EDINBURGH UNIVERSITY PROJECT BLACK HILLS 1999

Habitat Preference in Mule and White-Tailed Deer

Location: Southern Black Hills
South Dakota
USA

Duration: 6 July 1999 – 1 September 1999

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Introduction

Herds of white-tailed (*Odocoileus virginianus)* and mule deer (*O. hemionus)* are economically and recreationally important to the Black Hills, South Dakota. In recent years, however, population sizes of these species have been declining. Determining reasons for this trend forms the basis of ongoing analyses in this area. The desired outcome is a long-term management plan to be used in assisting population control and conservation both in the Black Hills and other regions of the country. To date, research has been limited to studying northern and central populations of the Black Hills. Ecological differences are pronounced between the southern and other areas of the Black Hills. Consequently, before management plans can be employed, additional information is required on the habitat use of southern deer populations. This aim of this study was to investigate factors governing habitat selection of mule and white-tailed deer in the southern Black Hills, thus providing much needed baseline information. These populations are migratory, and as such the study was restricted to habitat preference in the summer ranges.

Data was collected to investigate the potential influence of both man-made and biotic features on the habitat selection of individual deer. We attempted to see whether either species of deer exhibit a preference for habitats concerning any of the following factors:

- the species and density of trees
- the overstorey-understorey associations
- the species in the understorey vegetation
- the species and density of tall shrubs and saplings
- the amount of visual cover provided
- the distance to and the type of the nearest adjacent edge
- the distance to and the type of the nearest road
- the distance to the nearest water source and site of active logging

We also aimed to determine to what extent the habitats of the two species overlapped, which was aided by recording the elevations at which we found the deer.

Study area and methods

The summer ranges of the sample deer covered a 400 square mile area of the southern Black Hills (see fig. 1). This is approximately 6000ft above sea level, hence riparian habitats are rare. The major habitat types are pine forests (*Pinus ponderosa*), meadows, canyon lands and aspen stands (*Populus tremuloides).* There is a combination of both federal and privately managed lands, used for logging, farming and mining. Consequently, the woodland habitats are disrupted by roads, waterholes and domestic livestock grazing. In addition, there is widespread forest fire management. Particular aspects of the Black Hills biogeography are unique. This includes the local Black Hills spruce (*Picea glauca*), and mineral-rich geology. In addidtion to mule and white-tailed deer, other wild ungulates that occupied the study area included elk (*Cervus elaphus*). Potential predators of deer were coyotes (*Canis latrans*), bobcats (*Felis rufus*), mountain lions (*Felis concolor*) and golden eagles (*Aquila chrysaetos*). The annual variations in temperature are extreme, with mean July temperatures of about 25°C, and for January, about -4°C.

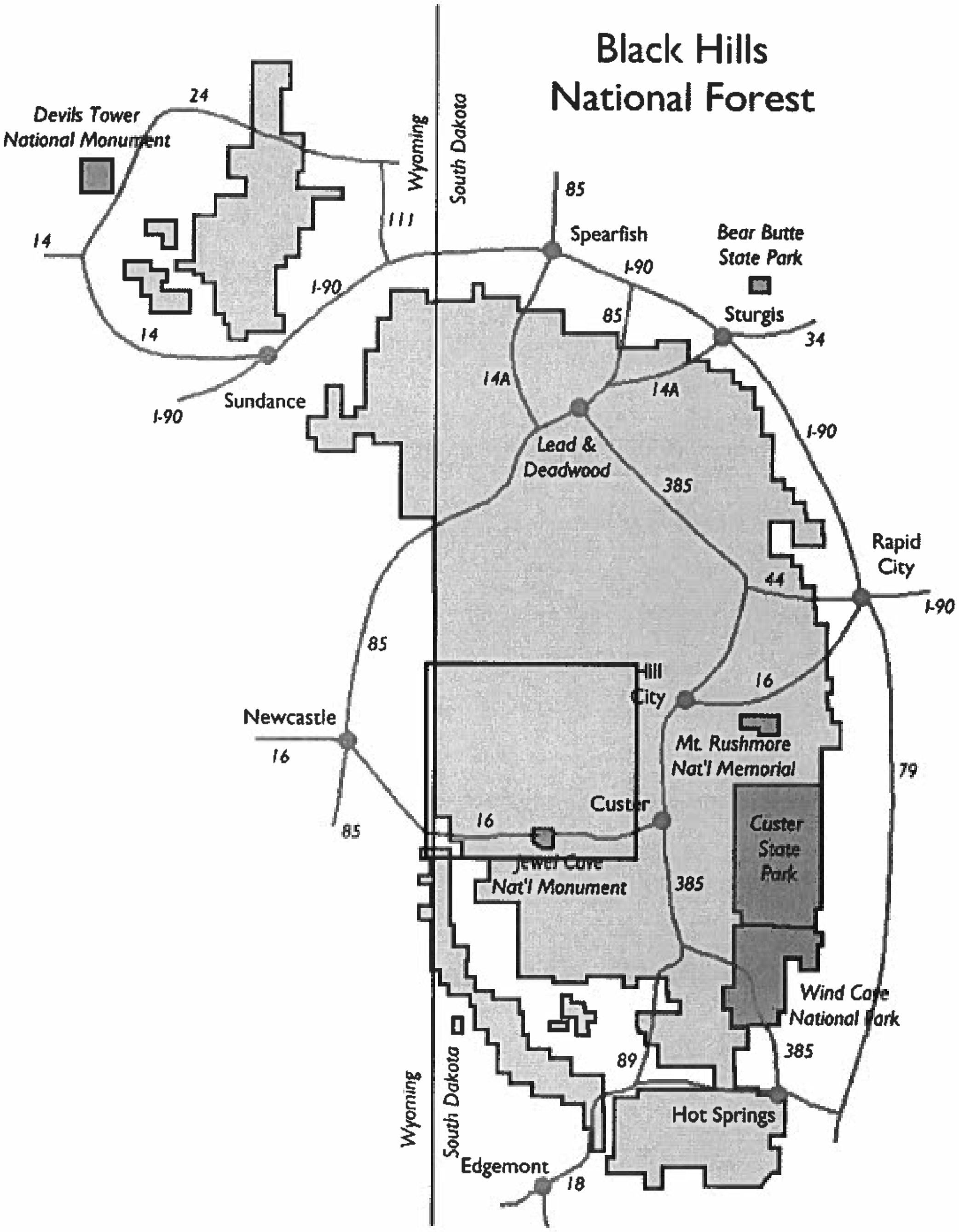
Twenty-nine white-tailed deer (three male, twenty-six female) and twenty-two mule deer (ten male, twelve female) were radio-collared prior to the onset of this study. The age and condition of the deer were unknown, and some of the does were observed with fawns.

