

WHITE-TAILED DEER USE OF CLEARINGS RELATIVE TO FORAGE AVAILABILITY

KELLEY M. STEWART,^{1,2} Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University–Kingsville, Kingsville, TX 78363, USA

TIMOTHY E. FULBRIGHT, Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University–Kingsville, Kingsville, TX 78363, USA

D. LYNN DRAWE, Rob and Bessie Welder Wildlife Foundation, P.O. Box 1400, Sinton, TX 78387, USA

Abstract: Use of woodland clearings by white-tailed deer (*Odocoileus virginianus*) may be in response to increased availability of forage within open patches or increased ability of deer to locate predators. We tested predictions, based upon the forage-maturation hypothesis, that white-tailed deer used areas with the greatest availability of high-quality forage, and that habitat use changed seasonally depending upon availability and quality of major types of forage in their diet. We tested those predictions in subtropical thorn woodland in South Texas, United States. Treatments included (1) areas with continuous woody cover as controls, (2) clearings with high availability of forbs and shrub sprouts, (3) clearings with low availability of shrub sprouts, (4) clearings with low availability of forbs, and (5) clearings with low availability of forbs and shrub sprouts. Intensity of use by deer during summer and autumn increased with increasing biomass of shrub sprouts and then declined with increasing shrub biomass as areas became dominated by mature shrubs with less accessible, usable forage. During spring, intensity of deer use increased in clearings with increases in forage availability and quality, indicated by an index to carrying capacity, then declined as vegetation matured. Responses of white-tailed deer to clearings supported the forage-maturation hypothesis in which herbivore responses to clearings resulted, in part, from the presence of shrub sprouts of high nutritional quality, particularly during summer and autumn when forage availability was low. Maintenance of clearings that are interspersed in a woodland matrix and maintaining high levels of immature shrub sprouts may alter the spatial distribution of white-tailed deer on the landscape.

JOURNAL OF WILDLIFE MANAGEMENT 64(3):733–741

Key words: concealment cover, forage-maturation hypothesis, forage quality, *Odocoileus virginianus*, South Texas, subtropical thorn woodland, white-tailed deer.

In the western and southwestern United States, white-tailed deer occupy more open ranges than deer in northern latitudes (Hirth 1977). Deer in the southwest often are seen feeding in large openings and savannas, but retreat into cover during periods of inactivity or when alarmed (Hood 1971, Hirth 1977, Naderman 1979). Use of open areas likely is related to food preferences for succulent vegetation or associated attributes of new plant growth such as nutrient content or tenderness of stems (Chamrad and Box 1968, Rollins et al. 1988).

The forage-maturation hypothesis predicts that net rate of energy intake for grazing herbivores should be maximized on patches of intermediate plant biomass, consisting of plants in early stages of maturity with higher levels of nutrients (Hobbs and Swift 1988, Wilmshurst et al. 1995). At low biomass, forage quality is high

but acquisition of nutrients is limited by the amount of food available; at high plant biomass, mature or senescent plants dominate and nutrient acquisition is limited by lower nutritional quality of forage (Hobbs and Swift 1988, Wilmshurst et al. 1995). Such maturational declines in forage quality have been well documented (Hobbs et al. 1981, Baker and Hobbs 1982). Following mechanical manipulation such as roller chopping, crude protein and phosphorus are greater in resprouts from stem bases of shrubs than in mature plants (Bozzo et al. 1992a, Everitt 1983, Powell and Box 1967, Wilmshurst et al. 1995). Moreover, nutritional quality of shrub sprouts remains elevated for 2–13 months following mechanical treatment (Everitt 1983, Asah et al. 1987, Fulbright et al. 1991, Bozzo et al. 1992a). The forage-maturation hypothesis predicts that herbivores select patches of intermediate forage biomass at early stages of maturity and high quality, and avoid patches low in biomass and those with high biomass dominated by poorly digestible, mature

¹ E-mail: ftkms1@uaf.edu

² Present address: Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

vegetation (Hobbs and Swift 1988, Wilmshurst et al. 1995).

Seasonal shifts in diets of deer may be reflected in seasonal changes in use of clearings, depending upon availability and quality of forage in the diet (Chamrad and Box 1968). In subtropical thorn woodland of South Texas, forbs are the primary components of deer diets during late winter and spring, whereas diets often are dominated by shrubs during summer and autumn when cool-season annual forbs are unavailable and warm-season forbs have matured (Chamrad and Box 1968, Drawe 1968, Meyer et al. 1984, Bozzo et al. 1992b). Consumption of forbs by white-tailed deer increases as forb biomass increases, but deer feed on browse as forb availability and quality diminishes (Chamrad and Box 1968, Drawe and Box 1968, Bryant et al. 1981). Mechanical removal of tops of woody plants may increase forb abundance temporarily and attract foraging deer (Bozzo et al. 1992a).

Most species of woody plants in subtropical thorn woodland sprout from stem bases and crowns after mechanical removal of mature shrubs to ground level (Powell and Box 1967). Increased deer use of treated areas may result from increased availability of immature shrub sprouts and increased availability of forbs. Following mechanical removal, shrub regrowth is more available to deer than mature plants because re-sprouts are of lower stature, and stems and thorns of shrub regrowth are less lignified (Powell and Box 1967). Deer preferred regrowth from woody plants in subtropical thorn woodland following mechanical removal compared with mature shrubs (Box and Powell 1965).

