5-1979

Feeding Behavior and Habitat Selection of Deer and Elk on Northern Utah Summer Range

William B. Collins
Utah State University

Utah State University
MERRILL-CAZIER LIBRARY

FEEDING BEHAVIOR AND HABITAT SELECTION OF DEER AND

ELK ON NORTHERN UTAH SUMMER RANGE

by

William B. Collins

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

UTAH STATE UNIVERSITY
Logan, Utah

1979

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

ABSTRACT

Feeding Behavior and Habitat Selection of Deer and Elk

on Northern Utah Summer Range

by

William B. Collins

Utah State University, 1979

Major Professor: Dr. Philip J. Urness

Department: Range Science

This study examined feeding behaviors and habitat preferences of
mule deer (Odocoileus hemionus hemionus) and elk (Cervus canadensis
nelsoni) in aspen (Populus tremuloides) and lodgepole pine (Pinus
contorta) types. Specific purposes were 1) to determine where deer and
elk, undisturbed by humans, prefer to graze and rest within these two
types and 2) to consider what species-specific characteristics contri-
bute to their differing forage and habitat preferences.

Tame free-ranging mule deer and elk were observed for 24-hour
periods biweekly through summer to determine their grazing and resting
preferences for various habitat subunits. Relative distributions of
deer and elk fecal groups were also recorded and compared with actual
distribution of the animals. Species dry-weight compositions of monthly
diets in the aspen type and lodgepole pine type were quantified by the
bite count technique and used as basis for assessing consumption rates,
intake and certain aspects of diet quality. In particular, relative
digestive capacities of deer versus elk were investigated by using
rumen inocula from each species in the fermentation of that animal's
diet, as well as in fermentation of the other species' diet. Crude
protein values of diets in the aspen type were also determined monthly

and compared with values reported for deer and elk in the lodgepole
pine type.

In either type, both deer and elk exhibited strong grazing prefer-
ence for open habitat subunits. However, elk most preferred highly
productive meadow bottoms, whereas deer most preferred less productive
clearcut lodgepole pine. Aspen forest subunits were also preferred by
deer. Clearcutting greatly increased deer and elk grazing use of these
areas in the lodgepole pine type, but aspen clearcuts were used about
equally to uncut aspen, even though forage production doubled. The
reason deer used meadow bottoms less than elk is attributed to the
deer's preference for a more digestible diet; deer were generally more
selective than elk, especially in meadow subunits where density of
vegetation and abundance of nonpreferred grasses and sedges apparently
interferred with forage selection and prevented maximum forage consump-
tion rates. Elk had significantly greater digestive capacity than deer
and were apparently better adapted to using a more diverse array of
plant species as food. In any case, consumption rates were highest on
subunits the animals most preferred to graze. The fact that both
species made considerable use of less preferred habitat, where consump-
tion rates were "suboptimal", suggests that deer and elk are innately
motivated to explore their environments for alternate food resources.

Elk generally preferred to bed near where they finished feeding,
although always in close proximity to cover. In contrast, deer gener-
ally retreated to specific beds which they used repeatedly throughout
the summer. Deer resting behavior made them better adapted than elk
to cope with biting insects.

Relative distributions of deer and elk pellet groups differed

significantly from actual habitat use by either animal. Importance of the most valuable habitat was underestimated by pellet group distributions, and value of less important habitat was overestimated.

(124 pages)

INTRODUCTION

As big-game summer ranges in the intermountain states are increasingly subjected to other uses, deer and elk welfare becomes more dependent on the manager's ability to distinguish between necessary and non-essential habitat and on his understanding of how habitat requirements are affected by habitat modifications. More specifically, managers of big game need to know where the animals spend their time and what requirements are being met by each segment of their habitat. They also need to know the acceptability and relative value of alternative habitat.

Competitive uses potentially cause changes in big game behavior, wherein the animal relocates itself in space and time with respect to its environment. Such change is not necessarily detrimental to the animal, but the nature of its effect is dependent on relative changes in the food supply, microclimate and cover which accompany the alternative use. Deer and elk use of summer range can be altered by livestock grazing, hunting, road construction, timber removal, and successional changes resulting from fire management. While physical alterations of habitat--forage removal by livestock, cover changes by timber harvest, and successional changes by fire--have significant effects on big-game habitat, simply the presence of livestock and human activity can change big game habitat use, as well.

This study attempts to evaluate the relative big game values of various subunits of the aspen and lodgepole pine types, two important summer ranges of deer and elk in the intermountain states. It also attempts to determine how clearcutting, recreational and other human activities may impact deer and elk.

Objectives

1. To determine activity-specific, habitat-subunit use by deer and elk in aspen and lodgepole pine ecosystems during the summer season.

2. To determine if important differences exist between habitat subunits in terms of potential intake and dietary quality for deer and elk.

3. To determine if the pellet-group count technique can be used to reliably estimate deer and elk habitat subunit preferences.

Hypotheses

The null hypotheses tested in this study were:

A. Hypotheses related to objective 1.

1. Percentage deer and elk use (grazing, resting, and all activities combined) of aspen and lodgepole pine subunits is not significantly different from the proportional availability of those subunits.

2. There is no significant difference between deer and elk habitat-subunit preferences.

B. Hypotheses related to objective 2.

1. Between subunits, there is no significant difference in selected qualitative characteristics (in vitro organic matter digestibility and crude protein) of deer or elk diets.

2. Consumption rates of deer and elk are not significantly higher on the subunits they most prefer to graze (assuming hypothesis A-2 is rejected).

3. Elk do not have significantly greater digestive capacity than deer.

4. Deer are not significantly more forage selective than elk.

C. Hypothesis related to objective 3. Relative distributions of deer
    and elk pellet groups do not differ significantly from actual
    subunit use by either animal.

LITERATURE REVIEW

Successful management of wildlife habitat requires that behavioral as well as physiological requirements of the animal be recognized and dealt with satisfactorily (Geist 1978, Moen 1973). Beament (1961) suggested that because an animal selects its environment, and not vice versa, it typically limits itself to a narrower range of habitat than that which is physiologically acceptable (i. e., some habitats which apparently meet all physiological requirements of the animal are unused, because they are behaviorally unacceptable).

Food

Early researchers believed big game habitat use was dependent almost entirely on forage supply (Elton 1936). Cheatum and Severinghaus (1950) found deer fertility directly related to the condition of their range. Indirect losses of big game through poor reproductive success are less obvious than winter malnutrition losses, but, in some cases, are more important. Julander et al. (1961) clearly documented this for mule deer in a comparison of excellent and poor condition Utah summer ranges, and also suggested that good nutrition during this season is vital to overwintering success. Similarly, Buechner and Swanson (1955) suggested that populations of elk maintained somewhat below carrying capacity have increased natality as a result of better nutrition of fewer individuals.

Mackie (1976) stated that interspecific competition for forage will likely exist between deer and elk wherever they occupy the same range. He also suggested elk are the most efficient competitor of the two and will likely survive at the expense of mule deer. However, there is little quantitative support for this. Smith and Julander (1953) and

McMahan (1966) suggest there is real potential for forage competition between deer and livestock, especially sheep. Elk likely compete more heavily with cattle, but in a 3-way interaction between deer, elk and cattle, elk will avoid the cattle areas (Julander and Jeffery 1964) and hence, even more severely compete with the deer (Mackie 1976).

Hofmann (1968) and Hofmann and Stewart (1972) compared stomach morphologies of a large number of African ruminants to their feeding habits and concluded that those with large ruminoreticulum:body weight ratios are generally more capable of digesting grasses than animals with relatively smaller rumen capacity. Leege et al. (1977) asserted that the same relationship is true for large versus smaller species of the deer family, because the ability to digest cellulose is correlated with the relative rate of food passage through the rumen; small species have relatively smaller rumens, and food retention time is short. Prins and Geelen (1971) gave the red deer (Cervus elaphus) ruminoreticulum: body weight ratio as 23 %, whereas, Short et al. (1965) reported the mule deer ratio as 10 %. Leege et al. (1977) further suggested that relatively poor digestion of cellulose in small ruminants results because cellulolytic protozoa are not maintained well in rumens where food retention time is short. Retention time is a critical factor in the digestion of grasses, because grasses are relatively high in cell wall constituents and require fermentation over a long period of time (Van Soest 1965). Forbs, especially legumes, are lower in cellulose and other structural carbohydrates, and thus digested more readily.

Cover

More recent studies have emphasized the importance of environmental conditions other than food. Cover can serve two functions for big game.

First, it provides a place of security from disturbance or harm from predators and man; it is often essential for full use of a habitat even when danger is not imminent (Black et al. 1976). Secondly, it buffers the animal against heat loss or gain (Moen 1973, Edgerton and McConnell 1976). In the case of elk, the exact requirement for either type of cover appears to be dependent on the potential for harrassment and on the relative availability of food. This is exemplified by the recent natural establishment of an elk herd in the sagebrush:grass type of the Hanford Arid Lands Ecology Reserve in Washington (Rickard et al. 1977), an area with little thermal or escape cover.

Optimization

In any event of habitat selection, animals appear to optimize. That is, they appear to choose the best trade-off between the benefits and associated costs of an activity, whether by minimizing costs or by maximizing net benefit (McCleery 1978). Behavior of this type has seldom been studied in large herbivores. However, Royama (1970) and Krebbs (1978) through studying great tits and pigeons, respectively, concluded that animals should prefer foraging in most profitable food patches, and use less profitable patches only when availability of good ones is low. Conversely, Smith and Sweatman (1974) found that great tits do not forage in most profitable patches exclusively, but still spend time foraging in less productive patches. They also found that when the most profitable patch was suddenly eliminated, the birds switched their efforts immediately to the second best patch, indicating their "sampling" effort served as a hedge against possible changes in the environment.

Bitterman (1975) proposed that animals do not optimize at all,

but that they "match" their efforts to the amount each patch "pays off" (i. e., the amount of time spent foraging on each patch is in direct proportion to the efficiency of food consumption on that patch). Sutherland and Mackintosh (1971), on the other hand, suggested that any time spent foraging on a less productive patch represents an animal's failure to perceive the true value of the patch.

Clearcutting

Regardless of the mechanism of habitat selection, alteration of the food and cover resources of big game does affect their subsequent preference for that piece of landscape. The direction this change in preference will take is not always the same (Peek and Hieb 1976, Wallmo et al. 1976). Taber (1953), Hooven (1973), Plummer et al. (1966) and Patton (1974) have reported that overstory removal or thinning of various communities increases forage availability, thereby benefiting big game. Regelin et al. (1974), working in stands dominated by lodgepole pine and Englemann spruce (Picea englemannii), demonstrated that clearcutting can increase forage production and deer use, however, relative nutritional values of forages on cut and uncut areas did not differ. Pengelley (1972) cautioned that benefits resulting from overstory removal in one ecological situation do not necessarily accrue in other situations, and suggested that, in the past, these benefits have most often been obtained accidentally rather than through planned vegetational manipulation.

Roads and Campgrounds

Aside from direct vehicular mortality, roads are most detrimental to deer and elk in that they frequently eliminate prime habitat (Peery and Overly 1976, Black et al. 1976). Habituation to traffic may allow big game to use areas within visual and auditory range of roads

(Wallmo et al. 1976), but if people step out of vehicles on the road's edge, the range of unacceptable habitat is greatly extended (Ward 1979). Ward found that any type of on-foot activity by humans caused elk to leave an area. Similarly, Rost and Bailey (1979) found that both deer and elk avoid areas within 200 m of roads, especially along more heavily travelled ones. Consequently, campground activity would also eliminate animal use of surrounding areas. In contrast, closed roads may serve as travel routes and increase production of preferred forages through secondary plant growth (Marcum 1975, Collins et al. 1978).

Pellet-Group Count Technique

The pellet-group-count technique has increasingly been used as an index to relative use of different habitats, subtypes and habitat modifications. Riney (1957) suggested that fecal counts can delineate preferred habitat and seasonal use by various mammals including red deer. Julander et al. (1963) stated that the pellet-group method can estimate relative intensity of use, trend in use from year to year, and total population numbers of a given area. While this technique can reliably estimate populations of general areas, its use as an index to habitat subunit preferences is questionable (Neff 1968, Collins and Urness 1979). Anderson (1969) cautioned against inferring "use" (total time herbivores spend in a specific habitat) through pellet-group counts, because the method assumes that the rate of fecal deposition is a linear function of time and that average deposition rates within individual adjacent habitats are similar. The validity of these assumptions has been investigated in only a few cases (Leckenby 1968, White 1960).

METHODS

Experimental Areas and Materials

The study was conducted in two major vegetation types—aspen and lodgepole pine. The study areas, typical of physiography and vegetation of much of northern Utah and the central and northern Rocky Mountains, represent important summering areas for deer and elk.

Lodgepole pine study area

The lodgepole pine study area was located on the Little Brush Creek drainage of the Ashley National Forest. This is a gently rolling, forested plateau at the east end of the Uinta Mountain range, about 50 km north of Vernal, Utah. The elevation ranges from about 2600 to 3000 m.

The soils are in the Typic Cryorthent-Typic Cryocrept-Mollic Cryoboralf association. Soils of lower elevations are characteristically loamy skeletal, mixed; while soils of higher elevations are fine loamy, mixed. Argicaquic Cryoboralf soils are found associated with semiopen parks scattered throughout the area (Wilson et al. 1975, L. Chamberlain, pers. comm.).

Annual precipitation on the study area is about 500 mm, as much as half in the form of snow (Wilson et al. 1975). Due to the location, elevation, and orientation of the mountains, the area receives frequent orographic and convective summer thunderstorms from moisture originating in the Gulf of Mexico (E. A. Richardson, pers. comm.). Snowmelt is usually complete by mid-June. Killing frosts generally end by late June and resume in mid-September.

Ninety percent of the study area has a lodgepole pine overstory with a small percent of Englemann spruce (Picea englemannii) and

subalpine fir (Abies lasiocarpa). About 10 percent of the area is meadow. The habitat type for upper elevations is Abies lasiocarpa/Vaccinium scoparium. Habitat types for the lower elevations have not yet been determined, but community types known to be present are Abies lasiocarpa-Picea pungens/Berberis repens-Carex geyeri, Pinus contorta/Vaccinium scoparium, Pinus contorta/Calamagrostis canadensis and Pinus contorta/Carex geyeri. Pinus contorta is a possible edaphic climax in close association with the Abies lasiocarpa/Vaccinium scoparium habitat type (Phister 1972, R. L. Mauk, pers. Comm.).

Most of the lodgepole pine forest is composed of even-aged stands, either mature or stagnated. Stagnated forest is so dense (11,000 to 22,000 trees/ha) that it is practically devoid of understory; foresters refer to it as a "dog hair stand." The primary understory species in the mature forest is grouse whortleberry (Vaccinium scoparium).

Dry meadow habitat subunits are the most common type of natural opening in the area. They range in size from less than 1 to 40 ha, are located on deeper and wetter soils than occur in the surrounding forest, and produce a diverse array of forbs, grasses, and sedges. Characteristic species are alpine timothy (Phleum alpinum), several species of Carex and Juncus, marsh marigold (Caltha leptosepala), western yarrow (Achillea lanulosa), forest fleabane (Erigeron superbus), trailing fleabane (E. flagellaris), American bistort (Polygonum bistortoides), and longstalk clover (Trifolium longipes).

Wet meadow habitat subunits are less widely distributed, and are restricted to areas immediately adjacent to water. They seldom exceed 15 m in width. Wet meadows have many of the same species as the dry meadows but are more productive and are dominated by water sedge (Carex

canescens), Oregon fleabane (Erigeron speciosus), and mountain bluebells
(Mertensia ciliatus).

Clearcut subunits are dryer than either of the natural openings,
but they support a wide array of forbs, grasses, and sedges. Primary
species are dandelion (Taraxacum officinale), goldenrod (Solidago
decumbens), aster (Aster chilensis), alpine timothy, bearded wheat-
grass (Agropyron subsecundum), shortstemmed sedge (Carex brevipes), and
elk sedge (Carex geyeri).

Deer and elk utilize the area from late spring to fall. Although
some animals are in the area prior to substantial snowmelt, most stay
at lower elevations until green-up is well advanced. A 2-month grazing
permit for 1,000 sheep has been issued for the area, but during the
1976 season, the permittee did not graze his animals in the area.
Therefore, diets obtained did not reflect within-year competitive rela-
tionships with livestock.

The area is the same as studied by Collins et al. (1978), Deschamp
et al. (1979), and Pallesen (1979).

Aspen study area

The aspen study area was centered on and around the Chicken Creek
drainages of the Davis County Experimental Watershed in north-central
Utah. This is an area 2280 to 2560 m elevation on the Wasatch range
approximately 8 km east of Farmington, Utah.

The area is characterized by small watersheds with perennial and
intermittent streams flowing through gently sloping meadow bottoms.
These are bounded by 12 to 45 percent side slopes. The landforms are
relatively "old surfaces" (Bell 1952). Side-slope soils are well drained
very deep loamy and very deep clayey, developed in colluvium. Bottoms

are underlain with moderately to poorly drained very deep loam. Ridges are characterized by shallow gravelly loam (Johnston and Doty 1972).

Annual precipitation averages 1140 mm, 80 percent occurring as snow (Johnston and Doty 1972). June through September is the driest period of the year, averaging only 130 mm precipitation received as convective thunderstorms. Summer temperatures are generally free of killing frosts from mid-June through mid-September.

Fifty seven percent of the area has an aspen overstory, with trees averaging 40 years of age. This vegetation is generally restricted to side slopes and includes a rich understory of grass, browse and forbs. Characteristic species are mountain brome (Bromus carinatus), bearded wheatgrass, bluebell (Mertensia arizonica), sweetpea (Lathyrus lanzwertii), western valerian (Valeriana occidentalis) and snowberry (Symphoricarpos oreophilus).

About 8 percent of the area was clearcut in 1974. Slash was cleared from most areas. The vegetation is similar to adjacent uncut stands, but more productive and characterized by 1 to 2 m aspen suckers. Figure 1 presents the U. S. Forest Service number designation of individual clearcuts.

Patches of Douglas fir (Pseudostuga menziesii) and subalpine fir, totalling 3 percent of the area, occupy northeast-facing slopes. Understory is sparse, and limited mostly to snowberry and a few forbs.