Locations were obtained using radio telemetry for each species on alternate weeks throughout July and August 1999. This helped to maintain independence between relocations (see Dunn & Gipson 1977). Independence was also promoted as deer were not relocated at the same time of day (see Carson & Peak 1987). Different signal patterns enabled the behaviours of the deer to be identified, distinguishing between walking, feeding, bedding and escape. There was also a mortality signal.

Random grid-references within the study area were computer generated. The microhabitats at these sites were examined, and presumed to represent the average habitat of the summer range. These measurements were used as a base-line comparison with used sites.

Three different levels of study were performed on used sites. The level depended on the accuracy of deer relocation. Micro studies were carried out on the habitat if the deer was sighted. From this a precise location could be identified by evidence of foraging, fresh droppings, hoof prints or a bed site. If a precise location on the deer was not gained then either a macro or a general study was conducted. These studies did not involve such detailed measurements and vegetation analysis. Behaviour, grid-reference and topography were all collected at general, macro and microsites. Macro studies included details of elevation, distances to man-made features, cover type and understorey associations. In addition to these, detailed vegetation analysis and estimations on visual obscurity were recorded at microsites.

Fig. 1: The study area (in box) within the Black Hills, South Dakota, USA.



Details of vegetation analysis:

- **Canopy cover**: a densiometer was used to calculate overstorey cover at the centre of the microsite.

- **Basal area (BA) and diameter at breast height (DBH) of trees**: the basal area of the microsite was calculated, excluding surrounding trees smaller than the 10-factor angle gauge. The DBH of trees included in the BA were measured.

- **Tall shrub density**: four 1m by 10m belt transects, originating from the microsite centre running in the four cardinal directions, were followed. Shrubs and saplings taller than one metre, falling within the transects, were counted and identified to species level.

- **Ground cover**: fifteen 1m by 1m quadrats (five each on three parallel transects) were laid. The amount of understorey vegetation and abiotic cover were estimated by Daubenmire cover classes (see Appendix 1).

- **Visual obstruction at the microsite**: a 1m by 1m black and white chequered cover board was held at the centre of the microsite. The percentage visual obstruction of the lower and upper half of the checkerboard was recorded from a crouched down position. This was performed from the end of the tall shrub/sapling transect belts. The distance at which the entire cloth would be 100% obscured was visually estimated in each direction.

One-way ANOVA was used to analyse differences between the three groups (mule deer, white-tailed deer and random data) for canopy cover, BA, DBH and visual obstruction. Whilst continuous, quantitative measurements lend themselves to parametric statistical tests, forest species composition data and abiotic classifications were nominal and thus qualitatively described after careful study. The non-parametric Mann-Whitney U test was used to compare categorical quadrat data between the three groups.

Results

Many general habitat surveys (n = 154) were obtained but these have insufficient data for inclusion in analysis for habitat preference. They will be of use, however, in home range studies. Thus the results of this study are limited to micro and macrosite data (n = 133), and some analyses exclusively to microsites.

Elevation

Large differences were observed in the elevations between the three groups (ANOVA, $F_{2,129} = 78.85$, $p < 0.001$, see fig. 2). The elevation of the random sites, (mean ± std. dev: 6111ft ± 611), fell between the mean elevations of the two species. White-tailed deer were found at the highest elevations (mean ± std. dev: 6740ft ± 228) and mule deer were found at the lowest (mean ± std. dev: 5665ft ± 458).

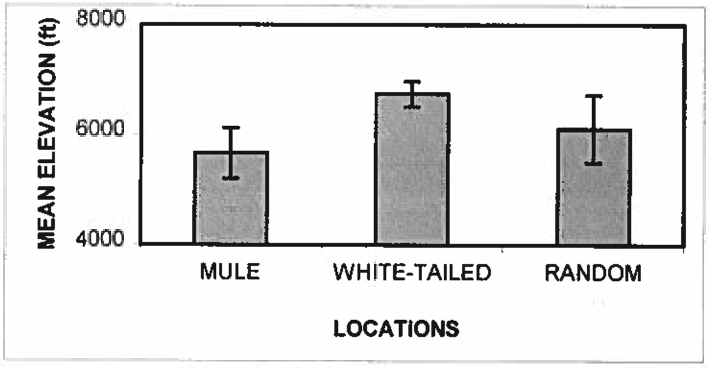


Fig. 2: Mean elevation (ft) ± std. dev. of the mule deer, white-tailed deer and random locations. White-tailed deer were found at higher elevations than randomly chosen sites, and mule deer at lower elevations.