Based upon the forage-maturation hypothesis, we tested the prediction that white-tailed deer use patches containing recent regrowth of woody plants more intensively than patches of mature woody plants or patches with low biomass of shrubs or forbs during summer and autumn. Moreover, we predicted that deer would use patches with a high biomass of forbs.

STUDY AREA

Our study was conducted on the Rob and Bessie Welder Wildlife Foundation Refuge, 11 km north of Sinton, Texas, United States (28°6'N, 97°25'W). The refuge consists of 3,158 ha adjacent to the Aransas River and lies on the transition zone between the Gulf Prairies and Marshes and the South Texas Plains (Gould

1975, Drawe et al. 1978). Elevation is about 12 m (Drawe et al. 1978) and the slope gradient is <1% (Guckian and Garcia 1979).

Climate on the Welder refuge was subtropical with mild winters and hot, humid summers (Drawe et al. 1978). Annual rainfall averaged 88.9 cm from 1956 to 1997, with bimodal peaks in precipitation occurring in late spring (May–Jun) and autumn (Sep–Oct). Mean daily temperature from 1982 to 1997 during winter ranged from 12.8–15.2 °C (Jan–Feb); during spring 18.3–27.7 °C (Mar–Jun); during summer 28.8–32.2 °C (Jul–Sep); and during autumn 22.8–18.3 °C (Oct–Nov). Vegetation in treatment areas included 2 plant communities that were characterized as a live oak (*Quercus virginiana*)–chaparral community, dominated by live oak, and a chaparral–mixed grass community (Drawe et al. 1978). Dominant species of shrubs in both communities were similar, and included blackbrush acacia (*Acacia rigidula*), lotebush (*Zizyphus obtusifolia*), brasil (*Condalia hookeri*), Texas persimmon (*Diospyros texana*), lime pricklyash (*Zanthoxylum fagara*), granjeno (*Celtis pallida*), agarito (*Mahonia trifoliata*), honey mesquite (*Prosopis glandulosa*), huisache (*Acacia smallii*), and twisted acacia (*Acacia schaffneri*). Plant nomenclature follows Hatch et al. (1990).

METHODS

Treatments and Experimental Design

We created open patches by mechanical removal of the woody plants to ground level using roller choppers pulled by a crawler tractor. A roller chopper is a large, heavy, cylindrical metal drum with metal blades mounted parallel to its central axis, which cuts down and chops above-ground portions of woody plants. We used chemical herbicide to manipulate the availability of forbs and shrubs within the open patches. Treatments were applied in a randomized complete-block design with 3 blocks. Each block contained 5, 4-ha plots; treatments were randomly assigned to each plot.

Treatments resulted in (1) an untreated control of continuous woody cover (i.e., mature shrubs in continuous woodland); (2) clearings with high biomass of both forbs and shrub sprouts; (3) clearings with low biomass of shrub sprouts and high forb biomass; (4) clearings with low forb and high shrub-sprout biomass; and (5) clearings with low biomass of both forbs and shrub sprouts. The treatment with high bio-

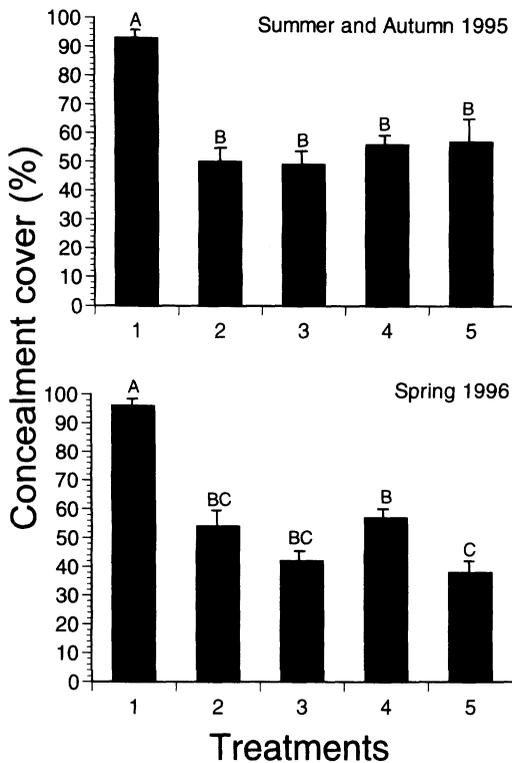


Fig. 1. Means (\pm SE) for concealment cover (%) among 5 4-ha treatment plots for summer and autumn 1995 and spring 1996, Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas, USA. Treatments consisted of (1) control, (2) chop only, (3) chop, reduce shrubs, (4) chop, reduce forbs, and (5) chop, reduce forbs and shrubs. Column means with the same letter are not significantly different (Tukey's HSD, $P > 0.05$) based on randomized complete block design ANOVA for arcsin-square-root-transformed values.

mass of forbs and shrubs had no herbicide application. Woody plants were chopped with a roller chopper in mid-June 1995.