Mountain brush (Stoddart et al. 1975) communities occupy about 10 percent of the area, predominately on southwest-facing slopes. This vegetation consists mostly of snowberry, chokecherry (Prunus virginiana), mountain brome, sweetpea, mulesears wyethia (Wyethia amplexicaulis), and bluebell. Sagebrush-grass vegetation often
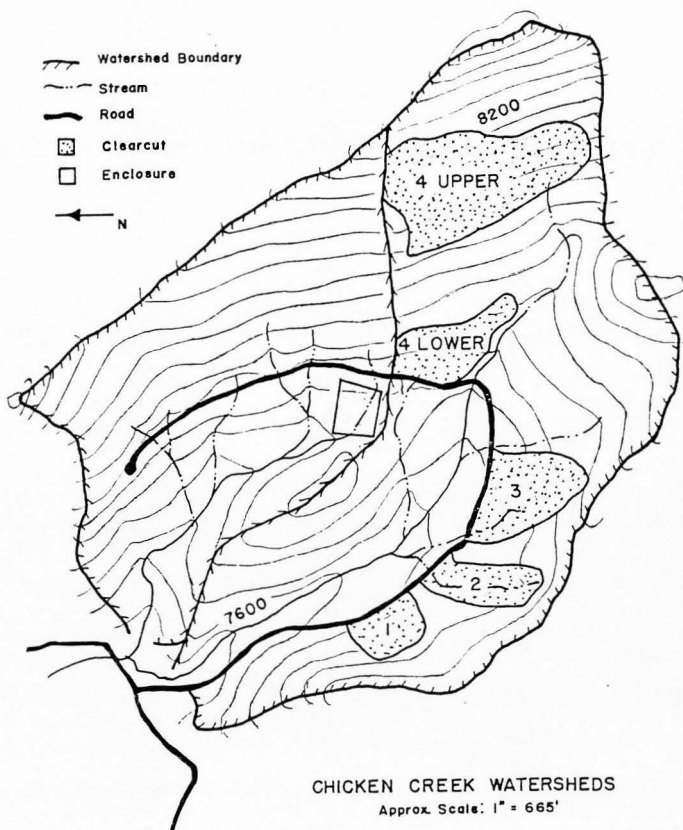
Figure 1. The Chicken Creek Watersheds, Davis County Experimental
Watersheds, Utah.

intergrades with the mountain brush on ridges.

Grass-forb vegetation occupies the bottoms and portions of ridges. Principal species are: mountain brome, bearded wheatgrass, bluebell, false hellebore (Veratrum californicum), alpine leafybract aster (Aster foliacious), tarweed (Madia glomerata), and wyethia. Small clones of aspen are found in association with streamside vegetation in bottoms, but understory composition is characteristic of grass-forb vegetation.

The area has been protected from livestock grazing for more than 40 years, to control erosion and flooding. Deer use the area from late spring to fall, but elk have not been reported on the area for many years.

Experimental animals

The deer and elk were obtained as 12-to-24-hour-old fawns and calves from the Utah Division of Wildlife Resources Green Canyon and Hardware Ranch facilities. They were fed fresh goat's milk the first 5 to 6 weeks, then weaned and maintained on alfalfa (deer), native grass hay (elk), and rolled barley (Collins 1977).

In addition to contact through bottle feeding, many hours were spent with the animals in the first year to ensure that they would be habituated to human activity. The elk were also trained to load into horse trailers and trucks which would be used for transport to study areas. The deer accepted loading into vehicles but became excited during movement; subsequently, they were transported in crates in which they were much less excitable and susceptible to injury.

Enclosures

Neff (1974) suggested that maintenance of tame deer in pens off the study area led to inefficient grazing and unsettled preferences

during diet observation trials. Consequently, enclosures of slightly more than 2.5 ha were built on the study areas to encompass habitats representative of those to be sampled. The enclosures also served to maintain the animals during non-sampling periods, providing sufficient feed for the animals until the last 2 or 3 weeks of the study periods, at which time the animals were supplemented with hay.

Field Equipment

Cassette tape recorders were used to accumulate field data on diet composition and behavior, because longhand methods were often inhibited by weather and/or rate of animal activity.

Insects were a major irritant to animals using the aspen type. To assess relative degrees of insect impact, a 12-inch-diameter, plastic beach ball, painted black and suspended from a stick 120 cm in front of the observer was used to record fly densities; flys were attracted by near infrared emissions from the ball. Stationary fly traps based upon those used by Thompson (1969) were also used to record fly density.

Rumen inocula from deer and elk were needed for in vitro digestibility trials. A vacuum aspiration apparatus consisting of a hand pump and a flexible plastic tube was used to extract rumen fluids. The tube was passed through the esophagus to the rumen. This eliminated the need to fistulate valuable research animals, an approach that involves high risk in excitable subjects such as deer and elk.

Procedures

Determination of habitat use and preference

Scan sampling, a technique described by Altmann (1974), was used to determine the time deer and elk spent grazing, resting, ruminating,

traveling, standing, sleeping, and playing on each of the habitat sub-
units in both types. Observation periods lasted 24 hours, the location
and activity or state of each animal being noted at 10-minute inter-
vals. Elk were observed in groups of 5 to 7 biweekly through the
summers of 1977 and 1978 in the aspen type, and biweekly during the
summer 1976 in the lodgepole pine type; the latter observations have
been published (Collins et al. 1978). Mule deer are not gregarious
during the summer as are elk; this necessitated observing them indi-
vidually or in pairs. Scan samples were obtained on alternate weeks
from that of the elk in summers 1977 and 1978 in the aspen type, and
summer 1978 in the lodgepole pine type.

Night observations were made with the aid of a flashlight. Also,
a pen light was attached to the collar of one animal to facilitate
following the animals without the use of a flashlight. Neither light
had any effect on animal behavior. At least one animal was equiped
with a radio transmitter, as well, to facilitate locating the animals
when I occasionally became separated from them.

The number of hectares of each subunit available to the animals
was determined by connecting the points of maximum peripheral deer or
elk movement as recorded over the entire summer and taking 900 point
samples on aerial photographs covering the same area. Percent avail-
ability was then calculated directly from the point distribution.

Forage production measurement

Forage production estimates for all subunits in the lodgepole pine
type were determined by Utah Division of Wildlife Resources biologist,
Dennis D. Austin. Forage production on the aspen and clearcut sub-
units of the aspen type was determined by U. S. Forest Service,

Intermountain Forest and Range Experiment Station personnel. Forage production on mountain brush, meadow, and logging road subunits of the aspen type was determined by use of a double-sampling technique (Wilm et al. 1944). Weight estimates for the road subunit were made on 40, 20 X 50 cm mechanically spaced plots. Weight estimates for the mountain brush, riparian, and meadow subunits were made on 120 such plots in each subunit. One out of every 5 plots was clipped for actual dry-weight determination. By means of regression analysis, the clipped weights were used to adjust the estimates.

Quantification of diets

Diet sampling was conducted from mid-June to mid-September in both types. In the lodgepole pine type, deer diets were sampled in 1976 by Deschamp (1977) and diets of the elk in 1976 by Collins (1977). Deer and elk diets in the aspen type were sampled in 1977.

In the lodgepole pine type, dietary information was obtained by individually observing 3 cow, 3 havier and 1 bull elk; 4 does and 1 havier deer. In the aspen type, observations were made on 2 cow, 2 havier and 1 bull elk and 4 does. The bite-count technique was used as described by Wallmo and Neff (1970), except animals were not restrained during sampling. All dietary information was estimated on a species-dry-weight basis. Samples of equal size were obtained for each animal, week and subunit in the lodgepole pine type. However, in the aspen type, the animals were observed only as they voluntarily entered each subunit, resulting in data of unequal sample size. Seventy five to 150 bites (simulated by hand clipping) of each species in each diet were collected, oven-dried and weighed to form the basis for weighting bite count totals. Initially, simulated bites were

collected biweekly on all species; thereafter, they were collected only on species still growing. Consumption rates were calculated as the average dry-weight consumption per minute of grazing time.

Diet quality indices

Diets were composited from plant species hand-clipped to be representative of plant parts consumed by the animals. Plants were collected for each period in which the diets were determined. Plants were oven dried within one day of collection and ground in a Wiley mill using a 40-mesh screen. The ground material was stored in jars and later combined with other dietary species in the same proportion as found in average deer and elk diets for each sampling period.

Moore's (1970) modification of Tilley and Terry (1963) in vitro organic matter digestibility (IVOMD) determination was used to estimate the digestibility of the composited diets. Inoculum for the procedure was obtained from animals grazing the aspen type. Inocula for the first 2 deer periods were obtained from sacrificed wild deer using the same area. In both cases, the inocula were placed directly into preheated 1-liter thermos bottles. The bottles were stoppered with Bunsen valves to maintain anaerobic conditions and placed in an ice chest maintained at 39° C with hot water. They were then transferred to the laboratory within 2 hours. Inocula from both deer and elk were used in the fermentation of both species' diets.

The macro-Kjeldahl procedure, as outlined by Harris (1970), was used to analyze representative diets for crude protein content (% nitrogen X 6.25). This analysis was done for deer and elk diets in the lodgepole pine type by Pallesen (1979).

Data analysis

Habitat use:availability data were analyzed by the z test of sig-
nificance of a binomial proportion (Snedecor and Cochran 1972). This
was also used to test for differences between deer versus elk habitat
subunit preferences. Chi-square goodness of fit was used to test for
differences between animal and pellet group distributions.

Data from the aspen type on forage species production and dietary
consumption rate were analyzed by use of a factorial analysis program
(BMD08V) written by Paul Sampson of the UCLA Health Sciences Computing
Facility. The model is a two-factor replicated, balanced factorial,
where forage class or species and subunit are treated as main effects.
Forage species production data from the lodgepole pine type were
analyzed by means of a general least-squares analysis program (FCTCVR)
prepared by Dr. Rex Hurst of the Utah State University Applied
Statistics and Computer Science Department. The main effects are the
same as for the aspen type.

Effects of rumen inocula source, animal species, subunit, and
sampling period were evaluated by the factorial analysis program. The
model is a four-factor unreplicated factorial analysis of variance.
Thus, the higher order interaction is assumed to equal 0 and, there-
fore, its mean square is an estimate of the error mean square. The
same factorial approach was used to evaluate the effects of animal
species, subunit, and period on crude protein content of diets in the
aspen type.

Significant differences among means were evaluated with the
Least Significant Difference (LSD) test (Sokal and Rohlf 1969).
Differences at $P \leq 0.05$ are considered statistically significant.

Diet selectivity was calculated by use of the percentage simi-
larity equation (Whittaker 1975), comparing species composition of diets
to species composition of the community. High values indicate greater
overlap of dietary composition with community composition, and hence,
lower selectivity than indicated by smaller values. Dietary overlap
between deer and elk was also determined in this way. Horn's (1966)
index of similarity was not used, because it is derived from the
Shannon-Weiner expression which is more responsive to changes in the
rarest species; in this study forage species consumption was seldom
limited by availability. The Friedman two-way analysis of variance
by ranks (Siegel 1956) was used to test for differences in selectivity
between deer and elk, because expression of greater selectivity by
either animal is probably not an interval measure of strength.

RESULTS

Habitat Subunit Use

In the aspen type, 24-hour scan sampling periods were completed for deer and elk each 2-week period of the summer. In the lodgepole pine type, deer were sampled for all but the first 2-week period of the summer season. Data from a series of 24-hour observations of elk in the lodgepole pine type were reported earlier (Collins et al. 1978), but are re-analyzed with the z test of significance of a binomial proportion and presented here for comparative purposes.

Tables 1 through 4 show percent deer and elk use of the different habitat subunits by all activities combined, grazing, and resting. Percent of the total area represented by each subunit the animals used and results of the z tests are also given. For the aspen type, the relative area proportions of the different subunits used by deer and elk are the same. Proportions used by the two species in the lodgepole pine type, however, are quite different, because the deer did not range over the same area as the elk.

Grazing use of the aspen type

Table 1 shows deer grazed aspen and associated conifer subunits significantly less than their availability. They grazed logging road and meadow subunits significantly more than their availability.

Elk (Table 2) grazed the aspen, mountain brush, clearcut and conifer subunits significantly less than their availability. The road and meadow[1] were grazed significantly more than their availability.

---

[1]Almost all use of the meadow type was restricted to the more mesic, riparian portion. However, this level of subunit classification was not recognized in the sampling scheme.

Table 1. Comparative deer use of different habitat subunits of the
aspen ecosystem, Wasatch Mountains, Utah. Sample sizes
are in parentheses.

	% Total area	% All activities[a]	% Grazing	% Resting
	(900)	(996)	(386)	(516)
Aspen	56.6	58.7	45.3 --[b]	70.7 ++
Clearcut	7.9	2.2 --	4.1 -	0.8 --
Conifer	3.2	0.1 --	0.0 --	0.0 --
Logging road	0.5	1.0	1.6 +	0.0
Meadow	14.4	31.2 ++	35.2 ++	28.5 ++
Mountain brush	17.5	6.7 --	13.7	0.0 --

[a]All activities combined includes traveling, grooming, standing,
and drinking, as well as grazing and resting.

[b]z test significance: - or + means animal use was significantly less
or greater than availability, $P \leq 0.01$; -- or ++ indicates signifi-
cance at $P \leq 0.001$.

Table 2. Comparative elk use of different habitat subunits of the
aspen ecosystem, Wasatch Mountains, Utah. Sample sizes
are in parentheses.

	% Total area	% All activities[a]	% Grazing	% Resting
	(900)	(3088)	(1120)	(1496)
Aspen	56.6	20.5 --[b]	17.9 --	14.7 --
Clearcut	7.9	4.1 -	7.0 --	1.6 --
Conifer	3.2	0.6 --	0.0 -	0.0 --
Logging road	0.5	2.3 +	3.2 ++	0.0
Meadow	14.4	68.4 ++	65.3 ++	83.2 ++
Mountain brush	17.5	4.0 --	6.7 --	0.5 --

[a]All activities combined includes traveling, grooming, standing,
and drinking, as well as grazing and resting.

[b]z test significance: - or + means animal use was significantly less
or greater than availability, $P \leq 0.01$; -- or ++ indicates signifi-
cance at $P \leq 0.001$.

Table 3. Comparative deer use of different habitat subunits of the lodgepole pine ecosystem, Uinta Mountains, Utah. Sample sizes are in parentheses.

	% Total area	% All activities[a]	% Grazing	% Resting
	(900)	(672)	(310)	(276)
Wet meadow	3.0	14.8 [++b]	30.6 [++]	0.0 [-]
Dry meadow	1.2	1.4	3.0 [+]	0.0
Clearcut	4.9	24.8 [++]	36.3 [++]	4.1
Mature forest	13.3	10.0 [-]	13.0	8.1 [-]
Stagnated forest	77.0	48.9 [--]	16.6 [--]	87.8 [++]
Revegetated roads	0.6	0.0 [-]	0.5	0.0

[a] All activities combined includes traveling, grooming, standing, and drinking, as well as grazing and resting.

[b] z test significance: − or + means animal use was significantly less or greater than availability, $P \leq 0.01$; −− or ++ indicates significance at $P \leq 0.001$.

Table 4. Comparative elk use of different habitat subunits of the
lodgepole pine ecosystem, Uinta Mountains, Utah. Sample
sizes are in parentheses.

	% Total area	% All activities	% Grazing	% Resting
	(900)	(4662)	(2307)	(2355)
Wet meadow	2.7	46.8 ++b	43.6 ++	50.5 ++
Dry meadow	11.7	20.6 ++	33.6 ++	15.6 +
Clearcut	4.4	8.4 ++	14.6 ++	0.7 --
Mature forest	11.9	12.4	3.3 --	20.7 ++
Stagnated forest	68.7	9.8 --	1.9 --	12.7 --
Revegetated roads	0.6	1.9 +	3.0 ++	0.0 --

[a]All activities combined includes traveling, grooming, standing,
and drinking, as well as grazing and resting.

[b]z test significance: - or + means animal use was significantly less
or greater than availability, $P \leq 0.01$; -- or ++ indicates signifi-
cance at $P \leq 0.001$.

The only obvious differences between deer and elk grazing use of the aspen type was that the elk grazed the meadow almost twice as much as the deer (65 versus 35 percent of the total grazing time), and the deer grazed in the forest twice as much as the elk (45 versus 18 percent).

If preference is considered to be proportional to the total time the animals grazed each subunit, it appears that the deer prefer to graze the aspen foremost, the meadow secondarily. Elk exhibit the opposite preference. Deer and elk grazing preferences were significantly different on all subunits, except the logging road and conifer subunit (Table 5).

Resting use of the aspen type

Deer and elk both used the aspen and meadow subunits as bedding areas more than their availability, while using the other subunits significantly less (Tables 1 and 2). The elk, however, showed much greater preference than the deer for resting in the meadow subunit (83 versus 29 percent of the total resting time). Deer showed greater preference for resting in aspen stands than elk (71 versus 15 percent). However, when deer and elk rested in the meadow subunit, they were generally within 2 to 3 m of cover; this cover usually consisted of riparian aspen or alder stands, not the aspen subunit proper. Resting area preferences of deer and elk were significantly different only on the aspen and meadow subunits.

Grazing use of the lodgepole pine type

The deer grazed wet meadow, dry meadow and clearcut subunits of the lodgepole pine type significantly more, and grazed the stagnated forest significantly less than their availability (Table 3). The

Table 5. Percent deer and elk use of different subunits of the aspen type, including z-test for significant difference between use by the two species. Sample sizes are in parentheses.

	All activities		Grazing		Resting	
	Deer	Elk	Deer	Elk	Deer	Elk
	(996)	(3088)	(386)	(1120)	(516)	(1496)
Aspen	58.7	20.5**	45.3	17.9**	70.7	14.7**
Clearcut	2.2	4.1*	4.1	7.0*	0.8	1.6
Conifer	0.1	0.6	0.0	0.0	0.0	0.0
Logging road	1.0	2.3*	1.6	3.2	0.0	0.0
Meadow	31.2	68.4**	35.2	65.3**	28.5	83.2**
Mountain brush	6.7	4.0**	13.7	6.7**	0.0	0.5
Percent similarity (overlap)	59.0		65.5		44.0	

** $P \leq 0.001$
* $P \leq 0.01$

difference between grazing use and availability of mature forest and
revegetated roads was not significant. The elk grazed the wet meadow,
dry meadow, clearcut, and revegetated road significantly more than
availability, but the forested subunits less than availability
(Table 4).

Deer preferred to graze the clearcut most, secondarily the wet
meadow. Elk preferred grazing the wet meadow, dry meadow, and clear-
cut in that order. Of note is that deer preferred grazing the
forested segments much more than elk, and dry meadows much less than
elk. Differences between deer and elk use of the lodgepole pine sub-
units were significant in all cases (Table 6).

Resting use of the lodgepole pine type

The deer rested in stagnated forest significantly more and the
wet meadow and mature forest significantly less than their availabil-
ity. There was no significant difference between resting use and
availability of dry meadows, clearcuts, or revegetated roads by deer
(Table 3). The elk used the wet meadow, dry meadow and mature forest
as resting areas significantly more than their availability, while
using the clearcut, revegetated roads and mature forest significantly
less than availability (Table 4).

The deer obviously preferred resting in the stagnated forest
subunits, while the elk preferred to rest in the wet meadow. Dry
meadow and mature forest were also preferred as resting sites by elk,
but much less so than the wet meadow. Resting area preferences of
deer and elk were significantly different in all cases except the
revegetated road (Table 6).

Table 6. Percent deer and elk use of different subunits of the lodgepole pine type, including z-test for significant difference between use by the two species. Sample sizes are in parentheses.