Overstorey and understorey vegetation associations

The Black Hills forests were composed primarily of ponderosa pine, with main understorey associations of grass, forbs and vegetative litter. At all the random sites (n = 33), ponderosa pine was the predominant tree, associated at 64% of sites with grass and forbs, and 18% of sites with litter and dead vegetation. Understorey associations of bearberry (*Arctostaphylos uva-ursi*), common juniper (*Juniperus communis*) and russet buffaloberry (*Shepherdia canadensis*) were recorded at the remaining sites. The levels of canopy cover provided by ponderosa pine varied considerably (mean ± std. dev: 58.3% ± 25.1).

Habitats of mule deer were only composed of ponderosa pine associations (n = 42, microsites and macrosites). Understorey unions were different to those found at random sites; fewer sites had predominantly grass and forb cover (24%), and shrubby cinquefoil (*Potentilla fruticosa*) associations were notably present (24%). In addition, wax current (*Ribes cereum*) and young ponderosa pine unions were found at a small number of sites. The number of sites with litter (10%) and bearberry appear in accordance with random forest sampling. The percentage of ponderosa pine canopy cover found in mule deer microhabitats also did not differ from that found at random sites (mean ± std. dev: 64.7% ± 26.6; ANOVA: $F_{1,53} = 0.80$, $p = 0.376$).

In contrast to the random and mule deer sites, the habitats of white-tailed deer ($n = 58$, microsites and macrosites) were not always composed of ponderosa pine communities. Quaking aspen provided primary overstorey cover at 16% of sites, and in a minority were found Black Hills spruce (3%). Grass and forbs constituted the main understorey union at the majority of sites (74%). A small number of sites showed associations with bearberry and young aspen, and at one site only was the understory union with litter. Ponderosa pine - cinquefoil associations were found at 14% of sites, a level that is comparable to that recorded in mule deer microhabitats. Aspen and pine provided similar amounts of canopy cover (mean ± std. dev: 62.4% ± 39.2 and 54.1% ± 22.0 respectively) and total amounts of canopy cover did not differ from random sites in the forest (ANOVA: $F_{1,64} = 0.09$, $p = 0.759$, two data points missing).

At the majority of microsites, the nearest adjacent edge types were grass and forb meadows, and occasionally, ponderosa pine stands with understorey unions of grass and forbs. There was great variability in the distance to the nearest adjacent edge with a mean ± std. dev. of 291m ± 200 from random sites. The mean distance to the adjacent edge for used sites of either species of deer did not differ from that seen at random sites (ANOVA: $F_{2,82} = 0.83$, $p = 0.439$).

Understorey vegetation types

Understorey vegetation in the Black Hills is predominantly composed of grass, forbs and litter, as reported above in the overstorey- understorey union data from random sites. Quadrat data from these sites supports this, with median values of between 26% and 50% cover by litter, 6% to 25% cover by grass and forbs. Slash cover was also relatively higher than other understorey components, with a median of nearly 5%. Small quantities of bearberry, oregon grape (*Mahonia repens*) and cinquefoil were also found at levels between 1% and 5% in the majority of random sites.

In comparison, the microhabitats of the mule deer show greater quantities of debris (51% to 75% litter and 6% to 25% slash), and associated vegetation, such as lichen (nearly 5%) (Mann-Whitney U tests; litter: $W = 733$, $p = 0.045$; slash: $W = 792$, $p = 0.003$; lichen: $W = 797$, $p = 0.002$). Buffalo berry and common ninebark (*Physocarpus opulifolius*) were also found in higher amounts (Mann-Whitney U tests: buffalo berry: 1% to 5%, $W = 706$, $p = 0.033$; ninebark: 1% to 5%, $W = 740$, $p = 0.006$). In contrast to the average random site, lower amounts of forbs, oregon grape, bearberry and cinquefoil were found in mule deer microhabitats (Mann-Whitney U tests; forbs: 6% to 25%, $W = 449$, $p = 0.004$; oregon grape: 1% to 5%, $W = 500$, $p = 0.041$; bearberry: 1% to 5%. $W = 474$, $p = 0.009$; cinquefoil: 1% to 5%, $W = 482$, $p = 0.017$).

White- tailed deer microhabitats had a greater degree of understorey vegetative cover than random sites (Mann Whitney U tests; bare ground: 1% to 5%, $W = 891$, $p = 0.005$; rock: 1% to 5%, $W = 98.5$, $p = 0.010$). Understorey plants that covered significantly more ground were grasses, forbs, bearberry and young quaking aspen

(Mann-Whitney U tests; grass: 26% to 50%, W = 1348, p = 0.016; forbs: 26% to 50%, W = 1405, p = 0.002; bearberry: 1% to 5%, W = 1341, p = 0.020; cinquefoil: 1% to 5%, W = 1343, p = 0.006). The only plant that was found in lower quantities in the white-tailed deer microsites was serviceberry (*Amelanchier alnifolia*) (Mann-Whitney U test: 1% to 5%, W = 1019, p = 0.016).