Treatment 3 with low shrub-sprout and high forb biomass was obtained by direct application of the herbicide Tordon 22K[®] (4-amino-3,5,6-trichloropicolinic acid) to woody plants with a carpet roller in November 1994 to minimize the effect of the herbicide on forbs. A carpet roller is a tractor equipped with a revolving drum on the front that is covered with carpet. Herbicides are applied via the carpet-covered drum to woody plants while minimizing impact on herbaceous vegetation; further description is provided in Mayeux and Crane (1985). Roller chopping in mid-June 1995 followed herbicide applications in treatments 3–5.

To obtain treatment 4 with high shrub-sprout and low forb biomass, the herbicide Grazon P+D[®] (4-amino-3,5,6-trichloropicolinic acid

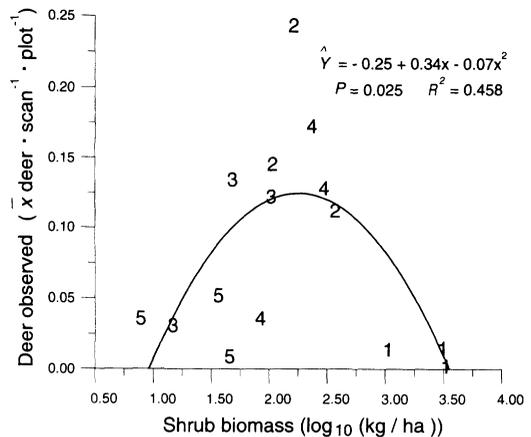


Fig. 2. Use of mechanically created patches in 4-ha plots by white-tailed deer (\bar{x} no. deer · scan⁻¹ · plot⁻¹) versus log₁₀-transformed shrub biomass with the parabola of best fit, summer and autumn 1995, Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas, USA. Numbers on graph correspond to treatments where 1 = control; 2 = chop only; 3 = chop, reduce shrubs; 4 = chop, reduce forbs; and 5 = chop, reduce forbs and shrubs.

and 2,4-dichlorophenoxyacetic acid) was applied at 2.7 L mixed with 11.2 L of water per ha from a helicopter during February 1995 and 1996. Herbicide application was timed to have maximum effects on forbs while minimizing effects on shrubs (i.e., woody plants were dormant and mostly leafless).

Treatment 5 with low biomass of both forbs and shrub sprouts received 567 g Tordon 22K and 567 g Remedy[®] (3,5,6-trichloro-2-pyridinyloxyacetic acid) mixed with 11.2 L of water per ha applied aerially from a helicopter in October 1994. This treatment was followed by hand application of equal parts Tordon 22K, Remedy, diesel, and water to surviving woody plants in May 1995. The herbicide Grazon P+D was applied from a helicopter at 2.7 L Grazon P+D mixed with 11.2 L of water per ha in February 1996, as in treatment 4, to reduce the abundance of annual forbs before spring sampling.

Observations of Deer

Deer were observed daily from August to December 1995 and from March to July 1996 to determine their seasonal use of each treatment. Observations were timed to activity patterns of deer (i.e., major peaks of activity were crepuscular hours; Hood 1971). Observation periods were timed to coincide with those peaks of activity; 2-hr sessions of observations were 30 min before to 1.5 hr after sunrise, and 1.5 hr before to 30 min after sunset. Deer in each

Table 1. Mean number of deer observed in 5 4-ha treatment plots as determined from the total observations from scan sampling, summer and autumn 1995 and spring 1996, Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas, USA.

Treatment ^a	\bar{x}^b	SE
Control	19B	6.6
Chop only	265A	17.6
Chop, reduce shrubs	148AB	37.5
Chop, reduce forbs	202AB	59.8
Chop, reduce forbs and shrubs	109AB	30.2

^a n = 3.

^b Column means with the same letter are not significantly (Tukey's HSD, $P > 0.025$) different based on randomized complete block design ANOVA.

treatment were observed with binoculars from a 4-m tall tripod stand. Deer in plots were counted by scan sampling at 15-min intervals (Altmann 1974).

Because concealment cover was greater in controls, values were weighted based on the estimated visible area in each treatment. Visible area was estimated in a polygon with the perimeter at points of final visibility and observations were weighted based on that area. Observations were weighted separately for each control plot where the weighted observations of deer (W) were equal to the number of deer observed (D) multiplied by the quotient of the plot size (4 ha) divided by area visible (A) to the observer $W = D (4ha/A)$. Visible area in controls ranged from 1.5 to 2 ha.

Vegetation Sampling

Post-treatment sampling of vegetation was conducted during July 1995 and mid-March to mid-April 1996. Sampling dates were selected to coincide with temporal variation in forage quality, where summer (Jul–Sep) was lowest in forage quality and early spring (mid-Mar to mid-Apr) was highest in nutritional quality of forage (Meyer et al. 1984).