	All activities		Grazing		Resting	
	Deer	Elk	Deer	Elk	Deer	Elk
	(672)	(4662)	(310)	(2307)	(276)	(2355)
Wet meadow	14.8	46.8**	30.6	43.6**	0.0	50.5**
Dry meadow	1.4	20.6**	3.0	33.6**	0.0	15.6**
Clearcut	24.8	8.4**	36.3	14.6**	4.1	0.7**
Mature forest	10.0	12.4	13.0	3.3**	8.1	20.7**
Revegetated road	0.0	1.9*	0.5	3.0*	0.0	0.0
Stagnated forest	48.9	9.8**	16.6	1.9**	87.8	12.7**
Percent similarity (overlap)	44.4		53.9		21.5	

** $P \leq 0.001$
* $P \leq 0.01$

Animal versus fecal group distributions

Table 7 presents the results of the tests for goodness of fit
made of the observed distribution of animal use versus the expected
distribution of animal use (distribution of fecal groups). The
results for elk use of the lodgepole pine type were previously
reported (Collins 1977), but are included here for easy reference.
Except for deer grazing use of the lodgepole pine type, pellet group
distributions for deer and elk were significantly different from the
animal grazing or general use distribution in the aspen and lodgepole
pine types.

Defecations occurred only during grazing or traveling activity.
Highest defecation rates occurred during most active periods (i. e.
during travel from one area to another). Roughly 40 percent of all
defecations occurred as the animals were traveling, yet traveling
represented only 3 to 6 percent of the deer or elk day. Mean defeca-
tion rates in the lodgepole pine type were 21 and 24 pellet groups
per day for deer and elk, respectively. In the aspen type, the rates
were 23 and 30 pellet groups per day for deer and elk, respectively.

Vegetation

Subunit forage production

Vegetal production for the various subunits of the aspen type is
reported in Table 8. Aspen and clearcut production information is for
clearcuts 1, 2, 3 and lower-4 and associated aspen plots. Upper-4 is
not included, because the animals never grazed that clearcut. Pro-
duction information for the lodgepole pine subunits was previously
reported (Collins et al. 1978) but is included here for reference
(Table 9).

Table 7. Chi-square goodness of fit tests of animal versus fecal group distributions for deer and elk using aspen and lodgepole pine types in northern Utah.

Type	Animal	Grazing	All activities
Aspen	Deer	$G = 19 > X^2_{0.01[4]} = 13$	$G = 19 > X^2_{0.01[5]} = 15$
	Elk	$G = 31 > X^2_{0.01[4]} = 13$	$G = 39 > X^2_{0.01[5]} = 15$
Lodgepole pine	Deer	$G = 1 < X^2_{0.01[5]} = 15$	$G = 67 > X^2_{0.01[4]} = 13$
	Elk	$G = 255 > X^2_{0.01[5]} = 15$	$G = 171 > X^2_{0.01[5]} = 15$

Table 8. Percent production by forage class on different habitat
          subunits in the aspen ecosystem, Wasatch Mountains, Utah.

	Habitat subunit					
	Aspen	Clearcut	Logging road	Meadow	Mountain brush	Riparian
Forbs	54.4	44.8	64.2	54.5	26.8	53.3
Grasses, sedges	32.1	29.0	33.0	43.8	18.2	42.8
Browse	13.5	26.2	2.8	1.7	55.0	3.9
Total production (kg/ha)	1774	3043	1245	2155	1570	2820

Table 9. Percent production by forage class on different habitat
          subunits in the lodgepole pine ecosystem, Uinta Mountains,
          Utah.

	Habitat subunit				
	Wet meadow	Dry meadow	Clearcut	Mature forest	Stagnated forest
Forbs	18.0	45.3	47.5	3.8	45.4
Grasses, sedges	80.8	54.7	36.5	2.6	7.6
Browse	1.2	0.1	16.1	92.5	45.3
Mushrooms	0.1	0.1	0.1	1.1	1.7
Total production (kg/ha)	2664	1148	484	335	37

In the aspen type, forage production almost doubled 3 years following clearcutting. Forbs, grass-likes, and browse were each significantly more productive in the clearcut stands than in the adjacent uncut areas (Table 10). Of the principal grass species, bearded wheatgrass increased significantly in the clearcut but mountain brome remained about the same. Important dietary browse species--aspen and snowberry--also increased significantly following cutting. Production estimates for Engelmann aster, peavine and western valerian were consistently higher in the clearcut, but were not significantly different from those in the adjacent aspen forest.

Eighteen years after clearcutting, lodgepole pine clearcuts were 13 times more productive than adjacent uncut stagnated stands. Forbs, grass-likes, and browse all significantly increased following cutting, but mushrooms decreased (Table 11).

Deer and Elk Diets

Monthly summaries of deer and elk diets by forage classes in the aspen type are presented (Figures 2 and 3). Diets by species dry-weight composition are presented in Tables 24 to 32 in the Appendix. Species dry-weight composition of deer and elk diets in the lodgepole pine type were reported by Deschamp (1977) and Collins (1977), respectively.

In both types, the deer were observed to consume little or no grass beyond the first 2 to 3 weeks of the season, as compared to the elk which consumed large quantities of grass all season. Deer diets were generally composed of greater than 50 % forbs, the remainder browse. Elk preferred forbs too, but to a lesser extent than deer.

Table 10. Mean dry weight production (kg/ha) ± SE of forage classes
and principal species occurring in deer and/or elk diets on
cut and uncut aspen stands.

| Forage | Habitat subunit | |
classes or species	Aspen	Clearcut
Forb	965 ± 174 a [1/]	1364 ± 142 b
Grass	569 ± 169 a	882 ± 173 b
Browse	240 ± 90 a	797 ± 257 b
Bearded wheatgrass	67 ± 10 a	426 ± 53 b
Mountain brome	346 ± 105 a	389 ± 81 a
Aspen	17 ± 18 a	268 ± 63 b
Snowberry	175 ± 96 a	504 ± 222 b
Engelmann aster	45 ± 29 a	58 ± 26 a
Peavine	114 ± 50 a	133 ± 44 a
Western valerian	175 ± 74 a	230 ± 54 a

[1]Means within rows followed by a common letter are not significantly
different (P ≤ 0.05).

Table 11. Mean dry weight production (kg/ha)$\pm$ SE of forage classes
and principal species occurring in deer and/or elk diets
on cut and uncut lodgepole pine stands.

| | Habitat subunit | |
	Lodgepole pine	Clearcut
Forbs	6.6 ± 2.4 a[1/]	307.8 ± 51.4 b
Grasses and sedges	2.7 ± 1.4 a	138.6 ± 43.1 b
Browse	16.9 ± 9.8 a	76.3 ± 55.9 b
Mushrooms	10.2 ± 5.0 a	0.0 ± 0.0 b
Heartleaf arnica	3.1 ± 1.2 a	1.1 ± 0.4 b
Pacific aster	0.1 ± 1.0 a	11.8 ± 5.2 b
Milkvetch	0.1 ± 0.9 a	92.9 ± 42.9 b
Goldenrod	0.3 ± 1.0 a	29.8 ± 9.8 b
Dandelion	0.0 ± 0.0 a	34.2 ± 5.3 b
Carex spp	2.2 ± 1.4 a	89.0 ± 17.2 b
Aspen	0.4 ± 1.1 a	73.1 ± 56.0 b
Grouse whortleberry	15.1 ± 8.9 a	0.1 ± 0.7 b

[1]Means within rows followed by a common letter are not significantly
different (P $\leq$ 0.05).
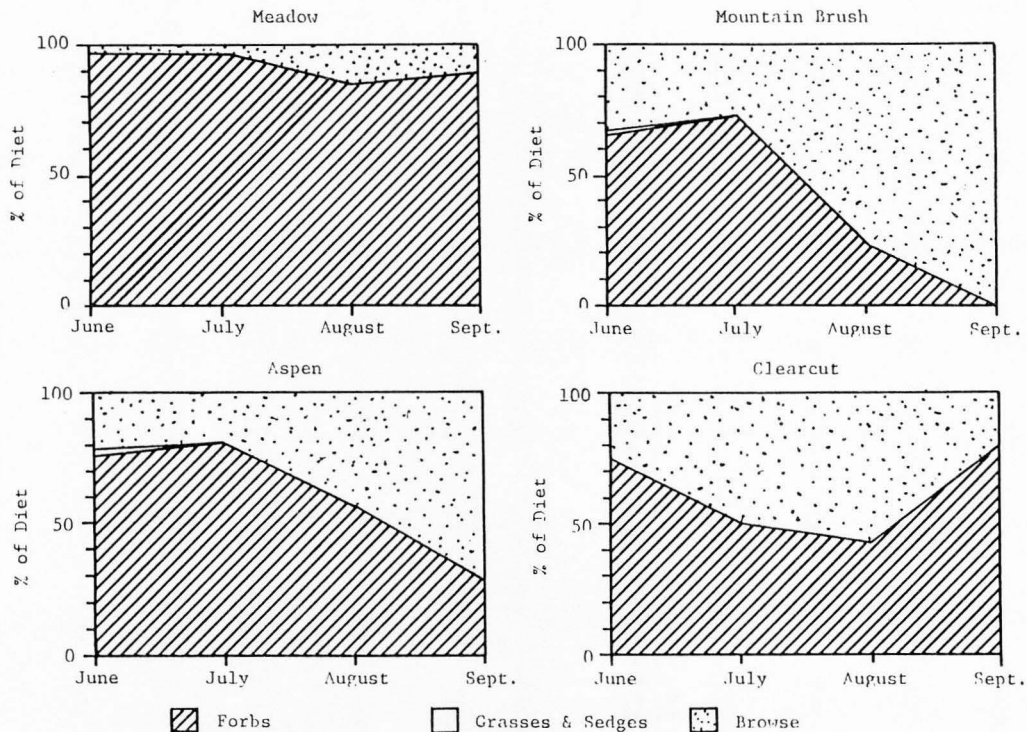
Figure 2.   Deer diets by forage class on four habitat subunits in the aspen ecosystem, Davis County Experimental Watershed, Utah.   Percentages are on a dry-weight basis.
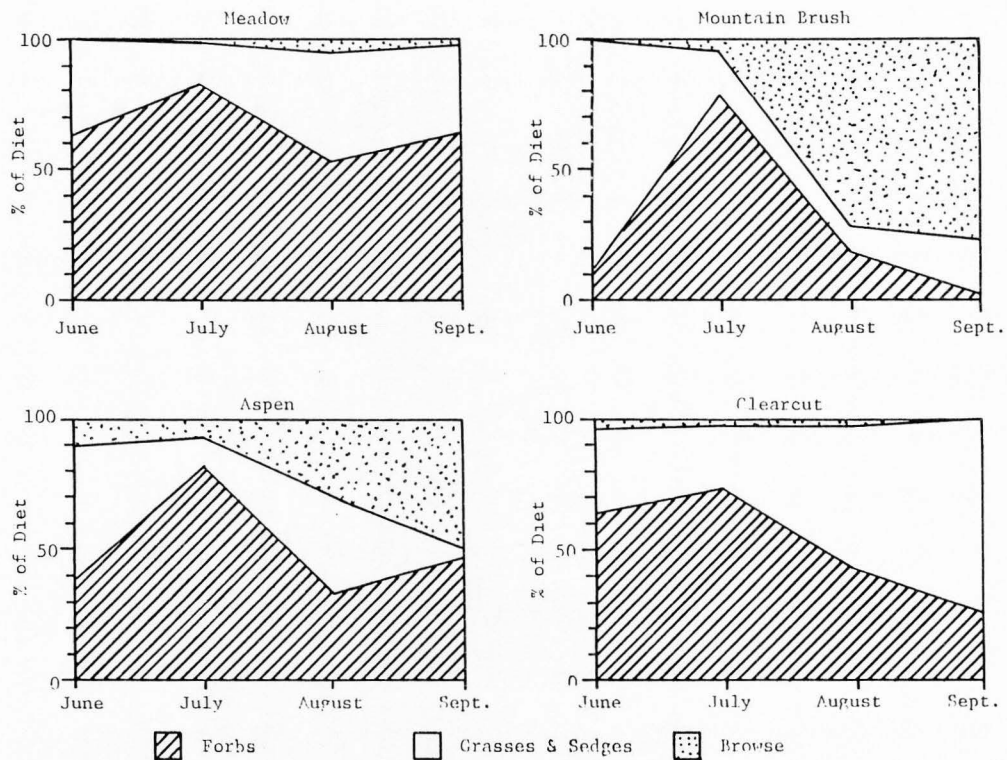
Figure 3. Elk diets by forage class on four habitat subunits in the aspen ecosystem, Davis County Experimental Watershed, Utah. Percentages are on a dry-weight basis.

Consumption rates and intake

Table 12 presents the consumption rates and daily intake of deer and elk on each subunit of the aspen and lodgepole pine types. Deer consumption rates were highest in the subunits they most preferred to graze; aspen and meadow subunits of the aspen type and the clearcut of the lodgepole pine type. In both types, elk consumed the most forage per unit time in meadow subunits which they highly preferred as foraging sites.

Neither deer nor elk grazed in the unproductive conifer stands of the aspen type, and consumed forage at only marginal rates in the forested subunits of the lodgepole pine type (Collins 1977, Deschamp 1977).

Unfortunately, exact weights could not be obtained for some of the animals used in the study. However, based on the weights which are known and on estimated weights of unweighed individuals, the mean weight of each group of animals was approximated. These weights were then converted to metabolic body weight (kg $BW^{0.75}$), and intake was computed as g/kg $BW^{0.75}$ (Table 12). Intakes were similar between types for each species.

Effect of clearcutting on forage consumption

Although overall consumption rates of deer were significantly lower on cut than uncut aspen stands, consumption rates of forage classes and species investigated were not significantly different (Table 13). The elk consumption rate was significantly higher on clearcut than on uncut stands (Table 14). Elk consumed sedges and mountain brome at significantly higher rates in the clearcut aspen, but consumed browse at significantly lower rates.

Table 12. Mean consumption rates and estimated daily intake (dry matter basis) of deer and elk on different habitat subunits of the aspen and lodgepole pine types in northern Utah.

	Deer			Elk		
	Consumption rate (g/min)	Grazing min/day	Intake (g/day)	Consumption rate (g/min)	Grazing min/day	Intake (g/day)
	Aspen type					
Aspen	2.6 a[1/]	249	647	10.7 a	99	1059
Clearcut	2.2 b	27	59	13.0 b	46	598
Conifer	0.0 c	0	0	0.0 c	0	0
Meadow	2.6 a	216	562	17.6 d	334	5878
Mountain brush	2.3 b	84	193	15.9 e	49	779
Logging road	0.0 c	0	0	16.2 e	14	227
total		576	1461		542	8541
g/kg BW$^{0.75}$			73			128
	Lodgepole pine type					
Wet meadow	2.7 a[2/]	202	545	13.5 a	311	4196
Dry meadow	2.8 a	21	59	10.6 b	240	2539
Clearcut	3.3 b	241	795	9.5 bc	104	989
Mature forest	2.2 c	86	190	6.2 c	24	146
Stagnated forest	1.8 d	110	198	3.7 d	14	52
Revegetated road	ND [3/]	---	ND	8.5 e	21	121
total		660	1791		714	8043
g/kg BW$^{0.75}$			77			156

[1] Means within columns followed by a common letter are not significantly different ($P \doteq 0.05$).

[2] Consumption rate data for the lodgepole pine type are from Deschamp (1977).

[3] ND indicates missing data; however, grazing use of the revegetated road by deer amounted to only 0.5 percent of deer grazing activity, and therefore, affects intake only slightly.

Table 13. Mean forage consumption rates (g/min) ± SE of deer for forage classes and principal species occurring in cut and uncut aspen stands.

Forage (classes or species)	Habitat subunit	
	Aspen	Clearcut aspen
Forb	1.47 ± 0.20 a[1]	1.26 ± 0.10 a
Grass	0.01 ± 0.01 a	0.00 ± 0.00 a
Browse	1.11 ± 0.46 a	0.84 ± 0.27 a
Aspen	0.18 ± 0.06 a	0.14 ± 0.03 a
Snowberry	0.80 ± 0.44 a	0.61 ± 0.26 a
Engelmann aster	0.07 ± 0.03 a	0.03 ± 0.02 a
Peavine	0.24 ± 0.10 a	0.14 ± 0.09 a
Western valerian	0.34 ± 0.10 a	0.25 ± 0.06 a

[1] Means within rows followed by a common letter are not significantly different ($P \leq 0.05$).

Table 14. Mean forage consumption rates (g/min) ± SE of elk for
forage classes and principal species occurring in cut and
uncut aspen stands

| Forage | Habitat subunit | |
(classes or species)	Aspen	Clearcut aspen
Forb	5.27 ± 0.30 a[1/]	6.36 ± 0.77 a
Grass	3.21 ± 1.53 a	6.68 ± 2.60 b
Browse	2.91 ± 1.27 a	0.44 ± 0.17 b
Bearded wheatgrass	2.39 ± 1.12 a	1.72 ± 0.38 a
Mountain brome	0.81 ± 0.46 a	4.66 ± 2.37 b
Aspen	0.50 ± 0.26 a	0.09 ± 0.02 a
Snowberry	2.37 ± 1.34 a	0.05 ± 0.04 a
Engelmann aster	0.31 ± 0.14 a	0.44 ± 0.36 a
Peavine	0.69 ± 0.43 a	0.14 ± 0.06 a
Western valerian	0.11 ± 0.06 a	0.27 ± 0.21 a

[1/] Means within rows followed by a common letter are not significantly
different ($P \leq 0.05$).

Collins (1977) and Deschamp (1977) reported overall consumption rates of elk and deer, respectively, to be much higher on clearcut than uncut lodgepole pine subunits. Table 15 shows deer consumed forbs at significantly higher rates in cut than uncut lodgepole pine, but grass at a lesser rate. All four important dietary forb species-- dandelion, pacific aster, goldenrod, and heartleaf arnica--were consumed by deer at significantly higher rates in the clearcut.

The elk also consumed forbs at a significantly higher rate in the clearcut lodgepole pine, but mushrooms at a lower rate (Table 16). The three most important forbs in the elk diet--dandelion, aster and goldenrod--were consumed at significantly higher rates in the clearcut.

Diet selectivity

Percent similarity (PS) was calculated as an index to forage selectivity (Tables 17 and 18). When all PS values from either type were applied to analysis of variance by ranks, deer were found to be significantly more forage selective than elk (P $\leq$ 0.05). In both types, the deer were substantially more selective than the elk when grazing in the meadows.

Deer and elk diet overlap

The greatest overlap of deer and elk diets in the aspen type occurred in the mountain brush subunit during the latter half of summer, when both species were concentrating their foraging efforts on snowberry, the predominate species still actively growing (Table 19). Considerable overlap also occurred in the aspen subunit and in the aspen clearcuts, yet the lodgepole pine clearcut consistently had the greatest overlap (Table 20).

Table 15. Mean forage consumption rates (g/min) ± SE of deer for forage
classes and principal dietary species occurring in cut and
uncut stagnated lodgepole pine stands.

