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Sexual Dimorphism in the Ecological Niche
of Wintering Rocky Mountain Bighorn Sheep

by

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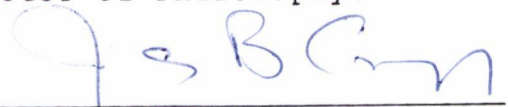
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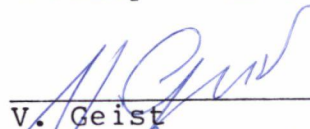
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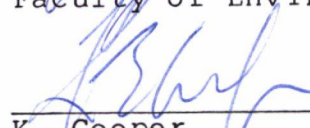
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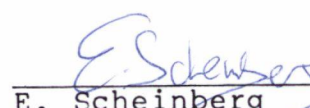
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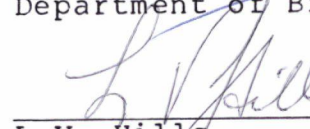
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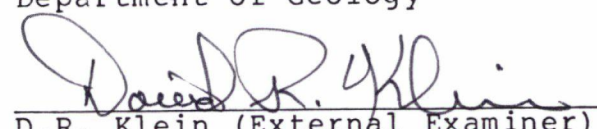
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ABSTRACT

This study consists of an examination of the winter ecology of Rocky Mountain bighorn sheep for the purpose of determining the extent to which the sexes differ ecologically.

The Cascade Valley bighorn population, located on the Palliser Range in Banff National Park, Canada, was studied during the winters of 1975-1976 and 1978. The sexes were found to be spatially segregated on the Palliser Range. Rams tended to remain on the northern end of the range whereas non-rams (ewes, lambs, yearlings) were largely confined to the extreme southern end. Rams utilized alpine meadow terrain, snow-covered areas, and higher elevations less than did non-rams. The vegetation of the favoured ram and non-rams ranges were significantly different. The ram range was characterized by Festuca while the non-ram range contained more Koeleria suggesting a more overgrazed condition. Diets were shown to vary significantly with respect to month, year, and age-sex class. Rams ate more Festuca, and less Carex, Poa, and Astragalus than did non-rams. These differences were shown to be attributable to an area effect rather than to class specific diet preferences. The diet of rams was of marginally higher quality than that of non-rams. Analysis of the sequencing of feeding behaviour showed lambs to exhibit a pattern consistent with a more specialized diet than that taken by

rams and adult ewes. There was no evidence for this in the faecal analysis. There was no noticeable difference between rams and non-rams in feeding mobility such as would be expected if they were utilizing patchily-distributed forages in different manners. Differences in mouthpart sizes of rams and ewes were shown to be of the order of magnitude expected in sympatric congeneric species. These differences were shown to be attributable to allometric relations and could not be demonstrated as being of ecological significance. The thermal advantages accruing to non-rams by remaining closer to the thermal inversion zone were shown to be negligible.

It was suggested that all niche differences are due to body size differences and spatial segregation and are not interpretable as an adaptation for the reduction of intraspecific competition. It was argued that sexual dimorphism in the ecological niche can never evolve as an adaptation for competition reduction since the inferior sex-specific niche will always tend to converge on the superior one. It was suggested that the distribution of resources and the presence of competitors make bighorn sheep particularly unlikely to exhibit large intrapopulational niche differences regardless of the nature of the selective pressures.

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Equipment was obtained on loan from various sources. The Warden Service of Banff National Park allowed me the use of a single-sideband radio. Altimeters were lent by the Departments of Geography and Geology of the University of Calgary. Meteorological equipment was provided by P.K. Anderson, Department of Biology and by the Environmental Sciences Centre (Kananaskis), both of the University of Calgary.

Many individuals assisted me in various ways. The Banff Warden Service, particularly A. Anderson, P. Whyte, S. Marty, and T. Auger helped with the logistics and kept a watchful eye for my return from the field. D. Gardiner and C. DeVries man-hauled huge sledge-loads to and from my camp. G. Sykes helped with the computer programming and J. Vrbik

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Special thanks go to Aalice Legat who provided encouragement, sympathy, and patience as required and to my supervisor, J.B. Cragg, who never failed to respond rapidly, effectively, and subtly to my needs.

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INTRODUCTION

It is usually accepted by ecologists that intraspecific ecological competition is in most cases more intense than is interspecific competition. Yet, little theoretical or field work has been devoted to the subject. An aspect of this problem that has attracted recent attention is the suggestion that the sexes may differ ecologically and thereby reduce intrapopulational competition. Like so many of the interesting modern problems of ecology, behaviour, and evolution, this suggestion is attributable originally to Charles Darwin (1888, first published in 1872). The idea was revived in the 1950's by Rand (1952) and Amadon (1959), elaborated in the 1960's (review in Selander 1972), and was recently the subject of a major review (Keast 1977). To date, sexual dimorphism in niches have been documented in such diverse groups as vascular plants (Putwain and Harper 1972, Freeman et al. 1976), fish (Feduccia and Slaughter 1974), reptiles, birds, and mammals. A list of some references to separation of niches by sex in terrestrial vertebrates is included as Table 1.

