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Role of thermal environment in habitat selection by male white-tailed deer during summer in Texas, USA

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Thermal cover may influence habitat selection by white-tailed deer *Odocoileus virginianus* in subtropical climates with hot summers. We 1) tested the hypothesis that thermal environment is more important in habitat selection at midday during summer than forage quality or quantity and concealment cover and 2) determined whether operative temperature, vegetation height, or woody plant canopy cover (or some combination of these) explain habitat selection at midday. We predicted that during crepuscular periods and at night habitat use increases with increasing forage quality and quantity and concealment cover and is unrelated to thermal environment. Male white-tailed deer were fitted with GPS collars to determine resources selected within habitats during June and July 2008 and 2009. A generalized linear mixed model using logistic regression was used to estimate resource selection functions. We used the first principal component in a principal components analysis (PCA) of forage standing crop, crude protein, and acid detergent fiber (ADF) to create a 'forage index'. This index and vegetation height, operative temperature and concealment cover, together with their interactions with activity period, were used to develop a priori candidate models. Akaike weights were used to compare candidate models. A model that included the forage index, vegetation height, operative temperature, concealment cover and their interactions with activity period was the best model out of 97 candidate models for explaining habitat selection by adult male white-tailed deer. Male white-tailed deer selected areas with taller vegetation in morning and midday activity periods but selected shorter vegetation during evening and nighttime. Forage quality was important in habitat selection in all activity periods. Male white-tailed deer did not select areas with greater concealment cover during any activity period. A combination of operative temperature, vegetation height, and woody plant canopy cover predicted midday habitat use better than any of these three variables alone. Thermoregulatory behavior in male white-tailed appears to include a combination of seeking cooler environments during midday but at the same time using areas with greater forage quality.

Temperature is an important factor influencing habitat selection by cervids (Schmitz 1991, van Beest et al. 2012). Effects of temperature, particularly cold temperatures, on white-tailed deer *Odocoileus virginianus* have been documented in temperate environments (Beier and McCullough 1990), but the effects of heat on habitat selection in subtropical environments are unclear. To reduce heat stress, cervids commonly become inactive and bed in areas with dense vegetation canopy cover (Sargeant et al. 1994, Mysterud and Østbye 1999, Germaine et al. 2004, Bowyer and Kie 2009). In southern Texas where maximum daily temperatures during summer may exceed 38°C, the need for thermal cover to reduce heat stress should be a major factor influencing selection of plant communities by white-tailed deer during midday.

Observations of several researchers suggest that thermal cover is important during hot weather for white-tailed deer in southern Texas and northern Mexico. For example, shrub canopy cover was unrelated to resource selection by white-tailed deer in southern Texas during autumn and winter, but during summer deer densities increased with increasing shrub canopy cover (Steuter and Wright 1980). Gallina et al. (2010) used vegetation canopy cover as a measure of thermal cover for white-tailed deer in Mexico. They concluded that deer selected bedsites with greater thermal cover and concealment cover (vertical vegetation cover that may visually obstruct detection by predators) during midday.

Some researchers, in contrast, have questioned the importance of thermal cover for cervids (Cook et al. 1998, 2004). Ungulates may employ other behavioral strategies than selecting thermal cover for reducing heat stress; for example, they may select open areas on windy days for convective cooling or they may orient their body to reduce exposure to solar radiation (Cain et al. 2008, Bowyer and Kie 2009). In addition, when deer select habitats with greater woody plant cover it is often unclear whether woody cover is being

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used for thermal cover, concealment, or for food (Pollock et al. 1994). Thermal cover and concealment cover are often confounded, however, making it difficult to determine if deer are selecting habitat for thermoregulatory reasons or to hide from predators (Bowyer and Kie 2009). Operative temperatures in areas that were used and avoided by deer have seldom been measured in habitat selection studies (Bakken and Gates 1975).

Including estimates of operative temperature with vegetation cover measurements may provide a more complete explanation of habitat selection by deer in response to temperature extremes (Bowyer and Kie 2009). Operative temperature integrates thermal characteristics of the environment experienced by an animal including ambient temperature, solar radiation, and thermal radiation (Dzialowski 2005). Operative temperatures provide an estimate of the thermal environment experienced by an animal by measuring the integration of convective and radiant heat transfer between an animal and the environment (Bakken and Gates 1975, Bakken 1976).

White-tailed deer should trade off use of plant communities with more concealment cover for plant communities with lower operative temperatures if thermoregulation is more important than avoiding predators during summer at midday. Although forage quality and quantity are often important resources in habitat selection (van Beest et al. 2010), deer would be expected to trade off selection for plant communities with greater forage quality and quantity for plant communities with lower operative temperatures, greater canopy cover, and taller vegetation during midday in summer to avoid heat stress.