Forage	Habitat subunit	
(classes or species)	Lodgepole pine	Clearcut
Forb	1.17 ± 0.16 a[1/]	3.08 ± 0.02 b
Grass	0.39 ± 0.07 a	0.16 ± 0.03 b
Browse	trace a	trace a
Mushroom	0.19 ± 0.10 a	0.03 ± 0.02 a
Heartleaf arnica	trace a	1.16 ± 0.11 b
Pacific aster	trace a	1.00 ± 0.15 b
Goldenrod	0.00 ± 0.00 a	0.22 ± 0.06 b
Dandelion	0.70 ± 0.17 a	0.15 ± 0.08 b
Carex spp	0.22 ± 0.05 a	0.11 ± 0.01 a
Aspen	0.00 ± 0.00 a	0.09 ± 0.02 a
Grouse wortleberry	0.36 ± 0.07 a	0.03 ± 0.01 b

[1/] Means within rows followed by a common letter are not significantly
different ($P \leq 0.05$).

Table 16. Mean forage consumption rates (g/min) $\pm$ SE of elk for forage classes and principal dietary species occurring in cut and uncut stagnated lodgepole pine stands.

| | Habitat subunit | |
	Lodgepole pine	Clearcut
Forb	1.01 ± 0.23 a[1]	8.00 ± 0.72 b
Grasses and sedges	1.20 ± 0.68 a	1.18 ± 0.38 a
Browse	1.39 ± 0.58 a	0.77 ± 0.37 a
Mushroom	5.87 ± 1.84 a	0.30 ± 0.14 b
Heartleaf arnica	0.19 ± 0.10 a	0.04 ± 0.02 a
Pacific aster	0.00 ± 0.00 a	1.91 ± 0.28 b
Goldenrod	0.06 ± 0.02 a	3.83 ± 0.24 b
Dandelion	0.00 ± 0.00 a	1.98 ± 1.50 b
Carex spp	1.12 ± 0.67 a	0.96 ± 0.28 a
Aspen	0.74 ± 0.34 a	0.22 ± 0.08 a
Grouse whortleberry	0.59 ± 0.26 a	0.04 ± 0.02 a

[1] Means within rows followed by a common letter are not significantly different ($p \leq 0.05$).

Table 17. Percent similarity (PS) estimates relating percentage dry weight composition of species in deer and elk diets to that of dry-weight species composition of habitat subunits of the aspen type, Davis County Experimental Watershed, Utah. High PS values indicate low degree of selectivity.

	June		July		August		September		Mean	
	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk
Aspen	26	34	21	35	35	35	36	32	29	34
Clearcut	25	27	27	39	40	29	36	27	32	31
Meadow	11	22	21	23	21	43	13	40	16	32
Mountain brush	24	17	28	47	53	65	46	60	38	47

Table 18. Percent similarity (PS) estimates relating percentage dry weight composition of species in deer and elk diets to that of dry-weight species composition of habitat subunits of the lodgepole pine type, Uinta Mountains, Utah. High PS values indicate low degree of selectivity.

| | 2-week periods | | | | | | | | | | | | Mean | |
| | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | | |
	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk
Wet meadow	7	27	4	18	9	16	9	18	9	32	9	38	8	25
Dry meadow	25	41	29	37	28	40	29	45	28	43	32	40	29	41
Clearcut	31	27	26	25	26	24	28	25	25	34	26	48	27	31
Mature forest	48	86	33	76	34	65	22	33	27	31	31	45	33	56
Stagnated forest	28	37	22	37	10	37	19	29	18	31	64	37	27	35

Table 19. Overlap of deer and elk diets on different subunits of the aspen type, estimated by the percent similarity index.

	Monthly periods			
	1	2	3	4
Aspen	23	41	59	42
Clearcut	17	15	24	10
Meadow	46	43	26	18
Mountain brush	16	32	81	78

Table 20. Overlap of deer and elk diets on different subunits of the lodgepole pine type, estimated by the percent similarity index.

	2-week periods					
	1	2	3	4	5	6
Wet meadow	51	57	54	53	39	19
Dry meadow	24	35	37	42	40	34
Clearcut	76	72	78	54	70	61
Mature forest	52	41	43	47	48	53
Stagnated forest	51	51	51	16	16	55

Diet quality

Elk diets were found to be significantly more digestible by elk rumen inocula than by deer inocula (Tables 21 and 22) except in the case of the highly digestible logging road diet. Deer diets were not always significantly more digestible by elk inocula; when they were, the difference was usually less than the difference occurring in tests of elk diets digested by elk versus deer inocula. Certainly there were far fewer differences (2 versus 9). The smallest differences in digestibility occurred with the most digestible diets, and are most apparent with diets consumed during the periods of most active plant growth (Tables 21 and 22).

Crude protein values of deer and elk diets in the aspen type are reported in Table 23. Elk generally consumed diets lower in percent crude protein than deer. In early summer, the lowest crude protein levels occurred in the meadow diets. By late summer the lowest values were for diets in the mountain brush.

Insects

Horse fly (Hybomitra opaca) disturbance to deer and elk in the aspen type was extreme during July (Figure 4), with peak levels in mid-July. Only slight differences in fly densities were recorded between subunits, but much greater densities were noted in and around the enclosure (Figure 5). Elk appeared to attract greater densities of flies than the deer (Figure 6). Another horse fly, Tabanus punctifer, also occupied the area, but in too few numbers for accurate assessment of densities. Neither fly became active unless ambient air temperature was at or above 17° C. As flies became active in all

Table 21. Mean in vitro organic matter digestibility values (%) of deer and elk diets in the aspen type, Wasatch Mountains, Utah. Diets were fermented in two trials, first with inocula from the appropriate species, and secondly, with inocula from the alternate species.

Type	Period	Deer diets		Elk diets	
		Deer inocula	Elk inocula	Deer inocula	Elk inocula
Aspen	I	69.0 abc[1]	72.5 ac	64.5 b	71.2 c
	II	64.6 a	66.6 a	73.0 b	72.6 b
	III	63.9 a	71.2 b	62.5 a	65.5 a
	IV	65.9 a	64.7 a	59.3 b	59.5 b
	mean	65.8 a	68.7 b	65.1 a	67.2 b
Clearcut	I	75.1 a	73.7 a	64.6 b	74.0 a
	II	73.2 a	73.1 a	72.5 a	72.9 a
	III	63.9 a	71.9 b	63.0 a	69.1 c
	IV	73.0 a	70.1 a	51.8 b	57.1 c
	mean	71.3 a	72.2 a	63.0 b	68.3 c
Logging road	I	ND[2]	ND	72.2 a	75.3 a
	II	ND	ND	76.2 a	75.7 a
	III	ND	ND	70.3 a	71.0 a
	IV	ND	ND	64.5 a	68.6 a
	mean	ND	ND	70.8 a	72.6 a
Meadow	I	74.4 a	78.0 a	75.7 a	77.7 a
	II	68.2 a	67.1 a	70.7 a	70.5 a
	III	59.4 a	59.9 a	65.6 b	71.9 c
	IV	60.8 a	64.2 a	64.3 a	70.2 b
	mean	65.7 a	67.3 ab	69.1 b	72.6 c

Table 21. Continued.

| Type | Period | Deer diets | | Elk diets | |
		Deer inocula	Elk inocula	Deer inocula	Elk inocula
Mountain brush	I	77.6 a	77.0 a	79.5 a	86.2 b
	II	72.8 a	69.4 a	71.8 a	73.0 a
	III	59.4 a	71.8 b	52.3 a	62.8 c
	IV	70.3 a	70.0 a	64.5 b	63.9 b
	mean	70.0 a	72.0 a	67.0 b	71.5 a

[1]Means within rows followed by a common letter are not significantly different (P ≤ 0.05).

LSD = 4.8 for specific period comparisons; LSD = 2.4 for comparisons of overall means.

[2]No data available.

Table 22. Mean in vitro organic matter digestibility values (%) of deer and elk diets in the lodgepole pine type, Uinta Mountains, Utah. Diets were fermented in two trials, first with inocula from the appropriate species, and secondly, with inocula from the alternate species.

Type	Period	Deer diets		Elk diets	
		Deer inocula	Elk inocula	Deer inocula	Elk inocula
Wet meadow	I	69.4 a[1/]	64.9 a	49.8 b	57.8 c
	II	63.4 a	63.9 a	47.6 b	56.3 c
	III	61.9 a	61.9 a	43.5 b	54.1 c
	mean	64.9 a	64.9 a	49.8 b	57.8 c
Dry meadow	I	65.9 a	67.2 ac	62.1 b	69.0 c
	II	59.0 a	59.6 a	63.5 b	72.7 c
	III	59.0 a	59.4 a	57.1 a	63.0 b
	mean	61.3 a	62.1 a	60.9 a	68.2 b
Clearcut	I	68.1 a	65.9 a	73.5 b	75.2 b
	II	58.1 a	56.1 a	68.3 b	71.8 c
	III	60.8 a	57.6 b	58.1 b	64.0 c
	mean	62.3 a	59.9 b	66.6 c	70.3 d
Mature forest	I	52.5 a	54.9 a	42.3 b	41.2 b
	II	52.8 a	53.3 a	57.9 b	58.3 b
	III	59.0 a	61.5 bd	54.0 c	61.1 d
	mean	54.7 a	56.6 b	51.4 c	53.5 d

Table 22. Continued.

Type	Period	Deer diets		Elk diets	
		Deer inocula	Elk inocula	Deer inocula	Elk inocula
Stagnated forest	I	50.2 a	49.5 a	ND[1/]	ND
	II	62.1 a	63.3 a	ND	ND
	III	61.1 a	62.6 ac	57.1 b	64.4 c
	mean	57.8 a	58.5 a	57.1 a	64.4 b

[1]Means within rows followed by a common letter are not significantly different (P ≤ 0.05).

LSD = 2.5 for specific period comparisons and for the comparison of stagnated forest elk diets in the overall mean comparison; LSD = 2.0 for comparison of the deer diet-elk inocula overall mean with the elk diet-deer inocula overall mean; LSD = 1.4 for all other overall mean comparisons.

[2]No data available.

Table 23. Percent crude protein (N X 6.25) content of deer and elk diets on different subunits of the aspen type, Wasatch Mountains, Utah.

	June		July		August		September	
	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk
Aspen	32.7 a [1/]	26.8 b	21.8 c	18.7 cd	16.7 de	15.0 ef	12.3 f	12.3 f
Clearcut	28.8 a	26.2 a	18.4 b	17.8 b	15.2 bc	12.9 cd	14.8 bc	9.9 d
Meadow	21.4 a	22.0 a	18.9 ab	17.7 bc	14.2 cd	15.7 bcd	16.3 bc	11.8 d
Mountain brush	26.3 a	25.8 a	18.1 b	16.9 bc	12.9 cd	10.7 d	10.8 d	10.0 d

[1] Means within rows followed by a common letter are not significantly different ($p \leq 0.05$).
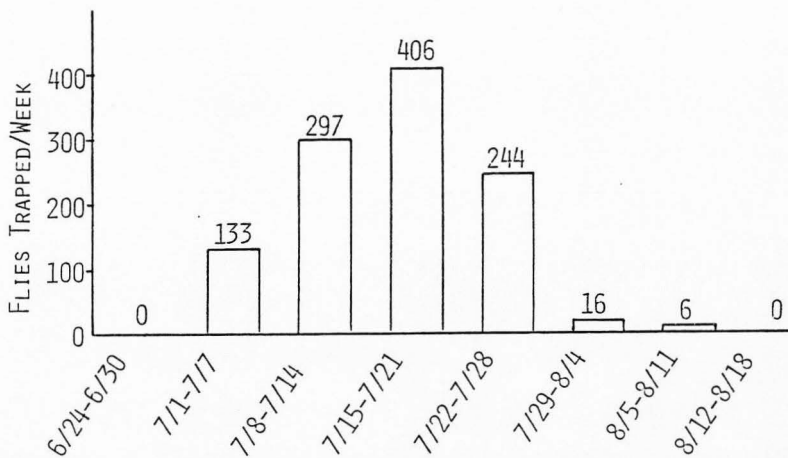
Figure 4. Seasonal occurrence of horse flies (<u>Hybomitra</u> <u>opaca</u>) in the Chicken Creek drainage of the Davis County Experimental Watershed, Utah.
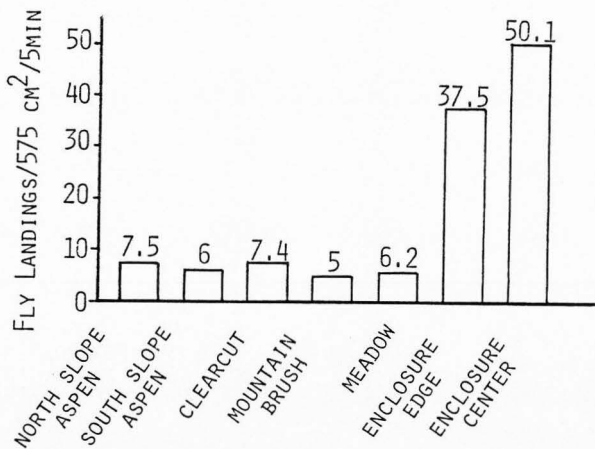
Figure 5.   Horse fly (<u>hybomitra</u> <u>opaca</u>) activity at different
locations in the Chicken Creek drainage of the Davis
County Experimental Watershed, Utah.
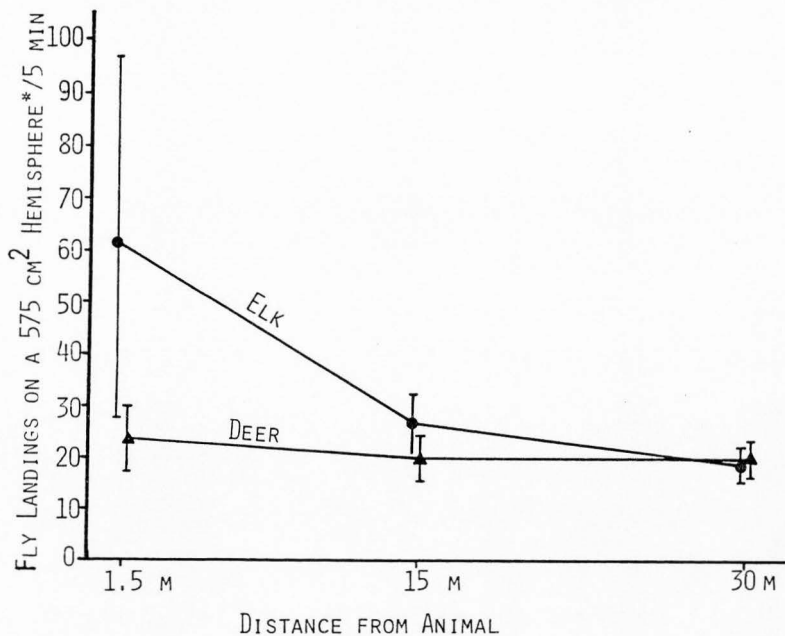
Figure 6.   Relationship of fly activity at various distances from deer versus elk.   Vertical bars represent 95 percent confidence limits.
*The hemisphere was the visible side of a black 12" diameter beach ball suspended by a pole 120 cm from observer and 120cm above ground.

subunits, the animals would frequently run to escape fly concentrations building up around them. In the case of deer, this behavior very characteristically involved running from one bed to another, then quickly bedding down again. Generally, these movements were back and forth between beds of a group of 4 to 7 beds located within 40 to 50 m of each other. Such beds often became as much as 30 cm deep with repeated use. The elk on the other hand, did not remain in one general area as they ran from flies, but would move several kilometers during the day. Sometimes an estimated 150 flies would swarm around each elk.

Large numbers of face flies (_Musca_ _autumnalis_) were also attracted to the deer and elk, but their activity did not seem to irritate the animals nor cause eye infection.

White-faced hornets (_Vespula_ _maculata_) were attracted to the animals, but their presence and landings on the hair coat was not disturbing. Apparently the wasps were attracted to the concentration of horse flies around the animals, as they were observed to methodically capture the flies, dismember them, and take only the fly abdomens back to the hives.

DISCUSSION

In practice it is extremely difficult to assemble all information pertinent to an explanation of any one example of habitat selection; presumably, this is why well documented examples are so scarce and deal mainly with animals behaviorally less complex than deer or elk. A rational explanation of animal choice must take into consideration all apparent advantages and disadvantages of behavior. That is, daily and hourly cost:benefit ratios as well as ultimate evolutionary consequences must be considered. Obviously, this study does not begin to address the entire scope of factors associated with deer and elk habitat selection. It does, however, help document the importance of certain environmental factors to these animals.

Grazing Behavior

Forage selection

The results of this study reject the null hypothesis that deer are not significantly more forage selective than elk. With one exception (grazing in the clearcut aspen), deer selected their diets from fewer species in a given subunit than elk. This is indicated by the percent similarity values which were calculated to measure the overlap of diets with forage availability in each subunit. Generally, both species exhibited the lowest degree of selectivity in subunits with lowest plant diversity or where choice was otherwise limited. For example, mountain brush and mature forest subunits mainly produce snowberry (aspen) and grouse whortleberry (lodgepole pine), respectively, and the costs of foraging on less abundant species apparently prevents their being selected at a rate much greater than their random occurrence in the path of the animal. Low selectivity was also exhibited in the dry

meadow subunit where the density and low profile of vegetation possibly made selection of individual plant species difficult for either animal.

The other factor of forage selectivity, that concerned with the various parts of a specific plant species, was not objectively dealt with in this study. However, deer were observed to be more discriminating in plant parts consumed. Discrimination may have resulted, in part, from restrictions in bite size (e. g. a deer may be able to readily fit only the terminal half of an American bistort leaf into its mouth, whereas elk can easily ingest the whole leaf). In many cases, deer fed exclusively on leaf versus stem, or leaf versus petiole.

Contrasts in selectivity may also reflect differences in digestive capacity that appear to dictate the type of forage which can efficiently be used by deer or elk. Elk were found to have significantly wider digestive capacities than deer. Elk diets were usually better digested by elk than by deer inocula, likely because elk rumen micro-organisms possess the cellulolytic enzymes necessary in the digestion of the fibrous portion of grasses (Leege et al. 1977). Deer diets were better digested by elk only when the diets were characterized by more fibrous plant materials. Schoonveld et al. (1974) demonstrated that mule deer have smaller rumen-reticula, omasa and abomasa than either sheep or goats of comparable size. They concluded that this characteristic of deer digestive physiology prevented fibrous food from remaining in the rumen long enough for adequate digestion of lignified fiber and that, consequently, large, abrasive food particles passing out of the rumen led to severe digestive upset and food impaction in the omasa. Hungate (1966, p. 414) suggested that large ruminants will be better

adapted to digest fibrous forages than smaller ruminants, because the relatively greater volume of their rumen allows them to retain ingesta for a longer time. Thus, the differences between in vivo digestibilities of the same diets by deer versus elk should be even greater than the in vitro differences, since food would be retained in the elk rumen longer than in the deer rumen. These observations help explain the lower degree of selectivity by elk, and indicate elk will more successfully compete with deer under poor range conditions, because they have a greater digestive capacity and wider food base (Wagner 1978).