There are also differences in the understorey microhabitats of the two deer species. White-tailed deer sites had higher amounts of grass, forbs, bearberry and cinquefoil (Mann-Whitney U tests; grass: W = 1157, p = 0.002; forbs: W = 1249, $p < 0.001$; bearberry: W = 1243, $p < 0.001$; cinquefoil: W = 1096, p = 0.015). In comparison, the mule deer sites had a greater degree of slash, buffalo berry, litter, lichen, rock, and ninebark (Mann-Whitney U tests; slash: W = 839, p = 0.030; buffalo berry: W = 870, p = 0.017; litter: W = 805, p = 0.006; lichen: W = 724, $p < 0.001$; rock: W = 769, $p < 0.001$; ninebark: W = 811, $p < 0.001$). These results are consistent with the differences highlighted by comparisons with the randomly chosen sites.

Size (DBH), density (BA) and species of established trees

The mean basal area (BA) for the mule deer sites was higher than the mean value for both the random and white-tailed sites (ANOVA, $F_{2,86} = 3.26$, p = 0.043, see fig. 3). However, the mean diameter of trees at breast height (DBH) in the mule deer sites was lower than both the other groups (ANOVA, $F_{2,86} = 4.44$, p = 0.015, see fig. 4). This indicates that although there is a greater density of trees in mule deer microhabitats, the less dense white-tailed and random sites have larger trees.

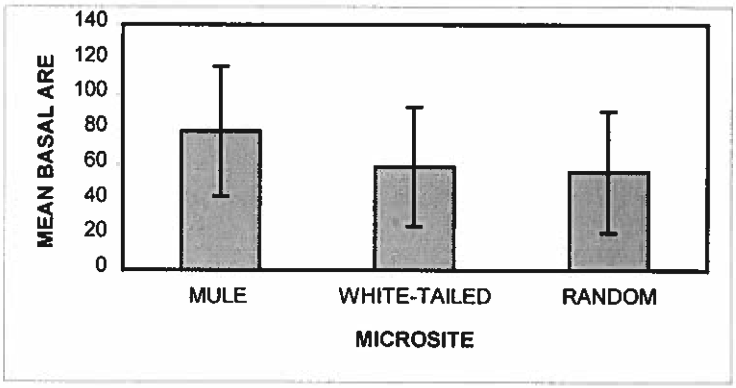


Fig 3: Mean basal area ± s.e.m (measured with the ten factor angle gauge) of mule deer, white-tailed deer and random microsites. The mean basal area of mule microsites is significantly higher than both white-tailed and random sites.

At all sites, the majority of mature trees included in DBH measurements were ponderosa pine (95% in random sites, 75% at mule sites and 72% at white-tailed sites). Aspen was also found in appreciable numbers at white-tailed deer sites (14%), but not at random or mule deer sites (0% and 4% respectively). The other trees included in the DBH measurements were burnt pine or aspen trunks, and occasionally Black Hills spruce.

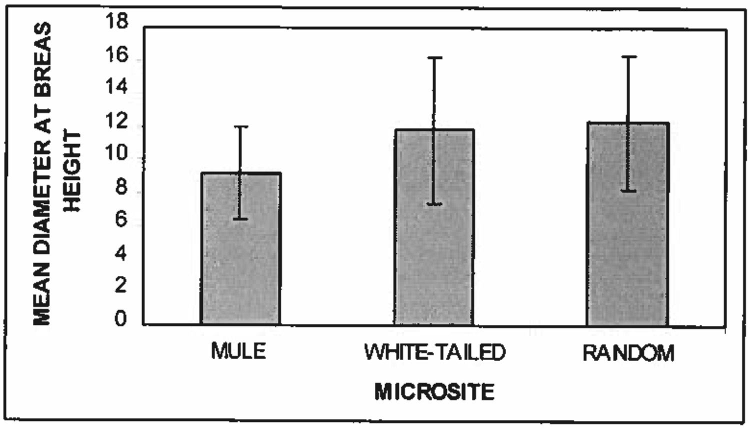


Fig 4: Mean diameter at breast height ± s.e.m. (inches) of mule deer, white-tailed deer and random microsites. The mean diameter at breast height of trees at mule microsites is significantly lower than both white-tailed and random sites.

Visual obstruction

During analysis of visual obstruction, the behaviour of the deer was taken into account. Bedding and feeding were the behaviours most commonly observed (white-tailed deer: bedding $n = 21$, feeding $n = 9$; mule deer: bedding $n = 12$, feeding $n = 10$). Means were calculated for visual obstruction by averaging the measurements taken from the four cardinal directions (see fig. 5).

Sites used by both feeding and bedded mule deer provided greater visual cover than at random sites (ANOVA: 0-0.5m: $F_{2,52} = 8.62$, $p = 0.001$; 0.5-1m, $F_{2,52} = 8.65$, $p = 0.001$). There were no differences in the amount of visual obstruction at sites used by feeding and bedded mule deer, at either height (ANOVA: 0-0.5m: $F_{1,20} = 0.03$, $p = 0.875$; 0.5-1m: $F_{1,20} = 1.44$, $p = 0.244$).

Sites used by bedded white-tailed deer had greater visual obstruction than feeding sites, at heights of 0-0.5m from the ground (ANOVA: $F_{1,28} = 5.19$, $p = 0.031$). Both types of used sites, however, were more obstructed than random sites, at this height (ANOVA: $F_{2,60} = 13.05$, $p < 0.001$). At heights of 0.5-1m from the ground, there were no differences between visual obstruction of random and feeding sites, although bedded sites were greater than both (ANOVA: $F_{1,40} = 0.21$, $p = 0.646$; $F_{1,52} = 18.53$, $p < 0.001$; $F_{1,28} = 6.07$, $p = 0.020$).