Our primary objective was to test the hypothesis that variables that may be associated with a cooler environment (operative temperature, vegetation height and woody plant canopy cover) are more important in explaining habitat use than concealment cover or variables associated with foraging, including plant nutritional quality and standing crop, during midday. We predicted that concealment from predators and forage quality and abundance are more important than thermal environment in explaining habitat use during activity periods other than midday.

Woody plant canopy cover is often mentioned in the literature as a measure of thermal cover (Demarchi and Bunnell 1993, Cook et al. 2004, Gallina et al. 2010). Whether woody canopy cover is an adequate descriptor of thermal cover, or if operative temperature or vegetation height provide a better measure of thermal cover has not been addressed in the literature. Our second objective was to determine whether operative temperature, vegetation height, and woody plant canopy cover explain habitat selection at midday better individually or in some combination.

Material and methods

Study area

We conducted research in a 5579 ha study area in Kleberg County, Kingsville, TX, USA (27°28′10″N, 97°37′26″W). Climate of the study area is subtropical, subhumid to semiarid (Norwine et al. 2007). The soil is Victoria clay (NRCS 2009) and vegetation is a mesquite *Prosopis glandulosa*–mixed brush community (Meyer and Brown 1985). In the southwestern and central location of the study area, 475 ha and 245 ha (i.e. consisted of 13% of the study area) were root plowed during spring and summer 2008. Clumps of brush averaging 40 × 60 m and 100 m apart were left in the cleared strips that alternated with 100 m-wide strips of uncleared brush. Plant communities within the study area were delineated using ArcGIS 9.3 software and an aerial photographic image with a scale and resolution of 1:1250. Ten plant communities were delineated based on woody plant species composition and density.

Operative temperatures and woody canopy cover

During summer 2008, ten 30-m transects were established in a stratified random manner within each vegetation community using Hawth's Analysis Tools 3.8 in ArcGIS 9.3 (Beyer 2004). Copper spheres, 15.24 cm in diameter were painted matted black and mounted 0.5 m above the ground to simulate the operative temperature a white-tailed deer may experience while laying down or standing. Fifty-one blackglobes (i.e. copper spheres) were deployed in 2008. From the origin of each of three transects in each plant community, the nearest woody plant representing similar canopy height and width of other woody plants in the community were selected. At each woody plant, a blackglobe was placed halfway between the trunk and canopy edge on the eastern and western sides of each woody plant. Six blackglobes were placed under three shrubs in each of seven woody plant communities. We placed three blackglobes in each of three grassland communities and in communities that contained minimal woody canopy cover.

A HOBO (Honest Observation By Observer, Cape Cod, MA, USA) pendant data logger was suspended in the center of each blackglobe and was programmed to measure operative temperatures every 30 min. Temperatures recorded in the blackglobes within each plant community were averaged every 30 min to represent temperatures available to deer at the plant community scale from17 June – 22 July 2008 and 2009 (i.e. 48 operative temperatures day^{-1} plant community^{-1}). The line intercept method was used to estimate percent woody plant canopy cover along each 30-m transect with each plant community during July 2009 and July 2009 (Canfield 1941).

Vegetation height

Light detection and ranging (LIDAR) data were collected on the study area during 26 October 2007 by AeroMetric, Inc. Bare ground and first return data were used to determine vegetation height using ArcMap ver. 9.3 (ESRI 2009). A triangular irregular network (TIN) was created representing the land surface (i.e. bare ground, first return) data within the geodatabase. Bare ground and first return TINs were used to create a 1.2 m digital elevation model (DEM) for each land surface. Vegetation heights were calculated by subtracting the first return DEM and bare ground DEM.

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Forage standing crop and nutritional quality

Vegetation was sampled during July 2008 and July 2009 using the 10 transects within each plant community. Mass of creeping bundleflower *Desmanthus virgatus*, false ragweed *Parthenium confertum*, western ragweed *Ambrosia psilostachya*, Texas nightshade *Solanum triquetrum*, spiny hackberry *Celtis ehernbergiana*, brasil *Condalia hookeri*, guayacan *Guaiacum angustifolia* and mistflower *Eupatorium odoratum* was ocularly estimated in four 1.5 m tall × 0.25 m^2 quadrats every 10 m along each transect (n = 436 total quadrats) (Ahmed and Bonham 1982, Ahmed et al. 1983). These species were preferred by white-tailed deer based on research conducted near the study area in a location with similar habitat (Meyer et al. 1984). We randomly selected one quadrat along each transect and harvested plant material in each forage class (109 of the 436 were harvested), dried samples at 40°C to a constant mass, and used the ratio of clipped mass to estimated mass to correct estimated standing crop values to dry mass (Bonham 1989: pp. 202–205). The sum of dry mass for the eight selected plant species that were present in each community is reported as forage standing crop herein.

A modified profile board measuring 1.2 m tall × 30.5 cm wide with six 20-cm squares was used to estimate concealment cover (Griffith and Youtie 1988, Bowyer et al. 1998). Percentage of vegetation covering each square was estimated when the profile board was placed in a randomly selected cardinal direction 15 m from the origin of each transect.