Woody and herbaceous biomass were estimated by double sampling of vegetation in 1.5-m-tall and 0.25-m² quadrats to estimate yield of forbs, graminoids, and shrubs (Ahmed and Bonham 1982, Ahmed et al. 1983, Bonham 1989). Relative mass (%) of each species was ocularly estimated in quadrats before clipping. We located quadrats using a stratified-random sampling design along permanently established transects within each treatment and block. We estimated mass in 30 quadrats and clipped a randomly selected subsample of 10 quadrats in

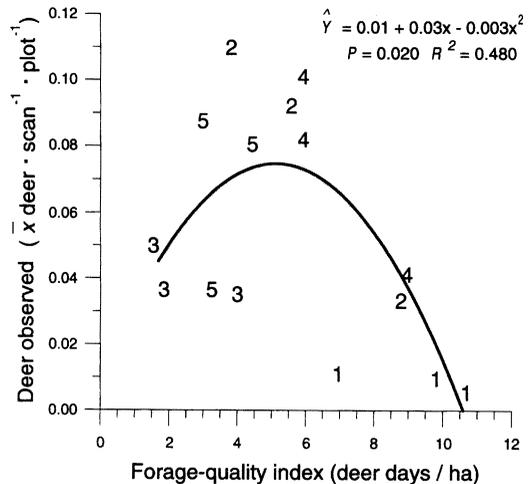


Fig. 3. Use of mechanically created patches in 4-ha plots by white-tailed deer (\bar{x} no. deer · scan⁻¹ · plot⁻¹) versus forage quality (indexed by carrying capacity) with the parabola of best fit, spring 1996, Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas, USA. Numbers on graph correspond to treatments where 1 = control; 2 = chop only; 3 = chop, reduce shrubs; 4 = chop, reduce forbs; and 5 = chop, reduce forbs and shrubs.

each block–treatment combination. The ratio of clipped to estimated plots was determined with equations of Bonham (1989: 202–205). Samples were placed in a forced-air drier at 40–45 °C and dried to a constant mass for about 48 hr to convert estimated wet mass to dry mass.

We determined canopy cover of shrubs with a point-intercept technique (Bonham 1989, Nolte and Fulbright 1997). Points were sampled at 10-m intervals along permanently established transects within each treatment and replication. A thin metal pole (1.3-cm diam by 3.0-m tall) was held vertically at each point and a hit was recorded if it touched a shrub or cactus. Percent canopy cover was quantified as the sum of cover values for each species in which a hit was recorded. Sample size (200 points/treatment–block combination) was determined by plotting number of species encountered versus number of points sampled (Gysel and Lyon 1980). Cover of woody plants and cacti was estimated within each treatment and replication.

Concealment cover for deer was estimated with a profile board about the length (1.5 m) and height (1.2 m) of a deer (Griffith and Youtie 1988). The profile board was covered with a checkerboard pattern and visual estimates of cover were made at distances of 50 m at a randomly selected cardinal direction. Sampling points along permanently established transects

were located with a stratified-random sampling design. We determined sample size (20 points/treatment-block combination) with Stein's equation (Bonham 1989:65–71).

Nitrogen content of shrubs, forbs, and grasses was determined by Kjeldahl analysis (Nelson and Sommers 1973). Dried plants from clipped samples for each forage class were composited, and a random sample was selected and analyzed for nitrogen content; thus, no specific plant species was selected for those analyses. Nitrogen was then multiplied by 6.25 to estimate crude protein (Nelson and Sommers 1973). A carrying capacity model, based on crude protein, from Hobbs et al. (1982) and Svejcar and Vavra (1985), was used as an index that incorporated forage quality (i.e., crude protein) and forage biomass for comparison across treatments. We assumed values calculated with the model provided an index to habitat quality, but made no assumptions about their value in estimating actual carrying capacity. The nutritional model for carrying capacity in summer and autumn 1995 included forbs and shrubs, which have been reported to be the primary diet components of deer during that season (Drawe and Box 1968, Bryant et al. 1981, Meyer et al. 1984, Bozzo et al. 1992b). For spring 1996, grass biomass also was included because deer foraged on new growth of grasses (>2% of diet) during spring (Chamrad and Box 1968, Drawe and Box 1968, Kie et al. 1980, Meyer et al. 1984).

Statistical Analyses

We combined juvenile deer and adult females into 1 age-sex class because juveniles generally followed the adults in their family group. During the course of sampling from August to November, however, fawns became increasingly independent of adult females. To avoid changing methods midway through the study we treated juveniles as independent samples and we lowered alpha (α) to 0.025 for data involving counts of deer, to compensate for any bias resulting from treating juveniles as independent observations.

The age-sex class of adult females and juveniles was compared with an age-sex class of adult males. Adult females and juveniles (af) were 3 times more abundant than adult males (am) on the Welder Refuge; thus we compared use of treatments by sex using the relative proportions of adult males (Pm) where $Pm = am / (af + am)$ (Bowden et al. 1984, Bowyer 1991).

The standard error of Pm was determined by the estimators appropriate for a binomial distribution (Bowden et al. 1984, Bowyer 1991), $SE(Pm) = [Pm(1 - Pm)/(af + am)]$.