The crude protein content of summer range deer and elk diets observed by Pallesen (1979) and myself are generally in excess of requirements of mature animals, since crude protein levels above 15 percent are degraded by rumen micro-organisms to approximately 15 percent, and levels above 6 to 7 percent are adequate for proper function of rumen micro-organisms (Dietz 1965). French et al. (1955) found optimum growth in white-tailed deer occurred with diets of 13 to 16 percent crude protein. The crude protein values of the deer diets are higher than associated elk values, because of the deer's selection of diets higher in proportions of leaf material and forbs, and not because they select for that nutrient, per se (Arnold 1964).

Overall, diets from different subunits within each type are probably of comparable quality in all respects except digestible energy, since the level of that nutrient is dependent on the digestibility of the diet. Hence, the profitability of grazing any given subunit will be a function of total intake X digestibility, assuming there are not significant differences in other environmental conditions which differentially affect the cost of grazing those subunits.

Intake

In both vegetation types, the estimated intakes (g/kg BW$^{0.75}$) of elk were much greater than those of deer. This is disturbing since one would expect them to be nearly equal. Deer and elk diets were of approximately the same digestibility, and hence, the intakes of the two species are legitimately compared on a metabolic weight basis.

After an extensive review of the literature, Cordova et al. (1978) concluded that intake estimates for grazing livestock are highly variable, but that those considered most valid fall in the range of 40 to 90 g/kg BW$^{0.75}$, the lower intakes being associated with mature and cured forages. Recalculation of data presented by Papegeorgiou (1978) suggests a maintenance intake requirement of 80 g/kg BW$^{0.75}$ for red deer.

Estimates of intake for deer in this study appear realistic from the standpoint of what Cordova et al. (1978) considered acceptable for livestock. However, by the chromic-oxide method, Fulgham (1978) found deer intake rates were 102 and 96 g/kg BW$^{0.75}$ while grazing on sagebrush-grass range in early and late winter, respectively. These values were much higher than what I observed, but when apparent digestibility of deer diets in the two studies were considered, it was found that his deer consumed 45 g apparent digestible dry matter per kg BW$^{0.75}$ per day compared to 48 and 46 g/day in the aspen and lodgepole pine types, respectively. Alldredge et al. (1974) found that mature deer consumed about 8 percent more forage in summer than in winter. This suggests that the intake rates for deer in my study, if in error, are underestimated slightly. In contrast, Fulgham (1978) found that the ocular method generally overestimated intake, when compared with the

chromic-oxide method; however, the great variability in Fulgham's ocular data prevents any firm conclusions about the relationship of the two methods.

The differences between the deer and elk intake values are probably not due solely to error in the method of estimation. In all but late summer and fall, I have observed strong differences between the intakes of deer and elk which were fed ad libitum at the Utah Division of Wildlife Resources' big game pens. There, as well as on the study areas, deer intake and weight gains were low until late August, whereas elk intake and body condition were high throughout summer. Possibly, elk metabolic rate and, hence, intake do not fluctuate annually as greatly as do deer's. This warrants further investigation. Elk intake was much greater in the lodgepole pine than in the aspen type, possibly because the elk were yearlings and still rapidly growing during that phase of the study.

Feeding site selection

The hypothesis that deer and elk use of aspen and lodgepole pine subunits is not significantly different than the relative availability of those subunits was rejected. The meadow and logging road subunits of the aspen type were grazed significantly more by both deer and elk than the relative amounts of those areas. In the lodgepole pine type, both species grazed significantly more on wet and dry meadows and clearcuts than their relative availability. However, in either type, areas further than 60 m from forested edge were never grazed, indicating they are behaviorally less acceptable than areas near cover; both deer and elk appeared anxious to cross wide open flats. It was also noted that the animals preferred to graze within the shade of edges during hot

clear days. Revegetated roads also incurred significantly greater use by elk. With the exception of the logging road, these subunits represented the most forage-productive areas in their respective types. This suggests that deer and elk prefer feeding in areas where they can obtain the most forage per unit of time. Clary and Larson (1971) likewise concluded elk may prefer areas of greater forage availability, since their distribution in the ponderosa pine type in northern Arizona was directly related to total herbage production and forb production. In the same study, deer distribution was determined to be "rather diffuse" and not correlated with forage production. This does not necessarily mean that deer distribution was any less dependent on food supply than was elk distribution, but may simply indicate that deer feeding area preference was more closely aligned with some aspect of food other than total herbage production.

Consumption rates. Deer and elk exhibited significantly higher consumption rates on subunits they most preferred to graze than on less preferred subunits. Thus, the animals obtained the most food per unit time on the preferred sites. However, deer and elk differ significantly in grazing area preferences on all but the conifer and logging road subunits, suggesting forage production, per se, is not the sole factor affecting feeding site selection.

Arnold (1964) and Bell (1969) both reported that the amount of forage available to an animal is greatly reduced when it is closely associated with large amounts of unused herbage. Interference by unpalatable species is greatest when the preferred species are sparse and of low stature in the general vegetal profile. Thus, forbs buried deep in a grass-sedge sward are of limited accessibility to a selective

feeder like deer that effectively utilize only a small amount of mature grass and sedges in their diet. This phenomenon was clearly evident in observations of deer grazing meadow subunits. When grass-likes were accidentally prehended with forbs, they were dropped. Presumably, this is why deer, consuming a greater proportion of forbs in their diet than elk, secondarily preferred the meadows as foraging areas. Clearcut lodgepole pine areas, on the other hand, produce fewer forbs, but since plant cover is much less dense, forbs are more accessible.

In both the aspen and lodgepole pine types, deer and elk most preferred grazing that subunit associated with highest consumption rates. However, if one assumes that the resting metabolic rates during grazing hours are approximately the same on each habitat subunit, the fact that the animals did not graze preferred subunits exclusively suggests that a daily cost-benefit approach to maximization theory does not adequately explain the feeding site selection. The amount of time spent grazing "less productive" subunits exceeds the degree of error Sutherland and Mackintosh (1971) suggested is acceptable on the basis that the animal will make some mistakes in value perception. Bitterman's (1975) theory on matching, likewise, is an inappropriate explanation because estimated digestible dry matter consumption rates regressed on grazing-subunit preferences yielded significant correlation only in the case of elk grazing the lodgepole pine type. Consequently, the observed pattern of grazing use by deer and elk is probably best explained in terms of both proximate and ultimate consequences of the behavior. For example, it is likely that natural selection has favored an animal which is motivated to explore its environment as a hedge against possible changes in the environment. Likewise, in a more proximate sense,

the exploratory animal may receive low-grade reinforcement for its be-
havior because its success at discovering new food sources is enhanced;
a new food source may simply be one where: (1) forage value relative
to other sites has improved with the season, (2) complete utilization
of forage at other sites has occurred, or (3) animals have been behav-
iorally excluded elsewhere.

Insect effects on grazing. Blood-sucking insects have been
reported to affect summer distribution of elk (Gruell and Roby 1976,
Anderson 1958), but the impact of insect attacks on deer and elk behav-
ior is generally poorly understood (Moen 1973). Mosquito attacks in
the lodgepole pine type caused deer and elk to graze inefficiently
during the day and to graze more at night or on upland sites where
breezes reduced mosquito activity. Stoddart et al. (1975, p. 261)
report that cattle on high mountain meadows are sometimes similarly
affected and fail to make satisfactory weight gains as a result. In
the aspen type, the most bothersome insect was the horsefly, and its
activity was fairly constant regardless of winds or openness of the
habitat when temperatures exceeded 17° C. Consequently, different
subunits of the aspen type were infested about the same, and the animals
benefited little by moving from one area to another. The exception to
this occurred when temperature lag in the aspen subunit attributable to
shading delayed the onset of fly activity and temporarily provided fly-
free habitat after flies had become active in open subunits. This
effect had little influence on deer feeding-area selection since they
typically were already feeding in the aspen stands. The benefit to elk,
although apparent, is of limited importance, and may not have occurred
at all, had the elk been allowed to vacate the area in preference for

less infested elevations or vegetation types. Fly disturbance in the
Chicken Creek area is unusually high, probably because the area has
a relatively large number of slow-moving streams and stagnant beaver
ponds in close association with substrata of high organic content; such
conditions are ideal for horsefly (Hybomitra) larvae (Teskey 1969).

Microclimatic effects on grazing. Microclimate can also play a
potentially important role in habitat selection by deer and elk (Allen
1977, Black et al. 1976, Edgerton and McConnell 1976, and Moen 1973).
Temperatures on aspen and lodgepole pine summer ranges are typically
well below the body temperatures of deer and elk, and, hence, unlikely
to cause thermal stress. Radiation, however, may play a much greater
role in the thermal balance of the animals. Unfortunately, my attempts
to collect data on animal response to temperature and radiation
regimes, and to determine whether or not either of these variables ever
increased the deer or elk daily cost of free existance, failed.
Certainly these characteristics contributed to comfort or discomfort of
the animals, but it is questionable whether or not comfort by itself
influenced habitat selection.

Resting Behavior

Cover has been identified as one of the most important factors
affecting bed selection by deer and elk (Allen 1977, Black et al. 1976,
Edgerton and McConnell 1976 and Moen 1973).

The results of this study indicate that, aside from their prefer-
ence for edges, elk generally bed near the spot where grazing ceases.
Whether or not the elk direct their feeding pattern so as to conclude
grazing in a certain place is not known. Hence, bedding following
grazing in the meadow most often was within a few meters of the

adjacent edge. Often the animals bedded just outside the edge, but
rarely did they ever bed in direct sunlight. Deer, in contrast, pre-
ferred bedding in specific areas, and were observed to use the same
beds repeatedly throughout the summer. The deer's preference for
specific resting sites may represent predator-defense behavior; greater
familiarity with resting local and possible escape routes may be more
essential for a solitary deer than for gregarious elk which benefit
from group surveillance of surroundings. Thermal cover apparently is
important for both deer and elk, since centers of clearcuts (having
good escape cover, but poor thermal cover) were not used for bed sites.

Insect effects on resting. The elk appeared to rest more fitfully
than the deer during fly attacks, likely because they attracted rela-
tively more flies than deer. Elk may have attracted relatively more
flies, because their greater size and gregarious nature provided a
larger, more visible target for the flies; flies find their prey by
detecting near infrared emissions of the hair coat. The distressed
behavior of one elk appeared to stimulate the behavior in others; thus,
when one would run, all would run. Such social facilitation would
never allow them to adopt the deer's fly-evading behavior of making
short dashes back and forth between beds. During fly attacks, elk pre-
ferred bedding in patches of false hellebore, deep stands of grass, or
under low-hanging trees, as this appeared to reduce fly activity. In
the enclosures, the elk preferentially bedded in the false hellebore
and deep grass sites until they were obliterated by frequent use; after
that time areas under low-hanging trees were the principal bed sites.
Deer, too, bedded under low hanging trees. Although horse flies
preferentially attacked the belly and undersides of the animals,

neither the deer nor the elk spent more time lying down during the fly season. In contrast, Espmark and Langvatn (1979) reported red deer spent twice as much time lying on days when head fly (Hydrotaea irritans) harassment was severe. Espmark and Langvatn did suggest that calm, hot, sunny weather associated with the appearance of head flies, may have been responsible for reduced locomotory behavior.

Deer and Elk Competition

Cliff (1939) concluded that elk would continue to be more productive than deer on poor winter and summer range in the Blue Mountains of Oregon, because they can use a wider array of forages. Bird as cited by Kramer (1972) reported that white-tailed deer populations in Manitoba are much lower in the presence of elk than in elk-free areas. Similarly, Cairns (1976) found that deer were more abundant in areas where elk were excluded. However, most discussion of deer and elk competition is inferential, speculative and controversial (Mackie 1976).

The results of this study do not provide any direct evidence of deer and elk competition, since populations were not manipulated or monitored for changes in productivity. However, data on the feeding niches and digestive capacity of the two species give some indication there is potential for exploitative competition between deer and elk.

Elk are generally broad spectrum feeders (Wagner 1978), and the data from my study reveal no exceptions. In both vegetation types, the feeding niche (plant species and structures ingested) of elk was wider and more flexible than that of deer. Not only were the elk less selective of plant species, they also ingested older and coarser plant parts. The relatively restricted nature of deer diets represented actual physiological limitations; deer simply could not digest some forages as

efficiently as elk. Deer rates of forage consumption were apparently restricted by interference from unpalatable species or plant parts, as well. Thus, deer were not capable of using the highly productive meadows to the extent that elk were.

Elk should be more capable of adapting to suboptimal forage supplies (species and communities) than deer. This is in agreement with Mackie (1970) who found that elk could more intensively use most plant communities, topographic sites and all forage classes than deer.

Mangement Implications

The strong differences in habitat subunit preferences and uses exhibited by deer and elk in this study clearly indicate that specific components of habitat should be recognized in the management of either species. The broad classification of a vegetation type as to habitat value is too general to recognize the specific animal habitat relationships which affect deer and elk. It is also important to recognize that deer and elk differ in their responses to specific modifications or alternative uses of the habitat.

Use of riparian habitat

Recent studies (Black et al. 1976, Lonner 1976, Marcum 1975, and Patton and Judd 1970) have shown deer and elk make disproportionately greater use of bottoms and areas near water; however, these studies have not identified the exact nature of this relationship. The deer and elk in this study appeared to have limited need for drinking water in either the aspen or lodgepole pine types. Apparently, the attraction of the wet bottoms is the availability and high quality of plants associated with high water tables. This is true for both species, but especially elk. Gentleness of slope appears to have little to do with

the preference for bottoms; in the aspen type, ridgetop grass-forb communities of species composition similar to meadow bottoms, but of limited productivity, are relatively unused by either species. This is in agreement with Julander and Jeffery (1964) who showed elk distribution on summer range in central Utah is little affected by any but very steep slopes. They also indicated that deer have slight preference for slopes greater than 30 percent.

Lodgepole pine meadows and aspen meadow bottoms provided the bulk of forage consumed by elk and almost the same amount of deer forage consumption as did the subunits most preferred by deer. This fact warrants special consideration of such meadows, especially since they are highly susceptible to disturbance. These areas commonly represent the most favorable terrain in which to build roads, campgrounds, and summer homes and to graze livestock.

Riparian habitat is of great importance to big game in unlogged or unburned lodgepole pine forest, because overstory thickening results in lowered forage production of poorer quality as measured in the mature and stagnated stands. Exclusion of deer and elk from meadow bottoms is probably less detrimental in aspen areas where adjacent plant communities apparently meet deer and elk habitat requirements, and in lodgepole pine areas where openings are created by logging or fire. However, a little management effort in controlling uses of bottoms will greatly enhance this valuable habitat for animals using either type. Such natural meadows, if well managed, are self perpetuating and do not require periodic reestablishment as do created openings. In regard to either type, there is perhaps more potential for enhancement of big game habitat through alteration of the uses of the landscape, than through alteration of the

landscape itself.

The results of this study indicate deer and elk use meadow bottoms even more than previously supposed. At least two explanations can be given for this: (1) since the study animals were accustomed to human activities, they were undisturbed by such activity and made greater use of the bottoms than would their wild counterparts; (2) the techniques used in this study more directly and accurately accounted for the relative distributions of the animals than do the commonly used techniques which record only the "signs" left by the animals.

Use of clearcuts

If competing uses in aspen or lodgepole pine types limit forage supply, clearcutting could be used to increase forage production (Wolfe 1978). However, as Pengelley (1972) cautioned, overstory removal is not necessarily beneficial to big game in all situations.

Due to the limited and fixed availability of highly productive natural openings in the lodgepole pine types, creation of small openings in extensive, unproductive timber stands would be of value to both deer and elk. This is especially true when livestock grazing or other human-generated activities eliminate a major portion of the forage resource in the bottoms. However, under conditions of low stocking rate, full access to meadow bottoms and limited inter- and intra-specific forage competition, clearcutting may be of little value to big game in the aspen type. Although these clearcuts were less preferred than adjacent aspen stands, they were used periodically throughout the day, suggesting that they are still marginally acceptable habitat. This combined with greatly improved forage production following timber removal, indicates that clearcutting of aspen may be beneficial to big game where range

conditions are more restrictive. This should be determined before clearcutting is justified on the basis that it will benefit big game.

Pellet Groups

My findings show that the pellet-group count technique does not reliably estimate deer or elk preference for various habitat subunits or modifications. The tendency of pellet-group counts to underestimate the importance of the most valuable habitat and overestimate the importance of least preferred habitat is even more serious.

Defecation rates were characteristically lowest in the areas where the deer or elk most preferred to graze, presumably because forage was most available there and required the least walking during grazing; the more the animals walked, the more frequently they defecated. Areas which incurred no grazing or resting use often were sites of many defecations, as the animals travelled through them. Similarly, J. M. Peek (pers. comm.) has observed that deer defecate at higher rates between feeding and bedding areas and that pellet data do not correlate with track data. He has also observed in the Gallatin Mountains that elk pellet groups are clumped along trails connecting feeding and bedding sites.

The daily defecation rates of deer and elk in this study are roughly double the accepted standard of 13 groups per day. Such high rates are likely a result of the quality and quantity of forage the animals consumed. Relatively good conditions on summer versus winter range can result in higher feed intake (Rogers et al. 1958), producing higher defecation rates. Likewise, high moisture content in forage has been found to coincide with higher defecation rates (Longhurst 1954). K. O. Fulgham (pers. comm.) observed that fecal volume doubled in deer

as they switched from a predominantly browse diet to a herbaceous diet
in spring. Hence, defecation rates determined for animals consuming
drier, more fibrous or limited forages are probably not applicable to
animals on summer range, and their use for estimating populations would
result in gross overestimates.

Tame Animal Methods

The use of tame deer or elk is expensive and requires long-term
investments in raising and training, but it appeared to be the method
best suited for this study. Other methods appeared unacceptable for the
following reasons: Fecal analysis (Free et al. 1970) does not allow
identification of the geographic area in which any species or portion
of the diet is consumed, and also probably underestimates the quantity
of highly digestible species occurring in the diet (Slater and Jones
1971). Wallmo et al. (1973) found both feeding-site (McCulloch 1955)
and foraging-minutes (Hahn 1945, Buechner 1950) analyses of diets over-
estimate importance of shrubby species and underestimate value of forbs
and grasses, even in open and easily observable types such as sagebrush-
grass. Rumen sample analysis (Rice 1970) requires the sacrifice of
many animals and does not allow identification of location where forage
was ingested.

Bite count observations using tractable animals have the following
advantages over the above methods: (1) positive identification can be
made of all species either eaten or consistently rejected; (2) observa-
tions can be planned in relation to the needs and design of the study;
(3) large amounts of data can be collected in relatively short time;
(4) the observer knows exactly where, geographically, any species or
portion of the diet was consumed; (5) tame animals can also be used as

a source of rumen fluid for subsequent forage digestibility analyses.