Creeping bundleflower, false ragweed, western ragweed, Texas nightshade, spiny hackberry, brasil, guayacan and mistflower were selected to index nutritional quality of forage available at the plant community scale (Meyer et al. 1984). Depending on availability, 1–3 woody plants were sampled at each transect to obtain ≥ 20 g (wet mass) for each woody plant species. Plants were then placed on dry ice at –10°C (Cash and Fulbright 2005). Plant samples from within each plant community were aggregated by plant species, freeze dried, and ground in a Wiley mill.

We used crude protein as one measure of forage quality because white-tailed deer foraging preferences are strongly associated with the protein content of plants (Dostaler et al. 2011). Nitrogen (%) in plant samples was determined using an elemental analyzer.

Plant communities with limited digestible energy may influence selection (Meyer et al. 1984); therefore we determined acid detergent fiber (ADF) of the eight plants species as an estimate of the available digestible energy. A fiber analysis system was used to determine ADF (Goering and VanSoest 1970).

GPS collar data

Male white-tailed deer were captured in a 1350 ha pasture in the center of the study area using the helicopter net gun technique (Barrett et al. 1982, Webb et al. 2008). Males ≥ 2.5 years based on tooth replacement and wear (Severinghaus 1949) were fitted with GPS collars that collected relocations every 30 min. Capture and handling procedures were approved by the Texas A&M University – Kingsville Institutional Animal Care and Use Committee (no. 2008-01-18A).

GPS collars were placed on 14 male white-tailed deer during 2008 and 2009. Collars were retrieved during September of each year following release by a drop-off mechanism. GPS collar data used in analyses were uncorrected because GPS radiotelemetry data loss was < 10% (D'Eon 2003). We considered the habitat available to each deer to be the area within the individual home ranges of each deer during 17 June – 22 July 2008 and 2009. Home range was calculated using the Home Range Tools third party extension in ArcGIS 9.3 (Rodgers et al. 2007, ESRI 2009). We used the fixed kernel home range estimator because it produces an unbiased density estimator and is not influenced by grid size or placement (Silveman 1986). Home ranges were constructed using a 95% probability contour to encompass frequently used habitats.

GPS collar locations during 17 June – 22 July 2008 and 2009 and home ranges of each deer during the same period were overlaid on the plant communities delineated within the study area to determine deer locations. Deer locations during these time periods were used so that vegetation variables would be representative of the conditions when deer location data were collected. Means of operative temperature, woody plant canopy cover, concealment cover, forage standing crop, forage crude protein and forage ADF were extrapolated within each plant community. Values for operative temperature every half hour and vegetation variables except for vegetation height for locations within each plant community were plant community means; means of the estimates within each plant community were used in statistical analyses.

Using ArcGIS 9.3 software, each GPS collar location within the home range of each deer was spatially joined with each plant community attribute (i.e. standing crop, concealment cover, crude protein, ADF and woody cover) based on the corresponding plant community where the deer was located. Plant community operative temperatures during each half hour by day were spatially joined to the GPS collar location based on the corresponding plant community where the deer was located. Using ArcGIS 9.3 software, deer relocations were spatially joined with the corresponding pixel of the raster that represented the height of the vegetation. As a result, each pixel represented a 1-m^2 surface within the raster and each pixel represented a vegetation height that corresponded to each deer location.

For each deer location, a random location was also generated within the deer's home range using Hawth tools extension in ArcGIS 9.3. Random locations were likewise joined spatially to the appropriate plant community attribute, operative temperature, and vegetation height following the same process as deer relocations. Joining each deer relocation and random location to a plant community attribute, operative temperature and vegetation height allowed the appropriate plant community characteristics to be associated with each deer relocation and random location.

Covariables

White-tailed deer habitat selection is influenced by agricultural fields, roads, and water availability and usage (Vercauteren and Hygnstrom 1998, Cooper et al. 2006, 2008, Webb et al. 2006). The distance of each deer to the

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nearest agricultural field, road, and water source (i.e. water sources included concrete troughs used for cattle with a continuous water supply) was calculated for each relocation using ArcGIS 9.3 Spatial Analyst software. Dry feeds in a pellet form were provided to deer in a pasture > 3 km away from the study area. In case presence of feed influenced habitat selection, we included distances of each deer to the nearest feeder. Distances to the nearest agricultural field, road, feed and water source were also calculated for random points.

Statistical methodology

Each deer relocation and random site was assigned values for habitat attributes (standing crop, crude protein, operative temperature, concealment cover, woody cover, vegetation height and ADF) that were averages of the plant community where it was located. It is likely that effects of habitat characteristics on resource selection also depend on time of day. Therefore, we identified four periods that coincided with daily crepuscular (morning, evening), diurnal (midday), and nocturnal activities. We delineated activity periods based on average daily patterns of movement. To do this, we calculated the average distance moved between consecutive GPS locations using all deer and plotted them (Fig. 1). We considered morning and evening periods of movement to constitute crepuscular periods and reduced midday movement to constitute the diurnal period. Nocturnal periods were from 1 h after sundown to 1 h before sunrise.