Deer responses (total no. deer/plot) to treatments for spring and autumn were analyzed with repeated-measures analysis of variance (ANOVA) for a randomized complete block design to compare treatment means and to test for significant treatment by season interactions. We used Tukey's honestly significant difference (HSD) for multiple comparisons to separate means when *F*-values were significant ($P \leq 0.05$). Planned contrasts are typically employed when treatment comparisons are known a priori; however, some comparisons among our treatments were not expressly predicted by our hypotheses. Nonetheless, those comparisons provided information valuable to correct interpretation of our observations, and in consequence, we employed Tukey's HSD for multiple comparisons instead of planned contrasts (Neter et al. 1996:724–725). Data were further analyzed by season when season by treatment interactions were significant ($P \leq 0.05$).

We used regression analysis to examine relationships between vegetation attributes (i.e., forb biomass, grass biomass, shrub biomass, shrub canopy cover, concealment cover, and nutritional carrying capacity) and number of deer observed in treatments (SAS Institute 1987). We used the variance inflation factor (VIF) to evaluate the effects of multicollinearity in the independent variables in regression (Myers 1990). Intensity of use by deer for ANOVA was determined by the total number of deer observed/plot for all observation periods and then a mean was determined for each treatment ($n = 3$). Mean number of deer observed per scan in each plot was the dependent variable for statistical analyses. Canopy cover of shrubs and values for concealment cover, were arcsine-square-root transformed to satisfy the assumption of the normality for ANOVA (Bonham 1989, Zar 1996). Data on biomass of plants were \log_{10} transformed because standard deviations were proportional to means.

RESULTS

Concealment cover (%) did not differ among treatments during pretreatment sampling in 1994. There was a significant time by treatment interaction ($F_{4,8} = 9.76$; $P < 0.001$) for concealment cover; thus, summer–autumn 1995

and spring 1996 were analyzed separately. During summer and autumn 1995 and spring 1996, concealment cover was significantly greater in control than cleared treatments (Fig. 1; Tukey's HSD, $P \leq 0.05$). During spring 1996, treatments that reduced the availability of shrub sprouts were lower in concealment cover than the treatments where shrubs were not chemically reduced (Fig. 1; Tukey's HSD, $P \leq 0.05$).

Data from deer use of treatments for summer and autumn 1995 and spring 1996 were combined for analysis because no season by treatment interaction occurred ($F_{4,8} = 3.10$; $P = 0.081$) for intensity of use (no. deer/plot) of treatments by deer. The chop only was used more intensively (Tukey's HSD, $P \leq 0.025$) by deer than the control (Table 1). There was no season by treatment interaction in the proportion of males in treatments ($F_{4,8} = 0.67$; $P = 0.209$); however, a significantly lower proportion of males were observed across treatments during spring 1996 than during summer and autumn 1995 ($F_{1,8} = 11.62$; $P = 0.009$). No differences occurred in proportion of males using treatments ($P = 0.310$), indicating that males and females did not differ in their responses to those treatments.

Intensity of deer use of clearings during summer and autumn 1995 showed a significant parabolic relationship with shrub biomass (Fig. 2). Biomass of forbs and graminoids, canopy cover of shrubs, concealment cover, and habitat quality (indexed by carrying capacity) was not related linearly to intensity of use by deer ($R^2 = 0.001$ to 0.229 , $P = 0.149$ to 0.932) or quadratically ($R^2 = 0.063$ to 0.271 , $P = 0.149$ to 0.780) during summer and autumn 1995.

A significant quadratic relationship ($R^2 = 0.507$, $P = 0.014$) existed between deer use and concealment cover during spring 1996; however, there was a relatively high degree of multicollinearity in the independent variables (VIF = 82.77). During spring 1996, intensity of deer use showed a significant parabolic relationship with our index to habitat quality (Fig. 3). Forb biomass, grass biomass, shrub biomass, and shrub canopy cover did not influence intensity of use by deer linearly ($R^2 = 0.014$ to 0.137 , $P = 0.174$ to 0.671) or quadratically ($R^2 = 0.040$ to 0.339 , $P = 0.360$ to 0.782) during spring 1996.

DISCUSSION

Greater use of open patches than continuous woodland by white-tailed deer during summer

and autumn crepuscular, activity periods was partly a response to presence of new sprouts produced by shrubs. Our findings support predictions of the forage-maturation hypothesis because deer used patches with greater new growth of shrubs and avoided controls, which were dominated by mature shrubs. Open patches containing the greatest biomass of shrub sprouts were used more intensively during summer and autumn 1995 than mechanically cleared patches with low biomass of shrub sprouts (Fig. 2). Moreover, few deer were observed in control plots, which had the greatest shrub biomass overall, resulting in a quadratic relationship between shrub biomass and intensity of deer responses (Fig. 2). This relationship supports our hypothesis that deer respond to areas with intermediate biomass of forage of high quality. Because concealment cover in the controls was about 2 to 2.5 times that of the cleared treatments, we believe that our visibility estimates in the controls were adequate for assessing deer use of those areas.