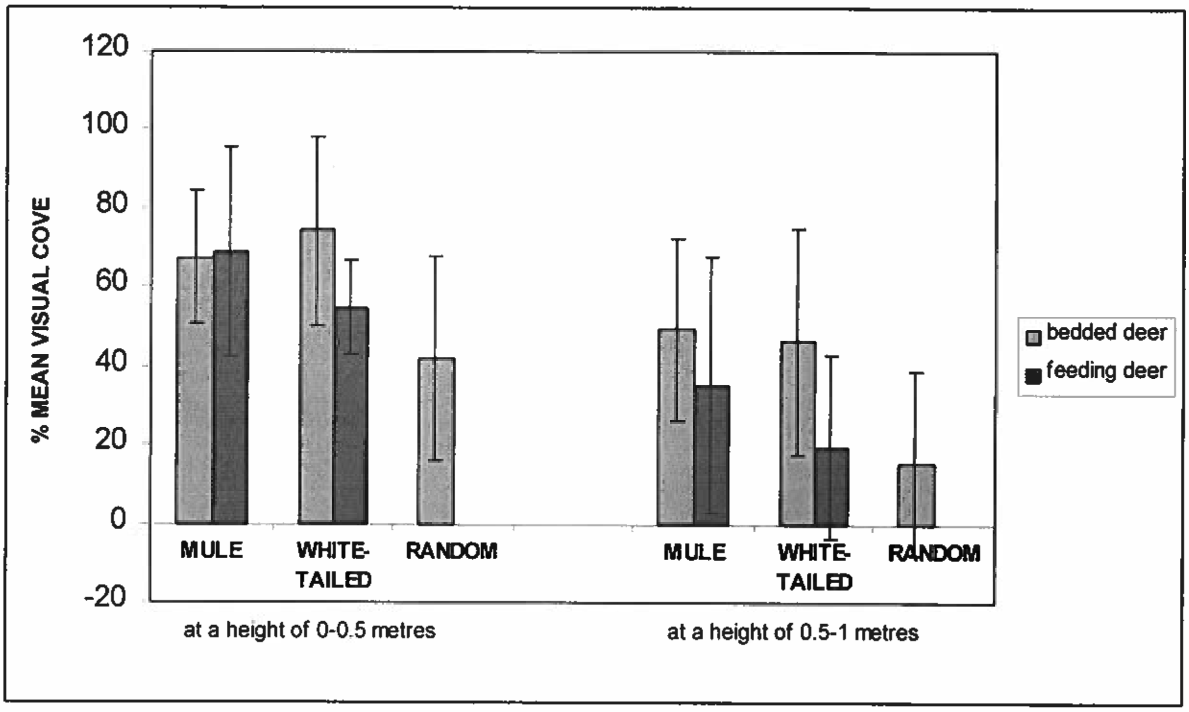


Fig. 5: The mean (± s.e.m) percentage visual cover at the microsites of feeding and bedded deer and at randomly chosen sites, at heights of 0-0.5m and 0.5-1m above the ground. Mule deer sites have significantly more cover than random sites at both heights, for both behaviours. There were no differences, however, between cover at feeding and bedded sites of mule deer. Sites used by bedded white-tailed deer have greater visual cover than random sites at both heights, but at sites used by feeding white-tailed deer, only the lower height has significantly more cover than random sites. At both heights, the visual cover found at bedded white-tailed deer sites was greater than at feeding sites.

Although sites used by both mule and white-tailed deer have greater visual cover than randomly chosen sites, no differences were found in the amount of cover between the microsites of the two deer species (see fig. 6).

Height of vegetation	**Differences in visual cover between sites used by mule and white-tailed deer when:**			
	Bedded		**Feeding**	
	$F_{1,31}$ value	p value	$F_{1,17}$ value	p value
0-0.5m above ground	0.71	0.407	2.16	0.160
0.5-1m above ground	0.10	0.748	1.41	0.252

Fig. 6: There are no significant differences in the amount of visual cover found between sites used by feeding white-tailed and mule deer, or between sites used by bedded white-tailed and mule deer, at either height.

The mean distances to 100% visual cover were calculated from the estimated distances taken in the four cardinal directions. At randomly chosen sites, the mean estimated distance to where visual obstruction would be 100% was 49.3m ± 27.3 s.e.m from the microsite centre. In contrast, 100% visual cover was maintained at distances closer to the microsite centre for both species of deer (mule deer: 30.7m ± 22.85; white-tailed deer: 41.37m ± 27.3), although these differences were only significant for mule deer (ANOVA: $F_{1,52} = 6.88$, $p = 0.011$).

Density and species of tall shrubs and saplings

Tall shrubs and saplings (>1m high) were found in approximately half of all microsites. The species found at randomly chosen sites were mostly ponderosa pine (84%), with small numbers of quaking aspen, Black Hills spruce and juniper bush. Similarly, sites used by mule deer only contained ponderosa pine saplings (100%). In contrast, the predominant species of tall saplings in white-tailed deer sites were aspen (60%). Ponderosa pine saplings constituted only 27%, although the proportion of spruce saplings was higher than at random sites (13% c.f. 6%).

White-tailed deer sites contained a greater number of tall shrubs and saplings than either random or mule deer sites, between which there was very little difference (ANOVA: $F_{2,86} = 4.37$, $p = 0.016$).