Objective 1. Variables important in explaining habitat use at midday

Woody cover and concealment were linearly related ($r = 0.9862$) and we removed woody cover from this analysis; pairwise linear correlations between remaining independent variables (concealment cover, operative temperature, vegetation height and the forage index ranged from $r = -0.027$ (forage index and operative temperature) to $r = 0.222$ (operative temperature and vegetation height). We conducted additional analyses as explained below to support biological interpretation of the data.

We used a generalized linear mixed model to estimate third order (Johnson 1980) resource selection functions (Manly et al. 2002). We modeled individual deer nested within year as a random effect; fixed effects of interest included vegetation height, operative temperature, the foraging index, and concealment cover; activity period and its interactions with each of these effects was also included. Distances to agriculture fields, roads, supplemental feed, and water were included in each model as fixed nuisance covariables. The four predictor variables together with their interactions with activity period were used to develop 97 candidate models. Akaike weights were used to compare models (Burnham and Anderson 2002) using program MuMIn (Barton 2013) in R. Effects of the concealment cover, vegetation height, operative temperature and forage (the latter effect through its derived index) were tested in each activity period in the selected model using contrast statements for this model in SAS ver. 9.2 in PROC GLIMMIX to test the prediction that habitat use during midday is reflective of the thermal environment and during all other activity periods the thermal environment is unrelated to habitat use.

We created a 'forage index' by using the first principal component in a principal components analysis (PCA) of forage crude protein, ADF and standing crop: the first principal component explained 84% of the variation in these variables. In order to better understand how the factors affecting the forage index influenced resource selection during the midday activity period, we used a generalized linear mixed model that included deer nested within year as a random effect and the fixed nuisance variables to analyze the direct effects of standing crop, crude protein, and acid detergent fiber on habitat selection; the model included activity period and its interactions with the forage variables.

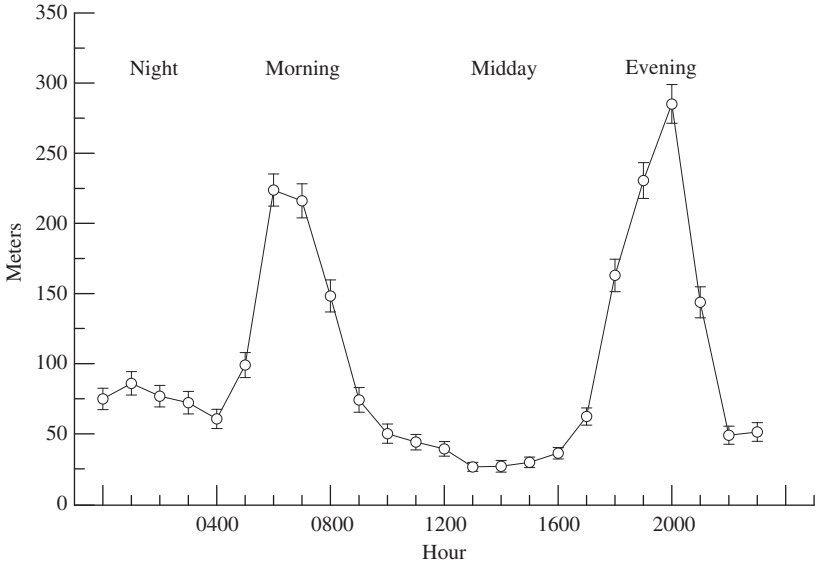


Figure 1. Mean distance moved / hour for male white-tailed deer during morning, midday, evening, and nighttime activity periods (± 95% CI, n = 14), 17 June – 22 July, 2008–2009, Kleberg County, TX, USA.

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Objective 2. Operative temperature, vegetation height and woody plant canopy cover

We used generalized linear mixed models and we fit three models to determine if operative temperature, vegetation height and woody cover explain habitat selection at midday better individually or in some combination. Each model included the fixed nuisance covariables and individual nested within year as a random effect. In addition to these variables, model 1 included woody canopy cover, vegetation height, and operative temperature; model 2 included woody canopy cover and vegetation height; and model 3 included operative temperature. We used Akaike weights to compare these three models; in addition, model 1 and 2, and model 1 and 3, were compared with likelihood ratio tests.

Results

One GPS collar malfunctioned, two males died in spring 2008, and five males left the study area; therefore, these individuals were excluded from statistical analyses. We also excluded four males that died in 2009 and two males that were outside of the study area from statistical analyses. The final sample size used in analyses was six males in 2008 and eight males in 2009, respectively.