A possible inherent limitation in the use of hand-reared, tame animals is that they may exhibit forage preferences different from their wild counterparts because they have not had the same early experience with food as those reared by the dam. Arnold and Maller (1977) have shown previous grazing experience can affect later grazing efficiency of sheep. However, generally little is known of the duration of this experience effect. For most grazing studies, a period of 7 to 10 days is considered adequate for the herbivore to adjust its feeding behavior to the characteristics of a new environment. It is noteworthy that, in addition to having 7 to 10 day adjustment periods, the animals used in this study had constant access to the same vegetation and physiography of the study areas throughout the course of the study. By all indications of animal response, this appeared to be effective in eliminating inefficient foraging and selection. At no time during the study were the animals observed to exhibit exploratory or unsettled feeding behavior described for mule deer artificially fed in small pens during non-sampling periods (Neff 1974). Arnold (1964) found that lambs require constant exposure to pasture conditions in order to maintain appropriate forage preferences in face of seasonal phenologic changes.

While little information exists as to the duration of the experience effect, at least two studies have demonstrated that tame animals will exhibit the same forage preferences as their wild counterparts. Longhurst et al. (1968) showed that deer raised in pens on a diet restricted to a single pelleted feed showed the same forage preferences as wild animals. Similarly, Regelin et al. (1976) demonstrated that deer receiving daily supplemental feed of alfalfa and concentrate

pellets, ad libitum, while at the same time having constant exposure
to native forage, exhibited virtually identical preference hierarchies
as tame deer subsisting entirely on native forage. Although further
testing for differences in forage preference may be desirable, these
studies, combined with the lack of information demonstrating that tame
deer or elk have different foraging preferences than wild animals,
indicates there is probably little bias associated with the use of
experienced, tame, generalist herbivores.

To my knowledge, free-ranging, domesticated big game animals have
not previously been used for the determination of habitat preferences;
thus, such use is even more subject to skepticism than their utility for
diet composition studies. A review by Partridge (1978) showed positive
effects of early experience on habitat selection have been demonstrated
for many different animal phyla. However, most of the species reviewed
are quite specialized in their use of habitat. Partridge suggested
that habitat selection by species living in spatially and temporally
variable habitat is not as dependent upon early experience, because it
is more adaptive for such animals to sample all other available habitat
to determine for themselves where they best acquire food or other
necessities.

A test for the reliability of this method is readily possible, but
lack of time and materials prevented such testing in this study. As a
consequence, my confidence in the method is based upon the large number
of consistencies observed between tame and wild animal use of the study
areas. The method offers a high degree of accuracy in pinpointing big
game use relative to habitat subunits and this warrants further consi-
deration as a research tool. Because animal response to environmental

conditions can be closely monitored, the method opens up new possibilities in the area of intensive behavioral and physiological research.

SUMMARY AND CONCLUSIONS

The feeding behaviors and habitat preferences of deer and elk
using aspen and lodgepole pine summer ranges are considered with respect
to possible interspecific competitive interactions and incompatability
with other range uses. The particular objectives of this study were to
determine activity-specific, habitat-subunit use by deer and elk in
aspen and lodgepole pine ecosystems for the summer season, and to deter-
mine what dietary and other behavioral constraints may exist for deer or
elk grazing each habitat subunit. The study resulted in the following
conclusions:

1. Free-ranging tame deer and elk were observed for 24-hour periods
periodically throughout the summer in aspen and lodgepole pine types to
determine their habitat subunit preferences. Deer and elk use of aspen
and lodgepole pine subunits is significantly different from the availa-
bility of those subunits, and there are significant differences between
deer versus elk subunit preferences.

2. In the aspen type, both deer and elk preferred to graze the meadow
subunit. However, elk use of the meadow was approximately double the
deer use (65 versus 35 percent). Deer use of the aspen subunit was
double that of elk (45 versus 18 percent).

3. In the lodgepole pine type, deer most preferred to graze the clear-
cut, the wet meadow secondarily. Elk preferred grazing wet meadow, dry
meadow, and clearcut, in that order. Deer used forested subunits more
than elk; even so, grazing use of these subunits was minor.

4. Deer and elk both preferred resting in aspen and meadow subunits,
but deer perferred the aspen most, whereas, elk preferred the meadow
most. Elk preferred resting near where they fed; hence, they preferred

the meadow subunit most. Deer preferred specific bedding areas and used the same beds throughout the summer.

5. In the lodgepole pine type, deer preferred specific bedding areas and most often in the stagnated forest, whereas, elk bedded most in the wet meadow where they did most of their feeding.

6. The relative distributions of deer and elk pellet groups differed significantly from actual habitat subunit use by either animal. In both types, deer and elk defecated most frequently while they were most active (i. e. travelling between feeding areas, or feeding in subunits of lowest productivity). Consequently, the pellet-group count method underestimates the importance of the most valuable habitat, and over-estimates the value of less important habitat.

7. The species-dry-weight composition of deer and elk diets in the aspen type was determined and compared with the compositon of diets in the lodgepole pine type. The deer generally consumed little grass after the first two weeks of summer, whereas the elk used the grasses through-out the summer. Deer preferred browse more than elk. Both species consumed large quantities of forbs.

8. The deer were significantly more selective of forage than elk in all except the aspen clearcut subunit. The least overlap between deer and elk diets also occurred on the aspen clearcuts. Deer were substan-tially more selective than elk in the meadow subunits of both vegetation types.

9. The deer and elk preferred grazing those areas where their consump-tion rates were highest. Their grazing use of suboptimal subunits indicates that they explore their environment and, thereby, know of alternative feeding sites should the principal one become relatively

less available.

10. Elk diets were significantly more digestible (in vitro) by elk than by deer, and deer diets of low digestibility were also better digested by elk. This difference in digestive performance helps explain why elk are less food selective and consume greater quantities of grass than deer, and indicates that elk will out-compete deer when highly digestible forages are in short supply.

11. Percent crude protein values (N X 6.25) in aspen subunit diets were all above minimum requirements, and most were above optimal levels required by deer and elk. Consequently, crude protein was not a biologically significant factor in the evaluation of dietary quality difference between aspen subunits.

12. Clearcutting significantly increased production of forage species important to deer and elk in both the aspen and lodgepole pine types. Consumption rates were lower on adjacent uncut areas for both deer and elk grazing in the lodgepole pine type, and for elk grazing in the aspen type. However, clearcuts in the aspen type had less deer and elk grazing use than adjacent uncut areas; grazing use of clearcuts in the lodgepole pine type was significantly increased over that in the forest. Thus, under conditions of low stocking rate and limited inter- and intra-specific competition for forage, as in this study, clearcutting in the aspen type is of little or negligible value to big game. In contrast, because of the limited forage supply in the lodgepole pine type, overstory removal and resultant increased forage production is of great value to big game.

13. In both the aspen and lodgepole pine types, meadow bottoms were strongly preferred as foraging areas by deer and especially by elk.

This preference for meadows is of practical importance to the manager, because other uses of the meadow resource include livestock grazing, recreation, and vehicular travel, all of which reduce the acceptability of this habitat by big game.

LITERATURE REVIEW

Alldredge, A. W., J. F. Lipscomb, and F. W. Whicker. 1974. Forage intake rates of mule deer estimated with fallout cesium-137. J. Wildl. Manage. 38(3):508-516.

Allen, E. O. 1977. A new perspective for elk habitat management. W. Assoc. State Game and Fish Comm. 57:195-205.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227-265.

Anderson, A. E. 1969. 2,4-d, sagebrush, and mule deer-cattle use of upper winter range. Colo. Div. of Game, Fish and Parks, Spec. Rep. 21, 21 p.

Anderson, C. C. 1958. The elk of Jackson Hole: a review of Jackson Hole elk studies. Wyo. Game and Fish Comm., Bull. No. 10, 184 p.

Arnold, G. W. 1964. Factors within plant associations affecting the behaviour and performance of grazing animals, p. 133-154. In: D. J. Crisp (ed.). Grazing in terrestrial and marine environments. Blackwell Sci. Publ., London, 322 p.

Arnold, G. W. 1969. Regulation of food intake in grazing ruminants, p. 264-275. In: A. T. Phillipson (ed.). Physiology of digestion in the ruminant. Oriel Press, New Castle Upon Tyne, England, 636 p.

Arnold, G. W., and R. A. Maller. 1977. Effects of nutritional experience in early and adult life on the performance and dietary habits of sheep. Appl. Anim. Ethol. 3:5-26.

Beament, J. W. L. 1961. The role of physiology in adaptation and competition between animals. In: Mechanisms in Biological Competition--a Symposia of the Society for Experimental Biology. Cambridge Univ. Press. 365 p.

Bell, G. L. 1952. Geology of the Northern Farmington Mountains. Utah Geological Society, Guidebook to the Geology of Utah, No. 8:38-51.

Bell, R. H. V. 1969. The use of the herb layer by grazing ungulates in the Serengeti, p. 111-124. In: A. Watson (ed.). Animal populations in relation to their food resources. Blackwell Sci. Publ., Oxford,

Bitterman, M. F. 1975. The comparative analysis of learning. Science 188:699-709.

Black, R., R. J. Scherzinger, and J. W. Thomas. 1976. Relationships of Rocky Mountain elk and Rocky Mountain mule deer habitat to timber management in the Blue Mountains of Oregon and Washington, p. 11-31. In: Proceedings of the Elk-Logging-Roads Symposium. Univ. Idaho; Forest, Wildlife and Range Exp. Sta., 142 p.

Brown, E. R. 1961. The black-tailed deer of western Washington. Wash. State Game Dept. Biol. Bull. 13, 124 p.

Buechner, H. K. 1950. Life history, ecology, and range use of the pronghorn antelope in Trans-Pecos, Texas. Amer. Midland Natur. 43(2):257-354.

Buechner, H. K., and C. V. Swanson. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. Trans. N. Amer. Wildl. Conf. 20:560-567.

Cairns, A. L. 1976. Distribution and food habits of moose, wapiti, deer, bison and snowshoe hare in Elk Island National Park, Alberta. M. S. Thesis. University of Calgary. 169 p.

Cheatum, E. L., and C. W. Severinghaus. 1950. Variations in the fertility of white-tailed deer related to range condition. Trans. N. Amer. Wildl. Conf. 15:170-190.

Clary, W. P., and F. R. Larson. 1971. Elk and deer use are related to food resources in Arizona ponderosa pine. USDA For. Serv. Res. Note RM-202. 4 p.

Cliff, E. P. 1939. Relationships between elk and mule deer in the Blue Mountains of Oregon. Trans. N. Amer. Wildl. Conf. 4:560-569.

Collins, W. B. 1977. Diet composition and activities of elk on different habitat segments in the lodgepole pine type, Uinta Mountains, Utah. M. S. Thesis. Utah State University, Logan. 82 p.

Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments . J. Wildl. Manage. 42(4):799-810.

Collins, W. B., and P. J. Urness. 1979. Elk pellet group distributions and rates of deposition in aspen and lodgepole pine habitats, p. 140 144. In: Elk Ecology Symposium. University of Wyoming, Laramie.

Cordova, F. J., J. D. Wallace, and R. D. Pieper. 1978. Forage intake by grazing livestock: a review. J. Range Manage. 31(6):430-438.

Deschamp, J. A. 1977. Forage preferences of mule deer in the lodgepole pine ecosystem, Ashley National Forest, Utah. M. S. Thesis. Utah State University, Logan. 76 p.

Deschamp, J. A., P. J. Urness, and D. D. Austin. 1979. Summer diets of mule deer from lodgepole pine habitats. J. Wildl. Manage. 43(1): 154-161.

Dietz, D. R. 1965. Deer nutrition research in range management. Trans. N. Amer. Wildl. Conf. 30:274-285.

Edgerton, P. J., and B. R. McConnell. 1976. Diurnal temperature regimes of logged and unlogged mixed conifer stands on elk summer range. USDA For. Serv. Pac. N. W. For. and Range Exp. Sta. Res. Note PNW-277, 6 p.

Elton, C. 1936. Animal ecology. MacMillan Press, New York. 209 p.

Espmark, Y., and R. Langvatn. 1979. Lying down as a means of reducing fly harassment in red deer (Cervus elaphus). Behav. Ecol. Sociobiol. 5:51-54.

Free, J. C., R. J. Hansen, and P. L. Sims. 1970. Estimating dry-weights of foodplants in feces of herbivores. J. Range Manage. 23(4):300-303.

French, C. E., L. E. McEwen, N. D. Magruder, R. H. Ingram, and R. W. Swift. 1955. Nutritional requirements of white-tailed deer for growth and anteler developement. Penn. Agr. Exp. Sta. Bull. No. 600, 50 p.

Fulgham, K. O. 1978. Influence of spring sheep grazing on the forage intake and quality of diets consumed by pen-reared mule deer under winter-range conditions. Ph. D. Dissertation, Utah State University, Logan. 159 p.

Geist, V. 1978. Behavior, p. 283-296. In: J. L. Schmidt and D. L. Gilbert (eds.). Big Game of North America: Ecology and Management. Stackpole Books, Harrisburg, Pa. 494 p.

Gruell, G. E., and G. Roby. 1976. Elk habitat relationships before logging on Bridger-Teton National Forest, Wyoming, p. 110-121. In: Proceedings of the Elk-Logging-Roads Symposium. Univ. Idaho; Forest, Wildlife and Range Exp. Sta. 142 p.

Hahn, H. C., Jr. 1945. The white-tailed deer in the Edwards Plateau region of Texas. Texas Game, Fish and Oyster Comm., Austin. 52 p.

Hansen, R. M., R. C. Clark, and W. Lawhorn. 1977. Foods of wild horses, deer, and cattle in the Douglas Mountains area, Colorado. J. Range Manage. 30(2):116-118.

Harris, L. E. 1970. Nutrition research techniques for domestic and wild animals. An international system and procedure of analyzing samples. Vol. 1. L. E. Harris, Logan, Utah.

Hofmann, R. R. 1968. Comparisons of the rumen and omasum structure in East African game ruminants in relation to their feeding habits. J. Zool. 21:179-194.

Hofmann, R. R., and D. R. M. Stewart. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36(2):226-240.

Hooven, E. F. 1973. A brief for the clearcut logging of Douglas-fir. J. For. 71(4):210-214.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

Hungate, R. E. 1966. The rumen and its microbes. Academic Press, New York and London. 533 p.

Johnston, R. S., and R. D. Doty. 1972. Description and hydrologic analysis of two small watersheds in Utah's Wasatch Mountains. USDA For. Serv. Intermountain For. and Range Exp. Sta. INT-127. 53 p.

Julander, O., and D. E. Jeffery. 1964. Deer, elk and cattle range relations on summer range in Utah. N. Amer. Wildl. Conf. 29: 404-414.

Julander, O., R. B. Ferguson, and J. E. Dealy. 1963. Measure of animal range use by signs, p. 102-108. In: U. S. For. Serv., Range Research Methods. USDA Misc. Publ. 940. 172 p.

Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. J. Wildl. Manage. 25(1):54-60.

Kramer, A. 1972. A review of the ecological relationships between mule and white-tailed deer. Alberta Fish and Wildl. Div. Occ. Paper No. 3. 54 p.

Krebbs, J. R. 1978. Optimal foraging: decision rules for predators, p. 23-65. In: J. R. Krebbs and N. B. Davies (eds.). Behavioural Ecology: an Evolutionary Approach. Sinaur Assoc. Publ., Sunderland, Mass., 494 p.

Leckenby, D. A. 1968. Influence of plant communities on wintering mule deer. Proc. Western Assn. State Game and Fish Comm. 48:201-208.

Leege, T. A., J. R. Nellson, and J. W. Thomas. 1977. Food habits and diet quality of North American elk, p. 221-241. In: M. Rechcigl, Jr. (ed.). CRC Handbook Series in Nutrition and Food, Section G: Diets, Culture Media, Food Supplements, Vol. 1: Diets for Mammals. CRC Press, Cleveland, O.

Longhurst, W. M. 1954. The fecal pellet group deposition rate of domestic sheep. J. Wildl. Manage. 18(3):418-419.

Longhurst, W. M., H. K. Oh, M. B. Jones, and R. E. Kemper. 1968. A basis for the palatability of deer forage plants. Trans. N. Amer. Wildl. Conf. 33:181-192.

Lonner, T. N. 1976. Elk use-habitat type relationships on summer and fall range in Long Tom Creek, southwestern Montana, p. 101-109. In: Proceedings of the Elk-Logging-Roads Symposium. Univ. Idaho; Forest, Wildlife and Range Exp. Sta. 142 p.

Lovass, A. L. 1958. Mule deer food habits and range use, Little Belt Mountains, Montana. J. Wildl. Manage. 22(3):275-283.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. No. 20. 79 p.

Mackie, R. J. 1976. Interspecific competition between mule deer, other game animals and livestock, p. 49-54. In: Mule deer decline in the west--a symposium. Utah State Univ. College of Natural Resources and Utah Agric. Exp. Sta. Pub. 134 p.

Marcum, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Ph. D. Diss., Univ. of Mont., Missoula. 188 p.

McCleery, R. H. 1978. Optimal behaviour sequences and decision making, p. 377-410. In: J. R. Krebbs and N. B. Davies (eds.). Behavioural ecology: an evolutionary approach. Sinaur Assoc. Publ., Sunderland, Mass. 494 p.

McCulloch, C. Y. 1955. Utilization of winter browse on wilderness big game range. J. Wildl. Manage. 19(2):206-215.

McMahan, C. A. 1966. Suitability of grazing enclosures for deer and livestock research on the Kerr Wildlife Managment Area, Texas. J. Wildl. Manage. 30(1):151-162.

Moen, A. N. 1973. Wildlife ecology. W. H. Freeman and Co., San Francisco, California. 458 p.

Moore, J. E. 1970. Procedure for the two-stage in vitro digestion of forages. Univ. of Florida. Dept. of Animal Science. Unpubl.

Nagy, J. G. 1970. Biological relations of rumen flora and fauna, p. 159-163. In: Range and wildlife habitat evaluation--a research symposium. USDA For. Serv. Misc. Pub. 1147.

Neff, D. J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. J. Wildl. Manage. 32(3):597-614.

Neff, D. J. 1974. Forage preferences of trained mule deer on the Beaver Creek watersheds. Ariz. Game and Fish Dept. Spec. Rep. 4, 61 p.

Pallesen, J. D. 1979. Nutritive value of mule deer and elk diets and forages on lodgepole pine summer range in Utah. M. S. Thesis. Utah State University, Logan. 114 p.

Papegeorgiou, N. K. 1978. Food preferences, feed intake, and protein requirements of red deer in central Greece. J. Wildl. Manage. 42(4):940-943.

Partridge, L. 1978. Habitat selection, p. 351-376. In: J. R. Krebbs and N. B. Davies (eds.). Behavioural ecology: an evolutionary approach. Sinaur Assoc. Publ., Sunderland, Mass. 494 p.

Patton, D. R. 1974. Patch cutting increases deer and elk use of a pine forest in Arizona. J. For. 72(12):764-766.

Patton, D. R., and B. I. Judd. 1970. The role of wet meadows as wildlife habitat in the Southwest. J. Range Manage. 23(4):272-275.