Implicit in the forage-maturation hypothesis is that large herbivores use areas with immature forage and avoid areas with mature forage (Fryxell 1991). Although this hypothesis was developed in areas dominated by graminoids, our data for use of clearings in response to shrub sprouts supported these predictions. The forage-maturation hypothesis partially explained use of our treatment patches by white-tailed deer because shrub biomass in the open patches consisted mainly of sprouts from stem bases of roller-chopped shrubs. Shrub regrowth resulting from mechanical top removal in South Texas is more palatable to white-tailed deer and is temporarily higher in nitrogen, phosphorus, and digestibility than mature growth (Everitt 1983, Asah et al. 1987, Reynolds et al. 1992). Increased use of shrub sprouts by deer in our study may not be consistent with deer use of patches in habitats where shrub sprouts contain high levels of secondary compounds to discourage herbivory (Chapin et al. 1985, Bryant et al. 1994, Bryant and Julkunen-Tiitto 1995). Whether these secondary metabolites occur in regrowth of granjeno, lotebush, brasil, or other shrubs that we sampled with increased palatability following top removal is unknown.

Mature shrubs in South Texas contain a lower percentage of plant material that is current annual growth than shrub sprouts and are protected by thorns and woody stems, which discourage her-

bivory (Powell and Box 1966). Optimal-foraging theory assumes that foraging decisions by herbivores are strongly influenced by physiological and environmental constraints on rates of nutrient uptake (Hobbs and Swift 1988, Wilmshurst et al. 1995, Kie 1999). Although bite size was not measured, energy gain likely was lower in controls because physical defenses of shrubs would require smaller bites, whereas shrub sprouts with nonglified stems and thorns allow greater energy gain with increased size of bites. Because mature woody plants are less accessible to browsers, less palatable, and less nutritious, large herbivores will tend to concentrate on forages where constraints are lessened (Powell and Box 1966, Bozzo et al. 1992a). This prediction is consistent with observed responses of *Acacia* species in Africa, where heavily browsed plants were more palatable than those with light browsing, because of increased production of shoots (du Toit et al. 1990).

At low levels of shrub biomass, energy gain is decreased with greater search time and less forage available once a patch of forage is located. Honey mesquite was the primary shrub present in the treatment where forbs and shrubs were reduced; although resistant to herbicide applications, honey mesquite is not preferred by white-tailed deer (Drawe 1968). The treatment with reduced forbs and shrubs can be regarded as a habitat patch that was less desirable to deer during summer and autumn because of low shrub biomass dominated by a single unpalatable species. Daily energy gain of deer was probably low in the control treatment, which had high shrub biomass, but supported mature shrubs of lower nutritional quality that were protected by thorns and woody stems.

Spring 1996 was characterized by severe drought. Spring is commonly a period of peak forage quality, and deer concentrate feeding on forbs and new grass growth (Chamrad and Box 1968, Drawe 1968, Meyer et al. 1984). Annual forbs that normally are exploited heavily by deer during spring were scarce or not available during our study, and leaf development of most shrubs was delayed following winter dormancy. Deer responses to treatments in spring 1996 probably differed from deer responses during periods of average rainfall and forage biomass, when annual forbs and new grass growth are more readily available. Although use of treatments shifted between summer–autumn and spring, we were unable to critically test if the responses shifted from shrub sprouts to forbs

because of the low availability of forbs and other forages during drought.

During spring 1996, deer responses were related directly to forage quality and availability. The quadratic relationship (Fig. 3) between deer use of treatments and our index of habitat quality indicated that deer responded to forage quality in cleared treatments and avoided controls. This relationship also supported our hypothesis that deer concentrate in areas with intermediate forage biomass of higher quality. Deer were more opportunistic during the drought and did not concentrate feeding on a specific forage class, as observed during summer and autumn 1995 with shrub sprouts.

Greater nutritional gain for deer may come from open patches where accessible forage was greater. This gain was likely either a function of greater bite size or greater time spent foraging. Length of time spent foraging is an important factor in acquiring the necessary resources for survival and reproduction. Fryxell (1991) suggested that aggregation patterns of large herbivores might be influenced simultaneously by maturational changes in forage quality, spatial variations in forage quality or productivity, and risk of predation. Young et al. (1995) proposed that congregation of wild herbivores in treeless glades in Kenya was a response to better food and protection from predators.

Although no treatment differences occurred in the proportion of males observed across treatments during the sampling periods, proportion of males observed during spring 1996 was significantly lower than during summer and autumn 1995. Adult males may have moved away from the study area. There was no hunting on the Welder Refuge prior to or during our study, thus fewer males resulting from hunting mortality is not a likely explanation for fewer bucks observed during spring. This movement may be attributed to differences in habitat use between females and males resulting from sexual segregation during spring. During the nonmating season, many ungulates exhibit pronounced sexual segregation (Bowyer 1984, Bleich et al. 1997, Main et al. 1996, Miquelle et al. 1992) and differences in habitat use between males and females on the Welder Refuge during the nonmating season have been observed (Kie and Bowyer 1999).

MANAGEMENT IMPLICATIONS

Maintaining shrubs at intermediate levels of biomass with mechanical manipulation enhances

habitat quality for white-tailed deer by providing overall higher quality and availability of forage. A caveat to this statement, however, is that reduction of shrub diversity with some types of mechanical manipulation reduces habitat quality. This statement is supported by poor responses to the low forb and shrub treatment, which was dominated by a single, unpalatable species of shrub. Maintaining mature thorn woodland for bedding and escape cover is also necessary to maintain suitable habitat for white-tailed deer (Rollins et al. 1988, Bozzo et al. 1992b), especially in this hot and humid environment.