Mean daily maximum ambient temperatures during 17 June – 22 July was 33°C in 2008 and 36.5°C in 2009 (Fig. 2). Among plant communities, operative temperatures were within a 5°C and a 3°C range in 2008 and 2009, respectively (Table 1). The study area received 483 mm and 99 mm of precipitation during 2008 and 2009, respectively, compared to a median (1977–2009) rainfall of 798 ± 41 mm (median ± SE). Male white-tailed deer were the least active during midday (Fig. 1). Home ranges averaged 652 ± 240 ha, n = 6, during 17 June – 22 July 2008 and 383 ± 44 ha, n = 8, during the same period in 2009.

Objective 1. Variables important in explaining habitat use at midday

A model that included vegetation height, operative temperature, concealment cover, and the forage index together with all of their interactions with activity period, had a Akaike model weight = 0.89 and was the best model out of 97 candidate models for explaining habitat selection by adult male white-tailed deer. Concealment was negatively related to relative probability of use during all activity periods whereas the forage index was positively related to relative probability of use during all activity periods. Vegetation height was most strongly (and positively) related to relative probability of use during midday, and strongly (and negatively) related to relative probability of use during night; in addition, vegetation height was less related to relative probability of use during morning and not related during evening. Operative temperature was negatively related to relative probability of use in midday but otherwise positively related (Table 2; these interpretations were confirmed with single-variable analyses).

When we considered the effect of our forage variables individually, their effects on habitat selection depended on activity period (Fig. 3). The relative probability of a deer using an area increased with increasing forage crude protein and declined with increasing ADF during all activity periods. Standing crop was negatively related to probability of use during all time periods except nighttime.

Objective 2. Operative temperature, vegetation height, and woody plant canopy cover

There was a three-way interaction between woody canopy cover, operative temperature and vegetation height on resource selection during midday (Fig. 4). The general shape of the response surface involving operative temperature and vegetation height became more convoluted as woody canopy cover increased. For example, regardless of

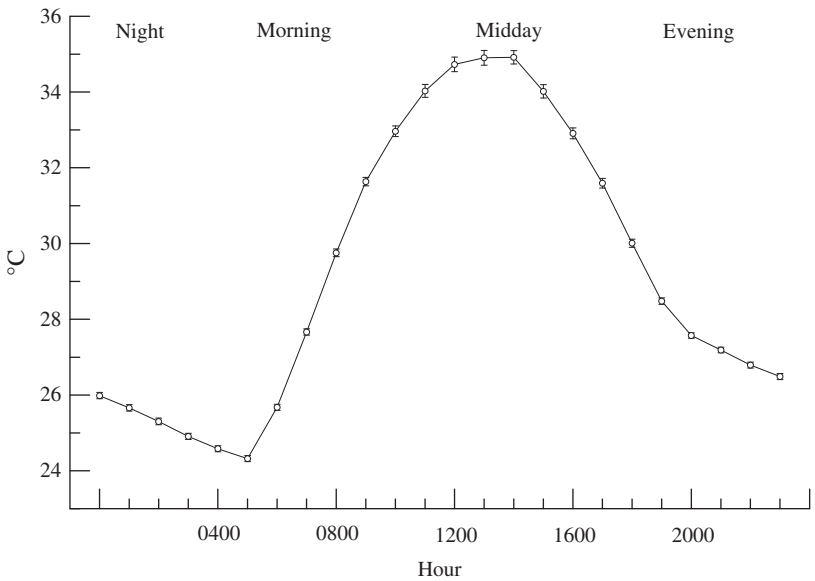


Figure 2. Mean ambient temperatures during morning, midday, evening, and nighttime activity periods, 17 June – 22 July, 2008-2009, Kleberg County, TX, USA.

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Table 1. Forage ADF, crude protein, standing crop, concealment cover (mean ± SE) and woody plant canopy cover (mean ± SE) for 10 plant communities across activity periods on the King Ranch, Kingsville, TX, USA, 2008–2009.

Plant community	ADF %	Crude protein g kg^{-1} DM	Standing crop g 10 m^{-2}	Concealment cover %	Woody cover %
Spiny hackberry	16 ± 8	25 ± 10	253 ± 127	85 ± 20	89 ± 22
Spiny hackberry interspersed with mesquite	13 ± 8	26 ± 11	54 ± 28	89 ± 15	85 ± 15
Large mesquite with spiny hackberry understory	15 ± 5	24 ± 10	38 ± 18	83 ± 26	81 ± 16
Mesquite interspersed with spiny hackberry	13 ± 9	28 ± 11	98 ± 42	71 ± 21	77 ± 16
Mesquite regrowth	14 ± 8	25 ± 12	29 ± 8	89 ± 17	84 ± 22
Mesquite savanna	14 ± 6	22 ± 6	17 ± 10	43 ± 27	23 ± 21
Mixed brush	14 ± 8	30 ± 11	234 ± 98	95 ± 12	88 ± 14
Grassland	14 ± 8	27 ± 8	17 ± 8	27 ± 17	7 ± 15
Mesquite regrowth < 0.50 m in height within oil pipeline	15 ± 5	23 ± 6	7 ± 1	23 ± 5	32 ± 31
Herbaceous and woody vegetation within root plow	10 ± 8	28 ± 10	34 ± 16	23 ± 7	12 ± 28

woody canopy cover percentages, deer selected areas with taller vegetation at high operative temperatures. However, deer also selected areas with taller vegetation at lower operative temperatures in plant communities with less woody canopy cover.