Man-made features

The nearest roads to the microsites were always gravel secondary roads, tertiary roads, trails or two-tracks. Random and white-tailed deer sites were nearest to gravel secondary roads, trails or two tracks (94% and 91% of sites respectively), whereas mule deer sites were nearly always closest to trails and two-tracks (63% of sites). There was great variability in the distances of all sites to the nearest road (e.g. random sites: mean ± std. dev. = 255m ± 244), with no differences between sites used by deer and random sites (ANOVA: $F_{2,86} = 1.93$, $p = 0.151$).

Only at very few microsites could the distances to the nearest water sources and nearest active logging be determined. Natural water sources are scarce and seasonal, and maps are old and inaccurate. Thus, data on water sources could only be recorded if the route to the microsite happened to pass by a cattle watering hole. Similarly, the actual site of active logging was rarely observed when in the hills, although evidence of past logging activity was frequently seen. Hence, no statistical analyses were attempted with this data, and qualitative examination of the results was also uninformative.

Discussion

All species show habitat selection to a greater or lesser degree (Begon *et al.* 1996). Species distributions depend on their specific niche requirements; this pertains to first order habitat selection. Home range fidelity is classified as second order habitat selection. Deer migrate to the Black Hills and settle in a specific area for the summer. Within these home ranges the microhabitats are not uniform, which leads to the potential selection of individual habitat components. This is third order habitat selection and forms the basis of this study. Measurements taken in these microhabitats of the two deer species may deviate from the random data. Hence, any differences observed infer selection for some factor of the habitat. Habitat segregation between the two species may indicate some habitat selection also. Caution should be taken, however, as selection may not be occurring for the measured variable, but for an associated component of the microhabitat. For example, some plants have the same ecological requirements. Selection may be for only one of these plants or an abiotic property of the niche. Identification of these possible associated factors in this study, such as elevation, reduces this problem.

The random sites are being used throughout this study as the average forest type of the southern Black Hills. Successional changes of the habitats of the Black Hills towards climax communities have been reported previously and are substantiated by this study. Ponderosa pine, the indicator of the climax community, is the main type of canopy cover in the used and random sites. Regeneration, fire control and livestock grazing maintain the pine.

Large differences in the mean elevations of the sites strongly suggest that there is habitat separation between the two species. The elevation of the average forest type, determined from the random sites, lying between that of the two deer species substantiates this division. Forest composition also reflects the habitat segregation of the deer species. As with white-tailed deer habitats, the canyonlands of mule deer mainly supported ponderosa pine communities. Therefore, the main understorey associations found were grass and forbs in all areas. However, in mule deer habitats, there were large quantities of litter and slash and fewer tall shrub saplings and nutritious plants, such as aspen saplings. This indicates that the habitats of mule deer are coarser than the habitats of white-tailed deer. White-tailed deer habitats are also much more diverse than the mule deer habitats, with many more types of associations. Furthermore, the vegetation associations of the random locations show some variability in composition but mainly fall between the associations of the white-tailed and mule deer sites. This again implies selection by the two deer species away from the average composition.

Food and selection

Osborn (1994) showed that white-tailed deer in the Black Hills depend on poor quality forage, while our study found that these deer reside in areas with more nutritious plants. This apparent discrepancy can be explained as Osborn (1994) found that ponderosa pine was eaten even when nutritious grasses, forbs and shrubs were present. Although the white-tailed deer of our study were found in areas of high quality food, this does not necessarily mean that this food type is being selected for.

The deer may be selecting for some other factor associated directly or indirectly with these food plants, for example, cover from either predation or environmental conditions.

Prior to this study no information was available on mule deer habitat selection in the Black Hills. In reference to food selection, mule deer were found inhabiting areas of poorer quality forage than white-tailed deer. In a comparison between feeding behaviour of mule deer and elk in northern Utah, the diet of mule deer was found to be more selective (Collins & Urness 1983). Digestive capacity mediates this. The physiology of the mule deer gut prevents fibrous foods from being adequately digested. Hence, the diet is generally composed of more than 50% forbs, with the remainder being browse. This implies that mule deer are selecting for food of higher quality. Mule deer may depend on more nutritious forage than white-tailed deer, but our results, however, show that there are higher amounts of grass and forbs both in the white-tailed deer and random areas. This suggests that another factor, other than food, may be more important in the habitat selection process.

Interspecific competition

When similar species appear together resource partitioning can occur to decrease interspecific competition (Begon *et al.* 1996). In other cases one species may outcompete the other causing a decline in the population size of the weaker competitor. In the Black Hills, through deer capture programmes, the white-tailed deer population appears to be larger than the mule deer population (Griffin *et al.* 1995; our sample demography). If there were no competition, then the two species would possibility inhabit the same type of areas. Our results indicate that there is a species separation in habitat use; mule deer are found in areas with poorer quality forage. This segregation in habitats is further evidence that competition is occurring. A combination of the population demography and our findings show the direction of this competition. White-tailed deer may be outcompeting the mule deer, and therefore may be restricting them to nutritionally inferior habitats.

An additional aspect, not considered by this study, is competition pressure from other ungulate species in the Black Hills. Elk live in herds and have a wide food base (Collins & Urness 1983) potentially making them better competitors for food than white-tailed and mule deer. This may place strain on the populations of both deer species. The presence of other species may also influence the relationship between the mule and white-tailed deer through apparent competition. For example, elk may restrict the mule deer (Collins & Urness 1983), but promote the white-tailed deer.