Mechanical top removal of shrubs may be used selectively to manipulate spatial distribution of white-tailed deer. Chemical removal of shrubs, particularly in summer, may be detrimental to habitat quality for white-tailed deer because biomass of immature shrub sprouts and shrub diversity are reduced; however, methods that stimulate shrubs to produce new sprouts, such as roller chopping or fire, may be used to improve and manipulate habitat for white-tailed deer. Maintenance of clearings interspersed in woodland matrix and maintaining high levels of immature shrub sprouts may alter the spatial distribution of white-tailed deer and other large ungulates on the landscape.

ACKNOWLEDGMENTS

Mention of a product or trade name does not indicate an endorsement by the authors or Texas A&M University-Kingsville. The authors thank H. Mayeux for applying herbicides with the carpet roller, R. Bingham for assistance in statistical analyses, and R. T. Bowyer, D. Hewitt, T. Ginnett, J. G. Kie, and B. Dick for reviewing our manuscript. The Rob and Bessie Welder Wildlife Foundation funded our research. This paper is Welder contribution number 542 and Caesar Kleberg Wildlife Research Institute number 98-111.

LITERATURE CITED

- AHMED, J., AND C. D. BONHAM. 1982. Optimum allocation in multivariate double sampling for biomass estimation. *Journal of Range Management* 35:777-779.
- , ———, AND W. A. LAYCOCK. 1983. Comparison of techniques used for adjusting biomass estimated by double sampling. *Journal of Range Management* 36:217-221.
- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- ASAH, H. A., T. E. FULBRIGHT, AND M. L. LAND. 1987. Effects of simulated browsing on spiny hackberry after top removal. *Texas Journal of Agriculture and Natural Resources* 1:16-18.
- BAKER, D. L., AND N. T. HOBBS. 1982. Composition and quality of elk summer diets in Colorado. *Journal of Wildlife Management* 46:694-703.
- BLEICH, V. C., R. T. BOWYER, AND J. D. WEYHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134.
- BONHAM, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York, New York, USA.
- BOWDEN, D. C., A. E. ANDERSON, AND D. E. MEDIN. 1984. Sampling plans for mule deer sex and age ratios. *Journal of Wildlife Management* 48:500-509.
- BOWYER, R. T. 1984. Sexual segregation in southern mule deer. *Journal of Mammalogy* 65:410-417.
- . 1991. Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* 72:138-145.
- BOX, T. W., AND J. POWELL. 1965. Brush management techniques for improved forage values in south Texas. *Transactions of the North American Wildlife Conference* 30:285-296.
- BOZZO, J. A., S. L. BEASOM, AND T. E. FULBRIGHT. 1992a. Vegetation responses to two brush management practices in south Texas. *Journal of Range Management* 45:170-175.
- , ———, AND. 1992b. White-tailed deer use of rangeland following browse rejuvenation. *Journal of Range Management* 45:496-499.
- BRYANT, F. C., C. A. TAYLOR, AND L. B. MERRILL. 1981. White-tailed deer diets from pastures in excellent and poor range condition. *Journal of Range Management* 34:193-200.
- BRYANT, J. P., AND R. JULKUNEN-TIITTO. 1995. Ontogenetic development of chemical defense by seedling resin birch: energy cost of defense production. *Journal of Chemical Ecology* 21:883-896.
- , R. K. SWIHART, P. B. REICHARDT, AND L. NEWTON. 1994. Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America. *Oikos* 70:385-395.
- CHAMRAD, A. D., AND T. W. BOX. 1968. Food habits of white-tailed deer in south Texas. *Journal of Range Management* 21:153-164.
- CHAPIN, F. S., II, J. P. BRYANT, AND J. F. FOX. 1985. Lack of induced chemical defense in juvenile Alaskan woody plants in response to simulated browsing. *Oecologia* 67:457-459.
- DRAWE, D. L. 1968. Mid-summer diet of deer on the Welder Wildlife Refuge. *Journal of Range Management* 21:164-166.
- , AND T. W. BOX. 1968. Forage ratings for deer and cattle on the Welder Wildlife Refuge. *Journal of Range Management* 21:225-228.
- , A. D. CHAMRAD, AND T. W. BOX. 1978. Plant communities of the Welder Wildlife Refuge. Welder Wildlife Foundation Contribution No. 5, Series B, Revised. Sinton, Texas, USA.
- DU TOIT, J. T., J. P. BRYANT, AND K. FRISBY. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savannah browsers. *Ecology* 71:149-154.
- EVERITT, J. H. 1983. Effects of plant shredding on