A model that included woody canopy cover, vegetation height, and operative temperature was a better fit than a model that used only woody canopy cover and vegetation height or a model that used only operative temperature when the variables that influence the thermal environment were tested as individual variables during midday (Table 3). Additionally, a model with all 3 structural variables differed ($\chi^2 = 43$, 1 DF, $p < 0.001$) from a model with only woody canopy cover and vegetation height, and also differed ($\chi^2 = 1352$, 2 DF, $p < 0.001$) from a model with only operative temperature. Although all three variables were important in explaining habitat selection, a model with woody canopy cover and vegetation height explained habitat selection by adult male white-tailed deer better than a model with operative temperature.

Table 2. Partial regression coefficients, standard errors of regression coefficients, and p-values (35,338 error DF) for effects of predictor variables in each activity period in a multiple logistic regression model that included 4 variables and their interactions with activity period to estimate resource selection functions for male white-tailed deer (n = 14 animals; n = 35 372 observations), Kleberg County, TX, USA, 17 June – 22 July, 2008–2009.

Activity period	Variable	Estimate	SE	*t*	p-value
Morning	Concealment	−0.011	0.0009	−12.48	< 0.001
	Forage index	0.038	0.0042	9.15	< 0.001
	Op temp	0.008	0.0037	2.10	0.035
	Veg ht	0.047	0.0228	2.06	0.039
Midday	Concealment	−0.006	0.0008	−7.31	< 0.001
	Forage index	0.035	0.0039	8.96	< 0.001
	Op temp	−0.016	0.0026	−6.05	< 0.001
	Veg ht	0.561	0.0163	34.43	< 0.001
Evening	Concealment	−0.014	0.0008	−17.40	< 0.001
	Forage index	0.044	0.0038	11.58	< 0.001
	Op temp	0.014	0.0033	4.17	< 0.001
	Veg ht	−0.032	0.0218	−1.46	0.146
Night	Concealment	−0.012	0.0008	−15.83	< 0.001
	Forage index	0.057	0.0037	15.48	< 0.001
	Op temp	0.019	0.0042	4.43	< 0.001
	Veg ht	−0.566	0.0301	−18.83	< 0.001

Discussion

Adult male white-tailed deer in southern Texas seek thermal cover provided by tall vegetation during midday when

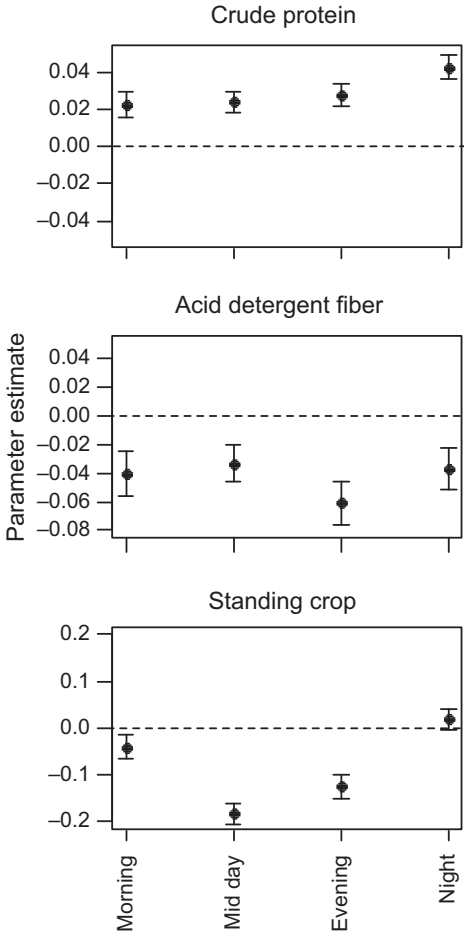


Figure 3. Parameter estimates derived from resource selection functions (number of used = 3306 locations and available = 3301 locations for morning; number of used = 5724 and available = 5721 locations for midday; number of used = 3829 and available = 3816 locations for evening; number of used = 4840 and available = 4835 locations for night) for forage standing crop, crude protein and ADF predicting the relative probability of use by male white-tailed deer (n = 14 animals, n = 35 372 observations), Kleberg County, TX, USA, 17 June – 22 July, 2008–2009.