Peek, J. M., and S. R. Hieb (eds.). 1976. Proceedings of the Elk-Logging-Roads Symposium. Univ. Idaho; Forest, Wildlife and Range Exp. Sta. 142 p.

Peery, C., and R. Overly. 1976. Impact of roads on big game distribution in portions of the Blue Mountains of Washington, p. 62-68. In: Proceedings of the Elk-Logging-Roads Symposium. Univ. Idaho; Forest, Wildlife and Range Exp. Sta. 142 p.

Pengelly, W. L. 1972. Clearcutting: detrimental aspects for wildlife resources. J. Soil and Water Cons. 27(6):255-258.

Pfister, R. D. 1972. Vegetation and soils in the subalpine forests of Utah. Ph. D. Dissertation. Washington State University, Pullman. 98 p.

Plummer, A. P., D. R. Christensen, and S. B. Monsen. 1966. Highlights, results and accomplishments of game range restoration studies. Pub. 67-4, Utah State Dep. Fish and Game. 45 p.

Prins, R. A., and M. J. H. Geelen. 1971. Rumen characteristics of red deer, fallow deer, and roe deer. J. Wildl. Manage. 35(4): 673-680.

Regelin, W. L., O. C. Wallmo, J. Nagy, and D. R. Dietz. 1974. Effect of logging on forage values for deer in Colorado. J. For. 72(5): 282-285.

Regelin, W. L., R. M. Bartman, D. W. Reichert, and P. H. Neil. 1976. The influence of supplemental feed on food habits of tamed deer. USDA For. Serv. Rec. Note RM-316. 4 p.

Rice, R. W. 1970. Stomach content analyses: a comparison of the rumen versus esophageal techniques, p. 127-132. In: Range and wildlife habitat evaluation--a research symposium. USDA For. Serv. Misc. Publ. 1147. 220 p.

Rickard, W. H., J. D. Hedlund, and R. E. Fitzner. 1977. Elk in the shrub-steppe region of Washington: an authentic record. Sci. 196:1009-1010.

Riney, T. 1957. The use of faeces in studies of several free-ranging mammals in New Zealand. New Zealand J. Sci. Technol. B 38 (6): 507-532.

Rogers, G., O. Julander, and W. L. Robinette. 1958. Pellet-group counts for deer census and range-use index. J. Wildl. Manage. 22(2):193-199.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. J. Wildl. Manage. 43(3):634-641.

Royama, T. 1970. Factors governing hunting behaviour and selection of food by the great tit (Parus major L.). J. Anim. Ecol. 39: 619-668.

Schoonveld, G. G., J. G. Nagy, and J. A. Bailey. 1974. Capability of mule deer to utilize fibrous alfalfa diets. J. Wildl. Manage. 38(4):823-829.

Short, H. L., D. E. Medin, and A. E. Anderson. 1965. Ruminoreticular characteristics of mule deer. J. Mammal. 46(2):196-199.

Slater, J., and R. J. Jones. 1971. Estimation of the diets selected by grazing animals from microscopic analysis of the faeces--a warning. J. Australian Inst. Agr. Sci. 37:238-239.

Siegel, S. 1956. Non-parametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

Smith, J. G., and O. Julander. 1953. Deer and sheep competition in Utah. J. Wildl. Manage. 17(2):101-112.

Smith, J. N. M., and H. P. Sweatman. 1974. Food searching behavior of titmice in patchy environments. Ecology 55:1216-1232.

Snedecor, G. W., and W. G. Cochran. 1972. Statistical methods. Iowa State University Press. Ames. 593 p.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman Press, San Francisco. 776 p.

Stoddart, L. A., A. D. Smith, and T. W. Box. 1975. Range management. McGraw-Hill Book Co., New York. 532 p.

Sutherland, N. S., and N. J. Mackintosh. 1971. Mechanisms of animal discrimination learning. Academic Press, New York. 559 p.

Taber, R. D. 1953. Studies of black-tailed deer reproduction on three chaparral cover types. Calif. Fish and Game 39(2):177-186.

Teskey, H. J. 1969. Larvae and pupae of some eastern North American Tabanidae (Diptera). Momoirs Ent. Soc. Canad. 63:147 p.

Thompson, P. H. 1969. Collecting methods for Tabanidae (Diptera). Ann. Entomol. Soc. Amer. 62:50-57.

Tilley, J. M. A., and R. A. Terry. 1963. A two-staged technique for the in vitro digestion of forage crops. J. of British Grassland Soc. 18(2):104-111.

Van Soest, P. J. 1964. Symposium on factors influencing the voluntary intake of herbage by ruminants: voluntary intake in relation to chemical composition and digestibility. J. Anim. Sci. 24:834-843.

Wagner, F. H. 1978. Livestock grazing and the livestock industry, p. 121-145. In: H. P. Brokaw (ed.). Wildlife and America. U. S. Government Printing Office, Washington, D. C. 532 p.

Wallmo, O. C., and D. J. Neff. 1970. Direct observations of tamed deer to measure their consumption of natural forage, p. 105-110. In: Range and wildlife habitat evaluation--a research symposium. USDA For. Serv. Misc. Pub. 1147. 220 p.

Wallmo, O. C., D. F. Reed, and L. H. Carpenter. 1976. Alteration of mule deer habitat by wildfire, logging, highways, agriculture, and housing developments, p. 37-47. In: Mule deer decline in the West--a symposium. Utah State Univ. College of Natural Resources and Utah Agric. Exp. Sta. Pub. 134 p.

Wallmo, O. C., R. B. Gill, L. H. Carpenter, and D. W. Reichert. 1973. Accuracy of field estimates of deer food habits. J. Wildl. Manage. 37(4):556-562.

Ward, A. L. 1979. Dispersed recreation impact on the big game resource. In: Dispersed recreation and natural resource management--a symposium. College of Natural Resources, Utah State University, Logan. (in press).

White, K. L. 1960. Differential range use by mule deer in the spruce-fir zone. Northwest Sci. 34(4):118-126.

Whittaker, R. H. 1975. Communities and ecosystems. MacMillan Pub. Co., New York. 385 p.

Wilm, H. G., D. F. Costello, and G. E. Klipple. 1944. Estimating forage yield by the double-sampling method. J. Am. Soc. Agron. 36:194-203.

Wilson, L., M. E. Olsen, T. B. Hutchings, A. R. Southard, and A. J. Erickson. 1975. Soils of Utah. Utah Ag. Exp. Sta. Bull. 492, 94 p.

Wolfe, M. L.   1978.   Habitat changes and management, p. 349-368.   In:
      J. L. Schmidt and D. L. Gilbert (eds.).   Big game of North
      America--ecology and management.   Stackpole Books.   494 p.

APPENDIX

Table 24. Diet composition by dry weight of deer grazing aspen meadow.

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Forbs					
Achillea lanulosa	0.0	0.0	0.1	0.0	+ [a]
Aconitum columbianum	0.3	+	1.4	2.2	0.9
Agastache urticifolia	0.0	0.1	0.0	0.5	0.1
Agoseris glauca	0.0	0.7	0.0	0.0	0.2
Arabis holboellii	0.1	0.0	0.0	0.0	+
Aster chilensis	0.0	0.1	0.8	0.0	0.3
Aster engelmannii	0.0	0.1	0.0	0.0	+
Aster foliaceous	2.2	8.6	7.1	7.2	6.8
Aster integrifolius	0.1	+	0.2	0.0	0.1
Camassia quamash	0.3	0.0	0.0	0.0	0.1
Castillegia spp.	0.0	0.0	1.6	0.0	0.5
Chenopodium fremontii	0.0	0.3	0.5	0.0	0.3
Collomia linearis	2.9	1.6	0.0	0.0	0.3
Delphinium nelsoni	0.2	0.0	0.0	0.0	+
Descurania spp.	0.3	0.1	0.1	0.0	0.1
Epilobium brevistylum	0.0	0.0	27.9	37.2	15.5
Erigeron perigrinus	0.4	0.2	0.0	0.0	0.1
Erythronium grandiflorum	0.2	0.0	0.0	0.0	+
Fragaria americana	0.0	0.1	0.0	0.0	+
Gayophytum nuttallii	2.0	13.2	9.0	1.0	7.9
Geranium fremontii	1.0	1.1	2.0	3.2	1.7

Table 24. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Habenaria dilatata	0.0	+	0.0	0.0	+
Hackelia floribunda	+	0.0	0.0	0.0	+
Heraculum lanatum	0.0	0.0	0.3	0.0	0.1
Lactuca scariola	1.3	0.1	0.1	0.9	0.4
Lathyrus lanszwertiii	2.6	5.4	0.0	0.0	1.3
Lepidium virginicum	0.0	0.0	0.0	1.0	+
Madia glomerata	0.0	4.7	1.4	6.1	3.1
Melilotus officinalis	2.9	0.9	1.5	0.1	1.3
Mertensia arizonica	0.1	+	0.0	0.0	+
Mimulus parryi	0.0	0.4	9.2	4.4	3.9
Osmorhiza occidentalis	0.0	+	0.0	0.0	+
Polygonum bistortoides	44.1	23.9	2.0	0.0	16.0
Polygonum douglasi	0.0	+	0.8	0.0	0.3
Potentilla gracillis	0.0	6.3	1.0	0.0	2.4
Rumex crispus	0.5	0.0	0.7	1.3	0.5
Sidalcea neomexicana	0.0	5.1	0.0	0.1	1.7
Stellaria jamesiana	0.0	0.1	0.0	0.0	+
Taraxacum officinale	2.0	0.9	1.9	17.7	4.2
Thalictrum fendleri	0.0	0.0	+	0.0	+
Tragopogon dubius	0.4	1.3	7.8	0.0	3.1
Trifolium sp	0.0	1.5	0.1	1.7	0.8
Valeriana occidentalis	0.0	+	0.7	0.0	0.2
Vicia americana	0.1	4.2	4.2	5.2	3.7

Table 24. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Viguiera multiflora	0.0	0.1	0.0	0.0	+
Viola spp.	28.5	7.7	0.1	0.0	7.4
Wyethia amplexicaulis	3.7	7.5	2.9	0.0	4.1
Grasses and Sedges					
Agropyron subsecundum	0.0	0.0	0.3	0.0	0.1
Bromus carinatus	0.0	1.6	+	0.0	0.5
Carex canescens	0.1	0.0	0.0	0.0	+
Phleum alpinum	1.1	0.0	0.0	0.0	0.2
Scirpus microcarpus	+	0.0	0.0	0.0	+
Browse					
Alnus tenuifolia	0.8	0.0	3.6	6.4	2.4
Amelanchier alnifolia	0.0	0.2	0.0	0.0	0.1
Populus tremuloides	1.9	1.2	2.9	1.8	2.0
Rosa woodsiii	0.0	0.0	0.1	0.0	+
Salix spp	1.1	2.1	0.5	0.0	1.1
Sambucus racemosa	0.0	0.0	3.3	0.0	1.1
Symphoricarpos oreophilus	0.0	0.7	1.5	1.6	0.7
Mushroom [b]	0.0	0.0	1.9	0.0	0.6

[a] + = trace item, less than 0.05% of diet.

[b] Mushrooms not identified.

Table 25. Diet composition by dry weight of deer grazing aspen forest.

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Forbs					
Achillea lanulosa	$+^a$	0.0	+	0.0	+
Aconitum columbianum	0.2	0.9	0.0	0.0	0.3
Agastache urticifolia	0.3	1.5	3.4	5.2	2.6
Aquilegia caerulea	3.0	1.3	0.0	0.0	0.9
Aster chilensis	0.0	0.5	0.0	0.0	0.2
Aster engelmanii	0.7	7.1	1.2	2.3	3.3
Aster foliaceous	4.8	19.6	15.1	1.5	12.6
Castillegia spp.	0.9	+	0.0	0.0	0.2
Chenopodium fremontii	0.0	0.0	0.1	0.0	+
Chlorocrambe hastatus	0.4	0.4	0.0	0.7	0.3
Claytonia lanceolata	0.1	0.0	0.0	0.0	+
Collinsia parviflora	0.1	0.0	0.0	0.0	+
Collomia linearis	0.7	0.1	0.1	0.0	0.2
Delphinium nelsoni	1.3	0.1	0.0	0.0	0.3
Descurania spp.	1.2	0.4	0.1	0.0	0.4
Erigeron perigrinus	1.8	0.1	0.0	0.0	0.3
Erysimum inconspicuum	0.1	0.0	0.0	0.0	+
Erythronium grandiflorum	3.4	0.0	0.0	0.0	0.6
Gayophytum nuttallii	0.3	1.7	1.5	+	1.1
Geranium richardsonii	1.1	0.9	0.6	0.7	0.8
Hackelia floribunda	0.6	+	0.0	0.0	0.1
Heraculum lanatum	0.0	0.0	0.7	2.5	0.7

Table 25. Continued

Plant Species	June	July	August	September	X̄
		Percent			
Hieracium scouleri	0.3	0.1	0.1	0.0	0.1
Hydrophylum capatatum	1.8	0.0	0.0	0.0	0.3
Lactuca scariola	0.0	0.1	0.0	0.0	+
Lathyrus lanzwertii	27.2	10.3	1.6	5.8	9.5
Mertensia arizonica	1.2	0.0	+	0.0	0.2
Nemophyla breviflora	0.2	0.0	0.0	0.0	+
Osmorhiza chilensis	0.0	0.1	0.0	0.0	+
Osmorhiza occidentalis	1.0	0.1	0.1	+	0.1
Polenonium foliosissimum	0.9	0.0	0.0	0.1	0.2
Polygonum bistortoides	0.2	0.0	0.0	0.0	+
Polygonum douglasi	0.0	0.0	0.3	0.1	0.1
Ranunculus spp.	0.4	0.0	0.0	0.0	0.1
Rudbeckia occidentalis	0.6	0.0	0.0	0.0	0.1
Rumex crispus	0.0	0.1	0.0	0.0	+
Senecio serra	0.2	0.0	0.0	0.0	+
Sidalcea neomexicana	0.0	0.1	+	0.2	0.1
Taraxacum officinale	0.9	0.6	0.3	0.1	0.5
Thalictrum fendleri	0.0	0.6	2.3	1.4	1.2
Tragopogon dubius	0.0	0.2	+	0.0	0.1
Valeriana occidentalis	4.7	14.4	23.2	6.3	14.4
Vicia americana	6.6	19.2	5.9	1.6	9.7
Viola spp.	0.3	1.3	0.0	0.0	0.5
Wyethia amplexicaulis	7.7	0.0	0.0	0.0	1.3

Table 25. Continued

Plant Species	June	July	August	September	X̄
			Percent		
Grasses					
Agropyron subsecundum	0.8	+	0.2	+	0.2
Bromus carinatus	1.4	0.0	0.0	0.0	0.2
Browse					
Acer grandidentatum	0.1	0.0	0.0	0.0	+
Alnus tenuifolia	0.0	0.1	0.0	0.4	0.1
Amelanchier alnifolia	0.0	3.9	3.0	4.0	3.0
Populus tremuloides	16.9	1.6	4.8	6.5	6.0
Prunus virginiana	1.2	0.1	0.0	0.0	0.3
Quercus gambelii	0.5	0.0	0.0	0.0	0.1
Ribes	1.7	0.0	0.0	1.9	0.6
Rosa woodsii	0.8	1.9	0.4	0.0	0.9
Symphoricarpos oreophilus	0.7	10.1	32.8	58.0	24.1
Mushrooms[b]	0.2	0.5	1.3	0.7	0.8

[a] + = trace item, less than 0.05% of diet.

[b] Mushrooms not identified.

Table 26. Diet composition by dry weight of deer grazing mountain brush.

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Forbs					
Achillea lanulosa	+[a]	+	0.0	0.0	+
Agastache urticifolia	0.5	2.0	0.0	0.0	0.2
Allium acuminatum	0.1	0.0	0.0	0.0	+
Aquilegia caerulea	0.6	0.0	0.0	0.0	0.1
Arabis holboellii	+	0.0	0.0	0.0	+
Aster chilensis	0.0	+	1.1	0.0	0.4
Aster engelmanii	0.0	0.1	0.0	0.0	+
Aster foliaceous	1.0	4.0	4.1	0.0	2.9
Aster integrifolius	0.1	0.1	0.0	0.0	0.1
Collomia linearis	2.9	0.2	0.0	0.0	0.6
Delphinium nelsoni	+	0.0	0.0	0.0	+
Descurania spp.	0.3	0.1	0.0	0.0	0.1
Erigeron perigrinus	10.0	1.7	0.0	0.0	2.2
Erythronium grandiflorum	0.3	0.0	0.0	0.0	0.1
Gayophytum nuttallii	0.7	13.0	6.1	0.4	6.6
Geranium fremontii	8.6	1.2	3.6	0.0	3.0
Hackelia floribunda	+	0.0	0.0	0.0	+
Hieracium scouleri	1.1	0.9	0.7	0.4	0.8
Lactuca scariola	0.0	0.4	0.0	0.0	0.1
Lathyrus lanzwertii	15.2	13.3	1.5	0.0	7.5
Lepidium virginicum	0.0	0.1	0.0	0.0	+
Madia glomerata	0.3	1.3	0.6	0.0	0.7
Mertensia arizonica	+	0.0	0.0	0.0	+

Table 26. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Penstemon	+	0.0	0.0	0.0	+
Phacelia heterophylla	0.3	0.0	0.0	0.0	0.1
Polygonum douglasi	0.0	0.0	0.2	0.0	0.1
Sidalcea neomexicana	0.2	1.3	0.0	0.0	0.5
Tragopogon dubius	0.0	5.8	1.1	0.0	2.3
Valeriana occidentalis	0.2	0.0	0.0	0.0	+
Vicia americana	3.5	6.0	2.6	0.0	3.5
Viola spp.	13.8	4.0	4.0	0.0	5.0
Wyethia amplexicaulis	5.4	1.2	1.3	0.0	1.7
Grasses					
Agropyron subsecundum	0.9	+	0.0	0.0	0.2
Bromus carinatus	0.6	+	0.0	0.0	0.1
Browse					
Amelanchier alnifolia	0.0	15.7	0.0	0.0	5.2
Populus tremuloides	5.6	0.1	0.8	0.0	1.2
Prunus virginiana	0.4	0.0	0.4	0.0	0.2
Quercus gambelii	0.4	+	+	0.0	0.1
Rosa woodsii	24.8	3.1	0.1	0.0	5.2
Symphoricarpos oreophilus	1.8	24.2	73.5	98.8	49.3
Mushrooms[b]	0.0	0.0	0.0	0.4	0.1

[a]+ = trace item, less than 0.05% of diet.
[b]Mushrooms not identified.

Table 27. Diet composition by dry weight of deer grazing clearcut aspen.