- nutrient content of four south Texas deer browse species. *Journal of Range Management* 36:779–781.
- FRYXELL, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138: 478–498.
- FULBRIGHT, T. E., J. P. REYNOLDS, S. L. BEASOM, AND S. DEMARIS. 1991. Mineral content of guajillo regrowth following roller chopping. *Journal of Range Management* 44:520–522.
- GRIFFITH, B., AND B. A. YOUTIE. 1988. Two devices for estimating foliage density and deer hiding cover. *Wildlife Society Bulletin* 16:206–210.
- GOULD, F. W. 1975. Texas plants—a checklist and ecological summary. Texas Agricultural Experiment Station Technical Bulletin, Texas A & M University, College Station, Texas, USA.
- GYSEL, L. W., AND L. J. LYON. 1980. Habitat analysis and evaluation. Pages 305–327 in S. D. Schemnitz, editor. *Wildlife techniques manual*. The Wildlife Society, Washington, D.C., USA.
- HATCH, S. L., K. C. GANDHI, AND L. E. BROWN. 1990. Checklist of the vascular plants of Texas. Texas Agricultural Experiment Station Report MP-1655.
- HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53.
- HOBBS, N. T., D. L. BAKER, J. E. ELLIS, AND D. M. SWIFT. 1981. Composition and quality of elk winter diets in Colorado. *Journal of Wildlife Management* 45:156–171.
- _____, _____, _____, AND R. A. GREEN. 1982. Energy- and nitrogen-based estimates of elk winter-range carrying capacity. *Journal of Wildlife Management* 46:12–21.
- _____, AND D. M. SWIFT. 1988. Grazing in herds: when are nutritional benefits realized? *American Naturalist* 131:760–764.
- HOOD, R. E. 1971. Seasonal variations in home range, diet, movement and activity patterns of white-tailed deer on the Rob and Bessie Welder Wildlife Refuge (San Patricio County, Texas). Thesis, Texas A&M University, College Station, Texas, USA.
- KIE, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* 80:1114–1129.
- _____, AND R. T. BOWYER. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy* 80:1004–1020.
- _____, D. L. DRAWE, AND G. SCOTT. 1980. Changes in diet and nutrition with increased herd size in Texas white-tailed deer. *Journal of Range Management* 33:28–34.
- MAIN, M. B., F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77: 449–461.
- MAYEUX, H. S., AND R. A. CRANE. 1985. Application of herbicides on rangelands with a carpeted roller: evaluation of four herbicides for control of honey mesquite. *Journal of Range Management* 38:233–237.
- MEYER, M. W., R. D. BROWN, AND M. W. GRAHAM. 1984. Protein and energy content of white-tailed deer diets in the Texas Coastal Bend. *Journal of Wildlife Management* 48:527–534.
- MIQUELLE, D. G., J. M. PEEK, AND V. VAN BALLEMBERGHE. 1992. Sexual segregation in Alaskan moose. *Wildlife Monographs* 122.
- MYERS, R. H. 1990. Classical and modern regression with applications. PWS-Kent Publishing, Boston, Massachusetts, USA.
- NADERMAN, J. F. 1979. Deer use of different size mechanically cleared openings in south Texas brush. Thesis, Texas Tech University, Lubbock, Texas, USA.
- NELSON, D. W., AND L. E. SOMMERS. 1973. Determination of total nitrogen in plant material. *Agronomy Journal* 65:109–112.
- NETER, J., M. H. KUTNER, C. J. NACHTSHEIM, AND W. WASSERMAN. 1996. *Applied linear statistical models*. Fourth edition. Richard D. Irwin, Homewood, Illinois, USA.
- NOLTE, K. R., AND T. E. FULBRIGHT. 1997. Plant, small mammal, and avian diversity following control of honey mesquite. *Journal of Range Management* 50:205–212.
- POWELL, J., AND T. W. BOX. 1966. Brush management influences preference values of South Texas woody species for deer and cattle. *Journal of Range Management* 19:212–214.
- _____, AND _____. 1967. Mechanical control and fertilization as brush management practices affect forage production in south Texas. *Journal of Range Management* 20:227–236.
- REYNOLDS, J. P., T. E. FULBRIGHT, AND S. L. BEASOM. 1992. Mechanical rejuvenation to dampen seasonal variation in chemical composition of browse. *Journal of Range Management* 45:589–592.
- ROLLINS, D., F. C. BRYANT, D. D. WAID, AND L. C. BRADLEY. 1988. Deer response to brush management in central Texas. *Wildlife Society Bulletin* 16:277–284.
- SAS INSTITUTE. 1987. *SAS/STAT guide for personal computers*. Version 6. SAS Institute, Cary, North Carolina, USA.
- SOIL CONSERVATION SERVICE. 1979. Soil survey of San Patricio and Aransas Counties, Texas. Soil Conservation Service, Washington, D.C., USA.
- SVEJCAR, T., AND M. VAVRA. 1985. The influence of several range improvements on estimated carrying capacity and potential beef production. *Journal of Range Management* 38:395–399.
- WILMSHURST, J. F., J. M. FRYZELL, AND R. J. HUDSON. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* 6: 209–217.
- YOUNG, T. P., N. PATRIDGE, AND A. MACRAE. 1995. Long-term glades in *Acacia* brushland and their edge effects in Laikipia, Kenya. *Ecological Applications* 5:97–108.
- ZAR, J. H. 1996. *Biostatistical analysis*. Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Received 21 May 1999.

Accepted 31 January 2000.

Associate Editor: Krausman.