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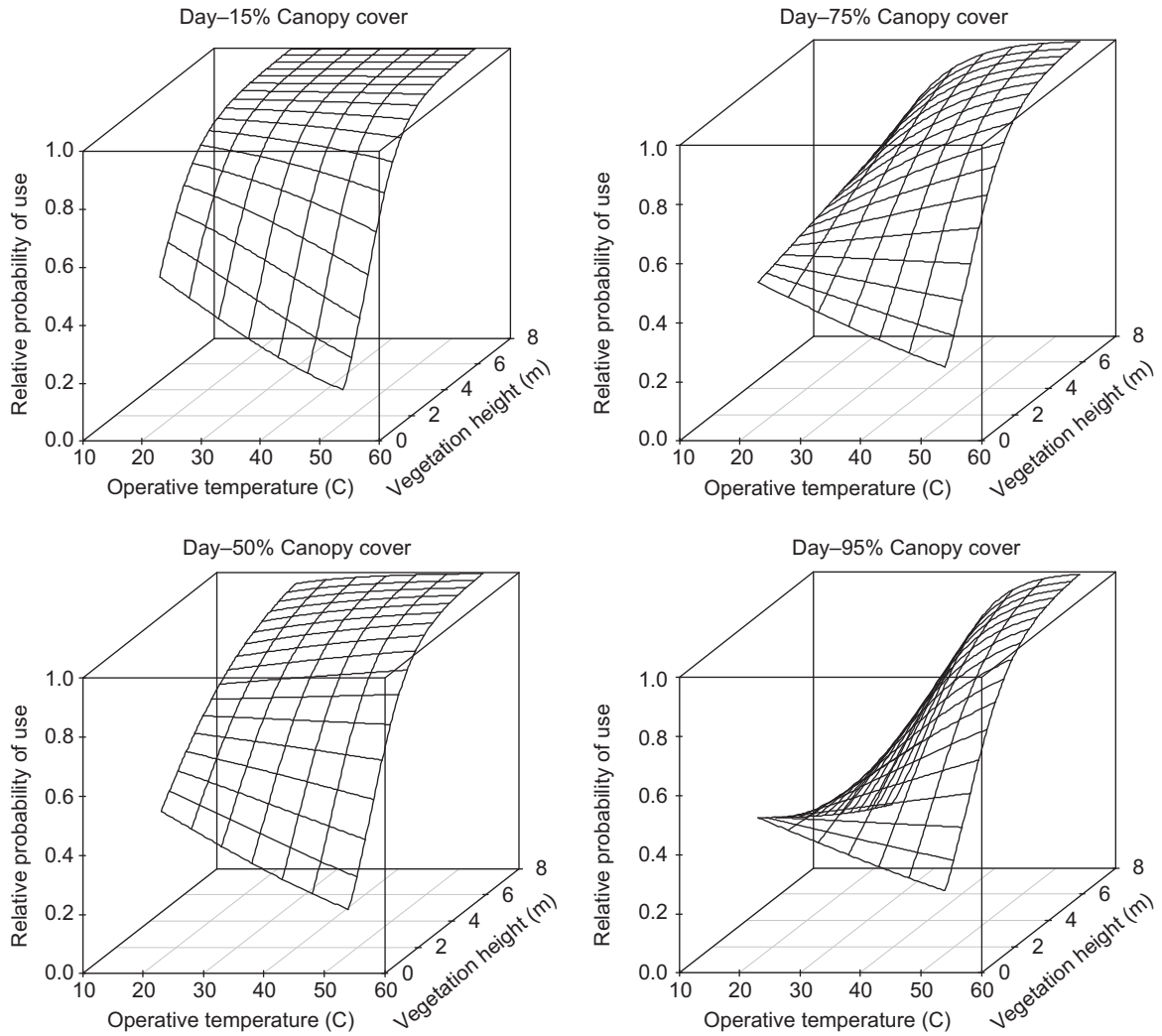


Figure 4. Relationships between relative probability of use of a location (number of locations used = 5724 and available = 5721) by deer, operative temperature, and vegetation height at midday (n = 14 animals, n = 11 455 observations) when woody plant canopy cover was 15, 50, 75 and 95%, Kleberg County, TX, USA, 17 June – 22 July, 2008–2009.

they are less active and incident solar radiation is greatest. Although operative temperature and vegetation height were important predictors of the relative probability of use by deer during midday, they did not trade off selection of food for selection of cover to avoid thermal extremes as ungulates commonly do (Mysterud and Østbye 1999). Instead, they selected locations with both thermal cover and food resources at midday in contrast to our hypothesis. Forage may be important in habitat selection during hot weather in part because food intake is important in maintaining energy balance when deer are exposed to temperature extremes. In Minnesota, Moen (1968) found that food was more important than cover in determining habitat selection by white-tailed deer during cold weather. Adequate nutrition enabled deer to withstand high winds and low temperatures in Moen's study; the same would likely be true for hot temperatures in southern Texas.