Predation

Predation is important in controlling population sizes (Begon *et al.* 1996). The main predators of white-tailed and mule deer in the Black Hills are mountain lions and coyotes. Selection for visual obstruction to prevent detection by these predators may be a significant factor in the third order habitat selection of deer. Our results of visual obstruction at close proximity are consistent with selection by deer for more covered areas. The habitats of both deer species had similar visual obstruction, and both had more than the random sites. Also, variation in the used sites is smaller than the random sites suggesting that cover was being selected for. Moreover, used sites, particularly mule deer locations, were totally obscured at a shorter distance than random sites. Finally, the number of tall shrubs and tree saplings can be a measure of cover and so may be selected for predator avoidance. Differences in this number, however, do not reflect the similarities in the amount of cover between the two species. White-tailed deer were found in areas with more tall shrubs and saplings. Therefore, the white-tailed deer may be selecting tall shrubs and saplings for unknown ecological associations or reasons other than cover; these may explain the presence of these plants. For example, the enhanced spacing of the large trees of the white-tailed deer habitats may allow the growth of younger trees.

Selection of more specific cover amounts is expected when behaviour of the deer is considered. In reference to horizontal cover (vegetation <1m in height; separated into two height classes: 0-0.5m and 0.5-1m), feeding deer may potentially require more cover above 0.5m than bedded deer. Our findings are not consistent with these predictions. In the mule deer microsites, no differences in cover at the two height classes between these behaviours were found. In white-tailed deer microsites, bedded deer inhabit areas of more cover than feeding deer at both height classes. Different degrees of cover may be required if the two species of deer have different escape responses to predators or experience different predation rates. The presence of fawns may also influence the amount of cover required.

Within the microhabitats, it appears that both species are selecting for increased cover and thus there is no apparent species segregation for this factor. This contrasts with habitat selection for food, which shows greater species separation. Both species may be requiring similar amounts of cover for predator avoidance. As habitat segregation is not observed with respect to cover, selection may be based primarily on some other factor, such as resource competition.

Man-made features

Proximity to man-made features was not found to be highly influential in habitat selection. Previous studies have shown that if human disturbance reaches a certain threshold, deer will avoid the area (see Collins & Urness 1983). Neither species of deer were found close to primary roads, but these types of roads are not found in the study area, as shown by the random data. Road disturbance could be a factor by which deer select their habitats, but it is difficult to separate road type from the physical geography of the area i.e. primitive roads will be found in rugged and remote areas. Thus, although mule deer were nearly always found near trails and two-tracks this could be purely a reflection of the type of habitat that is selected, rather than selection against human disturbance.

Logging and water are potentially important factors in habitat choice, but our study proved to be of limited use in determining this. The lack of developed roads in mule deer habitats will restrict the access to possible logging sites, which will in turn affect forest community structure. If there is less logging in mule deer habitats, then any human presence may disturb these deer to a greater degree. Nicholson *et al.* (1997) found that mule deer did indeed avoid human developments at all times. There is some suggestion, however, that logging is beneficial in terms of understorey vegetation regeneration. Our data supports this, as areas (white-tailed and random) that we suspect have more logging also have a richer understorey environment.

Conclusions

Our study has revealed definite habitat separation between the summer ranges of white-tailed and mule deer in the southern Black Hills. We have not been able to determine isolated factors by which deer select their habitat, however, and suggest that these habitat components interact complexly. Future studies could manipulate understorey vegetation. If site fidelity was affected by these experiments, important factors associated with selection could be identified.

Requirements can be simultaneous; for example, cover from predators is necessary whilst foraging. This simultaneous need may mediate a trade-off in the required conditions, and lead to a hierarchical selection process. The threat of predation is a constant pressure, which trades-off with the requirement for food. Other behaviours such as feeding, rutting, parturition and suckling also increase the risk of predation. We feel that our study would have been improved if the sample size had been large enough for us to consider behaviour in more analyses. In addition, both species of deer are migratory; a behaviour that is likely to have arisen as a consequence of seasonal food availability. Migration, however, is a clear trade-off with an increased risk of predation for the benefits of a better habitat (Nicholson *et al.* 1997). Selection of summer ranges may be the result of historical or life-history constraints. Therefore, if the environment has subsequently changed, components important in second-order habitat selection may not be easily identified or even present. If deer return to their natal areas, the importance of life-history in habitat selection could be investigated.

It was unusual that mule deer were not found in habitats with a greater abundance of high quality forage as they are thought to require good nutritional resources. This suggests that food may not be the determining selective factor. Two possible reasons for species habitat separation may be competition or human disturbance. It is possible that habitat preference may be confounded if there is interspecific competition. The results suggest that mule deer may be more selective than white-tailed deer, as the habitats of white-tailed deer were more similar to the average environment in the Black Hills. Consequently, shifts in community structure may result in white-tailed deer outcompeting mule deer. In accordance with this, white-tailed deer are found in habitats with more favourable food availability. The increased food availability may be associated with logging and thus has a possible disadvantage of greater human disturbance. The two deer species may be affected to a different degree by human disturbance, which may also explain why mule deer are found in more remote areas. If mule deer are being forced into less-than-favourable habitats, we predict that the decline in mule deer numbers may be more pronounced than in white-tailed deer numbers. Indeed, there has been some suggestion by local hunters that, contrary to the present species ratio, the population size of mule deer used to exceed that of the white-tailed deer population (D. Nielsen, pers. comm.). There is also the potential for competition with other ungulate species, for example, elk.