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Forbs					
Acconitum columbianum	0.1	0.3	0.3	0.0	0.2
Agastache urticifolia	0.6	1.5	6.4	11.9	6.7
Aquilegia caerulea	0.4	4.5	4.7	6.8	4.3
Aster engelmanii	0.9	3.3	0.0	0.0	1.3
Aster foliaceous	7.6	0.2	0.2	0.0	1.4
Castillegia spp.	0.5	0.0	0.0	0.0	0.1
Chenopodium fremontii	0.0	0.0	2.5	3.9	1.5
Chlorocrambe hastatus	0.0	4.5	2.8	0.0	2.4
Collomia linearis	0.0	0.3	0.0	0.8	0.2
Delphinium nelsoni	9.8	0.0	0.0	0.0	1.6
Descurania spp.	0.3	0.7	0.4	0.0	0.4
Erigeron perigrinus	3.5	2.5	0.0	0.0	1.4
Erysimum inconspicuum	0.7	0.0	0.0	0.0	0.1
Erythronium grandiflorum	2.1	0.0	0.0	0.0	0.3
Geranium nelsoni	2.7	0.7	0.1	0.0	0.7
Heraculum lanatum	0.0	0.0	10.1	27.4	7.9
Hydrophyllum capitatum	0.4	0.0	0.0	0.0	0.1
Lactuca scariola	0.0	0.0	+	2.2	0.4
Lathyrus lanzwertii	27.8	1.6	2.2	1.7	6.2
Lomatium spp.	0.1	0.0	0.0	0.0	+
Madia glomerata	2.1	0.0	0.0	0.0	0.4
Osmorhiza occidentalis	0.6	0.9	0.0	0.0	0.4
Phacelia heterophylla	0.3	0.0	0.0	0.0	0.1

Table 27. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Polemonium foliosissimum	0.0	4.2	0.0	0.0	1.4
Polygonum douglasi	0.0	0.0	2.4	3.6	1.4
Taraxacum officinale	0.8	1.7	0.0	0.0	0.7
Valeriana occidentalis	6.8	8.6	10.8	21.5	11.2
Vicia americana	3.1	10.9	2.4	0.0	5.0
Viola spp.	0.0	3.4	0.0	0.0	1.1
Wyethia amplexicaulis	3.9	0.0	0.0	0.0	0.7
Browse					
Populus tremuloides	11.8	6.5	6.0	3.0	6.6
Rosa woodsii	5.2	4.3	1.3	0.0	2.7
Salix spp.	6.6	1.2	2.2	0.0	2.2
Symphoricarpos oreophilus	1.4	38.1	45.2	17.3	30.9

[a] + = trace item, less than 0.05% of diet.

Table 28. Diet composition by dry weight of elk grazing aspen meadow.

Plant Species	June	July	August	September	$\overline{X}$
	———————— Percent ————————				
Forbs					
Achillea lanulosa	+[a]	0.0	+	+	+
Aconitum columbianum	0.0	0.0	0.1	0.0	+
Allium acuminatum	+	0.0	0.0	0.0	+
Aster chilensis	0.0	0.0	0.2	0.2	0.1
Aster engelmannii	0.0	0.0	+	0.0	+
Aster foliaceous	15.9	26.7	14.3	13.9	18.6
Aster integrifolius	0.0	0.2	0.7	0.0	0.3
Camassia quamish	+	0.0	0.0	0.0	+
Castillegia spp.	0.0	0.0	0.0	+	+
Chenopodium fremontii	+	0.0	0.9	0.0	0.3
Collomia linearis	0.0	+	+	0.0	+
Delphinium nelsoni	0.0	+	0.0	0.0	+
Epilobium brevistylum	0.0	0.0	2.0	1.3	0.9
Erigeron perigrinus	0.2	0.2	+	0.0	0.1
Erysimum inconspicuum	+	0.0	0.0	0.0	+
Erythronium grandiflorum	+	0.0	0.0	0.0	+
Gayophytum nuttallii	+	0.1	0.5	0.3	0.3
Geranium fremontii	0.5	0.6	0.7	0.0	0.5
Hackelia floribunda	0.1	0.0	0.0	0.0	+
Heraculum lanatum	0.0	2.8	18.8	12.9	9.4
Hieracium scouleri	0.1	0.0	0.0	0.0	+
Hydrophyllum capitatum	+	0.0	0.0	0.0	+
Lactuca scariola	0.0	0.9	1.1	0.0	0.7

Table 28. Continued

Plant Species	June	July	August	September	X̄
	————————— Percent —————————				
Lepidium virginicum	0.0	0.0	0.0	+	+
Madia glomerata	0.2	0.4	0.3	0.5	0.4
Mertensia arizonica	2.8	0.0	0.1	0.0	0.5
Mimulus parryi	0.0	0.0	0.8	+	0.3
Polygonum bistortoides	40.0	40.7	5.7	0.0	21.2
Polygonum douglasi	0.0	0.0	0.3	0.6	0.2
Potentilla gracillis	0.2	3.0	0.4	+	1.2
Ranunculus spp.	0.0	+	0.0	+	+
Rudbeckia occidentalis	0.0	+	+	0.0	+
Rumex crispus	0.0	+	0.1	0.0	+
Senecio integrimus	0.0	+	0.0	0.0	+
Sidalcea neomexicana	0.0	0.3	+	0.2	0.1
Taraxacum officinale	0.1	2.8	0.6	0.0	1.2
Thalictrum fendleri	0.0	0.5	2.7	6.6	2.2
Tragopogon dubius	0.0	0.5	0.1	0.0	0.2
Trifolium spp.	0.0	0.3	+	0.0	0.1
Vicia americana	0.0	0.3	0.8	1.1	0.6
Viguiera multiflora	0.0	0.1	+	0.0	+
Viola spp.	1.9	2.0	+	1.1	1.2
Wyethia amplexicaulis	0.3	+	0.0	0.0	0.1
Grasses and Sedges					
Agropyron subsecundum	30.5	1.3	14.0	2.4	10.6
Agrostis exarata	0.0	0.0	2.8	+	0.9
Agrostis stolonifera	0.0	0.1	0.2	14.4	2.5

103

Table 28. Continued

Plant Species	June	July	August	September	X̄
			Percent		
Bromus carinatus	4.6	7.0	16.7	24.6	12.8
Carex canescens	0.5	1.1	3.0	0.0	1.5
Juncus ensifolius	0.0	2.5	0.5	1.2	1.2
Juncus confusus	0.0	+	0.3	0.0	0.1
Phleum alpinum	0.0	3.6	3.3	7.5	3.6
Scirpus microcarpus	0.0	+	0.5	0.0	0.2
Browse					
Alnus tenuifolia	0.0	0.2	1.0	2.7	0.7
Lonicera involucrata	0.0	+	+	0.0	+
Populus tremuloides	0.2	0.4	0.1	0.1	0.2
Prunus virginiana	0.2	0.0	0.0	0.0	+
Salix spp.	0.0	0.7	0.7	0.4	0.5
Symphoricarpos oreophilus	+	0.1	2.4	2.5	1.3
Mushrooms[b]	0.0	0.1	0.3	0.0	0.1
Equisetum arvense	+	+	+	0.0	+

[a] + = trace item, less than 0.05% of diet.
[b] Mushrooms not identified.

Table 29. Diet composition by dry weight of elk grazing aspen forest.

Plant Species	June	July	August	September	$\overline{X}$
	————————— Percent —————————				
Forbs					
Aconitum columbianum	0.1	1.1	0.0	0.0	0.4
Agastache urticifolia	+[a]	0.0	0.0	0.0	+
Agoseris glauca	0.0	0.0	0.1	+	+
Aster foliaceous	5.8	32.5	6.4	8.6	15.4
Aster engelmannii	2.2	3.8	5.8	0.1	5.0
Aster integrifolius	0.0	0.0	0.4	0.0	0.1
Chenopodium fremontii	0.0	+	0.0	0.0	+
Collomia linearis	+	0.1	0.0	0.0	+
Delphinium nelsoni	+	0.0	0.0	0.0	+
Descurania spp.	+	0.0	0.0	0.2	+
Erigeron perigrinus	9.3	1.6	0.9	0.0	2.4
Erythronium grandiflorum	+	0.0	0.0	0.0	+
Gayophytum nuttallii	0.0	1.1	0.1	0.0	0.4
Geranium richardsonii	1.1	3.7	0.9	0.0	1.7
Habenaria dilatata	0.0	+	+	0.0	+
Hackelia floribunda	2.5	0.1	0.7	0.0	0.7
Heraculum lanatum	0.0	16.8	1.2	0.0	6.0
Hydrophyllum capitatum	+	0.0	0.0	0.0	+
Lactuca scariola	0.0	1.4	0.0	0.2	0.5
Lathyrus lanzwertii	0.1	2.6	5.0	13.9	4.9
Lepidium virginicum	0.0	0.1	0.0	0.0	+
Madia glomerata	0.0	0.3	0.0	0.0	0.1
Mertensia arizonica	12.7	0.0	3.9	0.0	3.4

Table 29. Continued

Plant Species	June	July	August	September	X̄
			Percent		
Osmorhiza chilensis	0.0	0.1	0.0	0.0	+
Osmorhiza occidentalis	3.5	1.2	1.4	0.0	1.1
Phacelia heterophylla	3.5	1.2	1.4	0.0	1.5
Polemonium foliosissimum	0.0	+	0.0	0.0	+
Polygonum bistortoides	0.0	0.0	0.0	0.4	0.1
Polygonum douglasi	0.0	0.1	+	0.1	0.1
Rudbeckia occidentalis	+	0.0	0.0	0.0	+
Senecio serra	+	0.0	0.0	0.0	+
Sidalcea neomexicana	0.0	0.2	0.0	0.0	0.1
Stellaria jamesiana	0.1	0.0	0.0	0.0	+
Taraxacum officinale	0.6	2.3	0.1	0.0	0.9
Thalictrum fendleri	+	.5.0	10.2	7.1	6.3
Tragopogon dubius	0.0	0.1	0.1	0.0	0.1
Valeriana occidentalis	+	0.2	2.0	1.4	1.0
Vicia americana	0.0	4.3	7.5	0.3	4.0
Viguiera multiflora	0.0	+	0.0	0.0	+
Viola spp.	0.5	3.7	0.0	0.0	1.3
Grasses and Sedges					
Agropyron subsecundum	34.2	6.8	3.5	30.8	14.3
Bromus carinatus	16.6	4.1	0.8	5.2	5.3
Poa reflexa	0.4	0.0	0.0	0.0	0.1
Poa spp.	0.2	0.0	0.0	0.0	+
Browse					
Populus tremuloides	9.6	2.4	4.0	0.9	3.9

Table 29. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Symphoricarpos oreophilus	0.4	1.7	44.5	29.6	20.4
Mushrooms[b]	+	2.6	0.6	0.0	1.1

[a] + = trace item, less than 0.05% of diet.

[b] Mushrooms not identified.

Table 30. Diet composition by dry weight of elk grazing clearcut aspen.

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Forbs					
Aconitum columbianum	0.0	1.5	+[a]	0.1	0.5
Agastache urticifolia	0.0	+	0.0	0.0	+
Aquilegia caerulea	0.0	0.1	0.0	0.0	+
Aster chilensis	0.0	0.0	0.0	0.1	+
Aster engelmannii	0.0	13.8	1.9	0.0	5.2
Aster foliaceous	12.6	29.6	+	10.9	13.8
Chenopodium fremontii	0.0	2.5	3.3	0.3	2.0
Collomia linearis	0.0	0.1	0.0	0.0	+
Erigeron perigrinus	0.0	2.7	0.0	0.0	0.9
Fragaria americana	0.1	0.0	0.0	0.0	+
Gayophytum nuttallii	0.0	+	+	0.0	+
Geranium richardsonii	0.0	2.5	0.0	0.0	0.8
Hackelia floribunda	0.0	0.2	0.0	0.2	0.1
Heraculum lanatum	0.0	8.0	19.1	5.0	9.9
Lactuca scariola	0.0	0.6	0.7	4.2	1.1
Lathyrus lanzwertii	0.0	2.2	0.5	1.3	1.1
Madia glomerata	0.0	0.7	0.0	0.0	0.2
Mertensia arizonica	31.8	0.0	0.0	0.4	5.4
Osmorhiza occidentalis	+	0.4	0.0	0.0	0.1
Polemonium foliosissimum	0.0	0.0	0.0	0.1	+.
Polygonum douglasi	0.0	0.5	0.1	0.8	0.3
Taraxacum officinale	11.8	3.1	0.0	0.0	3.0
Thalictrum fendleri	0.0	1.3	8.4	1.7	3.5

Table 30. Continued

Plant Species	June	July	August	September	X̄
			Percent		
Tragopogon dubius	0.0	1.9	0.0	0.0	0.6
Valeriana occidentalis	0.0	1.5	6.9	0.1	2.8
Vicia americana	0.0	0.4	1.2	0.2	0.6
Viguiera multiflora	0.5	0.0	0.0	0.0	0.1
Viola spp.	6.3	0.2	0.0	0.0	1.1
Grasses and Sedges					
Agropyron subsecundum	19.1	15.9	4.9	12.5	12.2
Agrostis exarata	0.0	0.0	+	5.6	0.9
Bromus carinatus	10.1	4.0	50.6	56.2	29.3
Carex canescen	0.0	1.4	0.0	0.0	0.5
Browse					
Populus tremuloides	1.0	0.3	1.0	0.5	0.7
Prunus virginiana	0.0	0.2	0.0	0.0	0.1
Ribes	0.0	+	0.0	0.0	+
Rosa woodsii	0.0	0.4	0.0	0.0	0.1
Salix spp.	6.7	3.4	0.0	0.0	2.3
Symphoricarpos oreophilus	0.0	0.2	1.3	0.0	0.5
Mushrooms[b]	0.0	0.2	0.0	0.0	+

[a]+ = trace item, less than 0.05% of diet.
[b]Mushrooms not identified.

Table 31. Diet composition by dry weight of elk grazing mountain brush.

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Forbs					
Agastache urticifolia	0.0	0.1	0.0	0.0	+ [a]
Agoseris glauca	0.0	0.0	0.0	0.1	+
Allium acuminatum	+	0.0	0.0	0.0	+
Aster chilensis	0.0	0.0	1.1	0.1	0.4
Aster engelmannii	0.0	3.8	0.5	0.0	1.4
Aster foliaceous	1.7	14.2	1.4	1.1	5.7
Aster integrifolius	0.0	1.5	1.9	0.4	1.2
Erigeron perigrinus	0.7	10.5	0.7	0.0	3.9
Gayophytum nuttallii	0.0	0.6	0.9	0.2	0.5
Geranium fremontii	3.8	15.1	4.2	0.0	7.1
Hieracium scouleri	+	+	0.4	0.0	0.1
Lactuca scariola	0.0	1.8	1.1	0.1	1.0
Lathyrus lanzwertii	0.0	0.1	1.2	0.2	0.5
Lepidium virginicum	0.0	0.1	+	0.0	+
Madia glomerata	0.0	0.0	1.3	0.5	0.5
Mertensia arizonica	+	3.0	1.9	0.0	1.6
Polygonum douglasi	0.0	+	0.3	0.0	0.1
Senecio integrimus	+	0.0	0.0	0.0	+
Sidalcea neomexicana	0.0	1.0	0.1	+	0.4
Stellaria jamesiana	+	0.0	0.0	0.0	+
Taraxacum officinale	0.3	3.6	0.0	0.0	1.3
Tragopogon dubius	0.0	0.0	0.2	0.0	0.1
Vicia americana	+	6.2	+	0.0	2.1

Table 31. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Viguiera multiflora	0.0	0.0	0.2	0.0	0.1
Viola spp.	6.0	16.1	0.1	0.1	6.4
Wyethia amplexicaulis	0.0	0.5	+	0.3	0.2
Grasses and Sedges					
Agropyron subsecundum	82.5	11.7	6.9	4.6	20.7
Bromus carinatus	2.3	2.7	2.8	14.8	4.7
Carex spp.	0.0	+	0.0	0.0	+
Browse					
Populus tremuloides	2.6	2.2	0.2	0.0	1.2
Quercus gambelii	0.0	1.1	+	0.0	0.4
Rosa woodsii	0.0	+	0.0	0.0	+
Symphoricarpos oreophilus	0.0	3.2	71.5	76.5	37.7
Mushrooms[b]	0.0	0.1	0.3	0.0	0.1

[a]+ = trace item, less than 0.05% of diet.
[b]Mushrooms not identified.

Table 32. Diet composition by dry weight of elk grazing logging road.

Plant Species	June	July	August	September	X̄
			Percent		
Forbs					
Agoseris glauca	0.0	0.2	0.3	0.0	0.2
Arabis holboellii	+[a]	0.0	0.0	0.0	+
Aster foliaceous	10.1	9.3	24.9	1.8	13.4
Collomia linearis	0.0	0.1	0.0	0.0	+
Delphinium nelsoni	0.0	+	0.0	0.0	+
Descurania spp.	0.0	0.1	0.0	0.0	+
Erigeron perigrinus	0.1	3.2	0.8	0.0	1.4
Gayophytum nuttallii	0.0	0.0	1.2	0.0	0.2
Geranium richardsonii	1.5	2.7	1.3	0.0	1.6
Hackelia floribunda	+	0.2	0.1·	0.0	0.1
Heraculum lanatum	0.0	0.0	0.2	1.4	0.3
Lactuca scariola	0.0	0.0	4.6	1.8	1.8
Lathyrus lanzwertii	0.0	0.0	0.8	4.8	1.1
Lepidium virginicum	0.0	+	0.1	+	+
Madia glomerata	0.0	0.0	0.6	0.0	0.2
Mertensia arizonica	7.0	0.0	0.0	0.0	1.2
Polygonum douglasi	0.0	0.0	0.0	5.8	1.9
Rudbeckia occidentalis	0.0	0.0	0.1	0.0	+
Taraxacum officinale	68.0	80.3	56.9	53.9	66.1
Tragopogon dubius	0.0	0.0	0.8	0.0	0.3
Vicia americana	0.0	0.7	0.1	0.0	0.3
Viola spp.	0.0	0.6	0.0	0.0	0.2
Viguiera multiflora	0.0	0.0	0.3	0.0	0.1

Table 32. Continued

Plant Species	June	July	August	September	$\overline{X}$
			Percent		
Grasses					
Agropyron subsecundum	12.9	1.6	6.6	9.5	6.5
Bromus carinatus	0.4	0.4	0.0	20.9	3.7
Browse					
Populus tremuloides	0.0	0.7	0.0	0.0	0.2

[a]+ = trace item, less than 0.05% of diet.

VITA

William Brian Collins

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Feeding Behavior and Habitat Selection of Deer and Elk on Northern Utah Summer Range.

Major Field: Range Science

Biographical Information:

Personal Data: Born 21 January 1950, Tucson, Arizona. Parents, John E. Collins and Mary P. Collins. Married Mardene Ellsworth, 17 November 1972; four children.

Education: Graduated from Whetstone High School, Columbus, Ohio in 1968. Graduated with a BS degree in Range Management from Brigham Young University in 1974. Graduated with a MS degree in Range Science from Utah State University in 1977, and completed requirements for a PhD degree in Range Science in 1979.

Professional Positions: Teaching Assistant, Brigham Young University, 1973-1974. Research Technician, USFS Intermountain Forest and Range Experiment Station (Desert Experimental Range) in 1974. Graduate Research and Teaching Assistant, Utah State University, 1975-1979.