Male white-tailed deer did not select areas with greater concealment cover during any activity period. Coyotes *Canis latrans* and bobcats *Lynx rufus* are the primary predators of white-tailed deer in southern Texas (Fulbright and Ortega-Santos 2013). These predators prey primarily on juveniles (Carroll and Brown 1977, Andelt 1985). Use of concealment cover may be less important for mature male white-tailed deer than for females and juveniles. For example, females with fawns used dense woody cover more than males did during summer in south Texas (Kie and Bowyer 1999). The authors attributed use of dense woody cover by females with young to avoidance of detection by

Table 3. Multiple logistic regression models with AICc values for predicting the relative probability of use by male white-tailed deer (n = 14 animals, n = 11 455 observations), Kleberg County, TX, USA, 17 June – 22 July, 2008–2009.

Effects	K	AICc	Delta AICc	AICc weight	Log likelihood
Woody canopy cover, vegetation height, operative temperature	9	14182	0	1	−7082
Woody canopy cover, vegetation height	8	14223	41	0	−7003
Operative temperature	7	15530	1348	0	−7758

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predators. Males used more open habitats where preferred forages were more abundant rather than seeking concealment cover.

Biologists commonly refer to the combined effects of horizontal (canopy cover) and concealment cover (vertical cover) as thermal cover (Collins and Becker 2001). One reason for this is that woody canopy cover and concealment, or vertical, cover may be confounded as they were in our study. Our results suggest that concealment cover is not a good index of thermal cover during the middle of the day when deer are exposed to direct solar radiation. Support for this conclusion is our finding that male white-tailed deer did not seek greater concealment cover during the middle of the day but they did seek taller vegetation and cooler operative temperatures.

Variables associated with forage were important in habitat selection behavior of male white-tailed deer in our study area during all activity periods. Negative relationships between height of vegetation at night probably occurred because white-tailed deer tend to select more open areas dominated by herbaceous vegetation for foraging. Our finding that deer selected open areas with shorter vegetation during night reflects findings of other researchers throughout the geographic range of the species that white-tailed deer tend to forage in herb-dominated areas and use woody-plant dominated areas for resting and rumination (Armstrong et al. 1983, Beier and McCullough 1990, Johnson et al. 1995).

We were interested in determining whether operative temperature, vegetation height, or woody plant canopy cover were more important in habitat selection by deer at midday because woody canopy cover has frequently been discussed in the literature as a surrogate for thermal cover (Demarchi and Bunnell 1993, Cook et al. 2004, Gallina et al. 2010). Our results show that woody plant canopy cover helps to explain habitat selection during the warmest period of the day. Models with vegetation height and operative temperature included with woody plant canopy cover, however, are much better than models with any of the three variables alone. Taller vegetation may be important to deer in shrub environments because tall woody plants attenuate more incoming solar radiation than shorter shrubs (Martens et al. 2000, Breshears and Ludwig 2010). For example, it would be theoretically possible to have two sites with similar canopy cover but the one with taller vegetation would likely attenuate more solar radiation and have lower operative temperatures because vertical width of the canopy is greater.

Operative temperature may be important in addition to vegetation height as a component of models of habitat use during midday because it is influenced by convective heat transfer as well as solar and thermal radiation. For example, because of convective heat transfer operative temperature in open areas with no woody vegetation on a hot, windy day might be lower than operative temperature in the shade where tall woody plants blocked the wind.

Selection of taller woody vegetation and lower available operative temperatures suggests deer were seeking the coolest possible sites at midday. We did not measure soil surface temperature in our study, however, interception of solar radiation by woody plant canopy cover reduces soil surface temperature in addition to operative temperature. Cooler soil surface temperature could also be a factor in habitat selection. Mesquite was the tallest woody plant species in our study area and maximum temperature in the upper 1 cm of soil during summer reaches 48 ± 3°C beneath mesquites compared to 61 ± 3°C in non-canopied areas (Fulbright et al. 1995). Reduction of soil surface temperatures under taller woody plants may be important for deer bedded during midday because cooler soil surface temperatures may reduce heat absorbed by conduction and re-radiation (Porter and Gates 1969).

Habitat selection at the plant community scale appears to be driven by combinations of variables interacting together in a dynamic fashion rather than any one variable acting independently. The relative importance of different environmental variables in habitat selection appears fluid and may change temporally in response to variation in temperature and other environmental cues. Deer spend the majority of daily activity periods foraging (Beier and McCullough 1990), however, and forage quality appeared to be the prevailing factor influencing habitat selection behavior at the plant community scale in our study. We make this conclusion because variables associated with forage quality were important in habitat selection throughout the day. Male white-tailed deer habitat selection at the plant community scale during crepuscular periods in our study was primarily driven by forage quality. Although forage is of underlying importance, male white-tailed deer select areas of habitat that provide the combination of resources that best meets their needs under particular sets of environmental conditions. Thermal cover is an important component of that combination of variables in hot environments.

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