study to test this hypothesis, although easily designed from an intellectual standpoint, presents numerous logistical difficulties due to its relatively long duration and thus large economic cost.

Management Implications

As stated, deer are generalists but also have preferences for highly palatable plant species. Many ornamental plants are among their favorites. Choosing less palatable herbaceous and woody plants can lower the level of deer browsing (Cummings et al. 1980; Fargione et al., 1991; Craven and Hygnstrom 1994; Curtis and Richmond, 1994; DeNicola et al., 2000). Lowering the number of ornamentals and the use of certain repellents, may minimize the damage caused by foraging deer in areas with low to moderate feeding pressure. It may be less successful in areas where the feeding pressure is very high (Warren, 1995; DeNicola et al., 2000).

This management strategy could also lower the population size, decrease the structural size of the deer, and lower the number of deer-vehicle accidents. By lowering the number of plants with high palatability, the deer will likely return to a more pre-development diet and this will hopefully allow the population to return to a more normal and sustainable population size and body size.

A possible future study on these deer populations, maybe to tag, remove some deer and transplant them onto an undeveloped island or to a penned area. By moving the

deer to an undeveloped island and returning them to a more normal habitat, the deer should after some generations return to normal size. The island would need to have no deer present and would need to be absent of almost all natural predators.

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