Limitations and Evaluations

The conclusions that can be drawn from this study have some limitations. The majority of the radio-collared deer, around which this study was based, were females. In addition, the ages of the deer, and whether or not they had fawns, were not known. Thus, generalisations that we have made concerning habitat selection should be considered with caution. It is highly plausible that sex, age, condition and lactation do affect habitat preference. For example, differences in niche requirements may be present between the two sexes. As the female provides all the parental care, a lactating female requires areas of high nutritional food and increased cover for her fawn(s). Single females without young and males require food and shelter also but to a lesser degree than lactating does. Such differences may be revealed in studies of longer duration but were necessarily overlooked in the present study. We also feel that behaviour will be highly important in immediate habitat selection, and with a larger sample size, this could be examined.

Radio-tracking studies are always limited by non-independence of locations, as data is collected from repeated measures on only a small number of collared individuals. Deer were relocated at different times of the day to lessen the effects of non-independence. On average, two micro or macrosites were obtained for each deer, although it is possible that some individuals were more easily tracked to microsite level than others and thus may be over-represented in the sample. The use of non-parametric tests meant that repeated measures could not be controlled for, and often multiple tests had to carried out, increasing the risk of type 1 errors.

Generalisations are also limited as radio-tracking could only be carried out in fine weather during day-light hours. Habitat use may vary depending on the weather and lighting conditions.

We feel that the results concerning the estimated distance to 100% visual obstruction may not be entirely reliable. Estimates are likely to vary considerably between people and in retrospect we should have standardised estimates between individuals whilst in the field.

Visual cover was considered in reference to predator avoidance. It should be remembered, however, that carnivores are also strongly dependent on olfactory senses whilst hunting, although our study cannot take the importance of this into account. Escape responses of both deer species are different and may reflect the specific behaviour at time of detection. Behavioural studies into escape responses could reveal any differences between species in the importance of visual cover and escape cover.

Ideally, we would have liked to collect a larger number of sample microsites. This may then have enabled us to identify the components important in habitat collection to a more specific degree. The terrain of the southern Black Hills did not allow easy radio-tracking, however, and obtaining a precise location of a deer proved to be quite difficult to achieve. The rough, steep roads also proved to be quite unforgiving on our vehicle, and regularly, data collection was prevented when the vehicle needed repairing. In addition, no data could be collected in electrical storms or rain. As well as the obvious dangers of carrying the metal aerial, radio signals suffered from interference and roads quickly became unusable.

Acknowledgements

We would like to thank Josephine Petley a PhD student from South Dakota State University and her technician Susan Cheyne who trained us in the use of the radio-telemetry equipment, vegetation analysis, and showed us the layout of the study area.

To Dr. Joesphine Pemberton who helped us greatly with our expedition proposal, giving us invaluable information on the day to day running of a research project and who also agreed to be our referee to so many funding bodies.

To Professor. J Jenks of South Dakota State University who agreed to be our referee in the USA.

To the community of Custer, who were so welcoming and made our time in America highly enjoyable.

To all the private landowners in the study area who gave us permission to access their land.

To the Expeditions Committee of Edinburgh University and Edinburgh University Court for the approval of the expedition.

Project Black Hills was funded with support from the following bodies:

The Blue Cross
The Davis Fund (Edinburgh University)
The James Rennie Bequest (Edinburgh University)
The Institute of Biology (Royal Geographical Society with the Institute of British Geographers)
The International Fund for Animal Welfare
MacDonalds Restaurants Plc
The Mathew Swann Travel Fund (Edinburgh University)
The Student Travel Fund (Edinburgh University)
The University of Edinburgh Development Trust (Small projects grant)
The Weir Fund (Edinburgh University)

References

Begon, M, JL Harper & CR Townsend. 1996. *Ecology: individuals, populations and communities (3rd edition).* Blackwell Science.

Carson, RG & JM Peak. 1987. Mule deer habitat selection patterns in northcentral Washington. *J. Wildl. Manage.* **51**: 46-51.

Collins, WB & PJ Urness. 1983. Feeding behaviour and habitat selection of mule deer and elk on northern Utah summer range. *J. Wildl. Manage.* **47**: 646-663.

Dunn, JE & PS Gipson. 1977. Analysis of radio telemetry data in studies of home range. *Biometrics* **33**: 85-101.

Griffin, SL, CS DePerno, JA Jenks, LA Rice & DA Flory. 1995. Capture success of white-tailed deer in the central Black Hills, South Dakota. *Proc. South Dak. Acad. Sci.* **74**: 71-76.

Nicholson, NC, RT Bowyer & JG Kie. 1997. Habitat selection and survival of mule deer: trade-offs associated with migration. *Journal of Mammology* **78**: 483-504.

Osborn, RG. 1994. *Winter diet and nutritional condition of white-tailed deer in the northern Black Hills, South Dakota.* MS Thesis, South Dakota State University, Brookings, SD, USA.

Sieg, CH. & KE Severson. Managing habitats for white-tailed deer in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming.

For information on the Black Hills vegetation, we consulted:
Plants of South Dakota grasslands. Bulletin 566. Agricultural Experiment Station, South Dakota State University.

Appendix 1

Daubenmire cover classes

Daubenmire cover class	% understorey ground cover
1	1 - 5%
2	6 – 25%
3	26 – 50%
4	51 – 75%
5	76 – 95%
6	96 – 100%

(Daubenmire & Daubenmire 1968; as cited in Carson & Peak 1987)