Few of the references listed in Table 1 pertain to those large mammals commonly termed "big-game animals". Since intraspecific competitive relations have been so rarely investigated, it is unclear whether this is because the phenomenon has simply not been observed or that it rarely exists. Big-game animals are often intensely managed

Table 1. A review of some literature pertaining to sexual niche differentiation in terrestrial vertebrates. An asterisk (*) following the description indicates that the author(s) suggested but did not demonstrate the separation.

Common Name	Taxon	Separation Type	Author
MAMMALS			
<u>Myotis</u> bats	<u>Myotis auriculus</u> ,	prey type	Husar 1976
	<u>M. evotis</u>		
Hamadryas baboons	<u>Papio hamadryas</u>	foraging behaviour	Kummer 1971
Olive baboons	<u>Papio anubis</u>	more hunting by males	Harding 1973
Human beings	<u>Homo sapiens</u>	various divisions of labour	Boserup 1970, Brown 1970, Ember & Ember 1971, Sanday 1973
Long-tailed weasels	<u>Mustela frenata</u>	prey type and size*	Brown and Lasiewicki 1972
European weasels	<u>Mustela nivalis</u>	prey type and size	Erlinge 1975
Coatis	<u>Nasua narica</u>	prey type and size, hunting behaviour	Smythe 1970
Roosevelt elk	<u>Cervus canadensis</u> <u>roosevelti</u>	proportion of forage species	Harper et al. 1967
Red deer	<u>Cervus elaphus</u>	food type	Dzieciolowski 1969
Bighorn sheep	<u>Ovis canadensis</u>	different foods*	Geist and Petocz 1977
BIRDS			
Flightless cormorants	<u>Nannopterum harrisi</u>	range of food type*	Snow 1966
Sharp-shinned, Cooper's and Goshawks	<u>Accipiter striatus</u> ,	Size of prey	Storer 1966
	<u>A. cooperi</u> , <u>A. gentilis</u>		
Sharp-shinned hawks	<u>Accipiter striatus</u>	size of prey	Storer 1952, Mueller and Berger 1970
Peregrine and gyrfalcons	<u>Falco peregrinus</u> & <u>F. rusticola</u>	food habits*	Cade 1970
Hawks and owls	Orders Falconiformes Strigiformes	prey type and size	Snyder and Wiley 1976

Table 1--Continued

Common Name	Taxon	Separation Type	Author
Pygmy owls	<u>Glaucidium gnoma</u>	prey type	Earhart and Johnson 1970
several owl	Order Strigiformes	prey size*	Earhart and Johnson 1970
Hairy woodpeckers	<u>Dendrocopos villosus</u>	foraging behaviour*	Selander 1965
Hairy woodpeckers	<u>Dendrocopos villosus</u>	foraging behaviour	Kilham 1965
Red-cockaded and	<u>Dendrocopos borealis</u> &	foraging behaviour	Ligon 1968
Arizona woodpeckers	<u>D. arizonae</u>		
Downy woodpeckers	<u>Dendrocopos pubescens</u>	foraging behaviour	Kilham 1970, Jackson 1970
White-headed woodpeckers	<u>Dendrocopos albolarvatus</u>	foraging behaviour	Koch et al. 1970
Melarnipine woodpeckers	<u>Centurus</u> spp.	"different niche"	Selander & Giller 1963, Selander 1966
Huias	<u>Neomorpha acutirostris</u>	foraging behaviour	Darwin 1888
Carrion crows	<u>Corvus corone</u>	foraging behaviour & food size	Holyoak 1970
Pygmy nuthatches	<u>Sitta pygmaea</u>	foraging behaviour	Norris 1958
Spruce-wood warblers	<u>Dendroica magnolia</u> , <u>D. coronata</u> , <u>D. fusca</u> , <u>D. virens</u>	foraging behaviour	Morse 1966
Dusky & grey flycatchers	<u>Empidonax oberholseri</u> & <u>E. wrightii</u>	size of prey*	Johnson 1966
Red-eyed vireos	<u>Vireo olivaceus</u>	foraging heights	Williamson 1971
Goldfinches	<u>Carduelis carduelis</u>	food species	Darwin 1888, Newton 1967
Henslow's sparrows	<u>Ammodramus henslowii</u>	separate foraging areas	Robins 1971
Black-faced dionchies	<u>Quelea quelea</u>	food size	Ward 1965
Warbler finches	<u>Certhidea olivacea</u>	foraging behaviour	Lack 1945
REPTILES			
<u>Anolis</u> lizards	<u>Anolis conspersus</u>	size of prey	Schoener 1967

in the wild to maintain their population numbers at a level which is best suited to man's uses. Central to the practice of wildlife management is a detailed knowledge of the relationship between available resources and population requirements. Using these data, managers can estimate the relationship between observed population levels and the maximal ones and subsequently manipulate the habitat in such a manner as to produce the desired population response. Almost always, wildlife managers have of necessity treated the requirements and resource base of a population as being typical of the group as a whole. If, however, the relationship between animals and the resource base differs by sex, determination of "carrying capacity" or planning a management programme would be more precisely determined if consideration were given to sex-specific requirements.

Geist and Petocz (1977) discovered that Rocky Mountain bighorn sheep (Ovis canadensis canadensis) in Banff National Park, Canada, sexually segregate onto separate portions of their winter range and occupy cliff and alpine meadow terrain in differential proportions. They suggested that such segregation might entail niche separation for the purpose of reducing intraspecific competition.

I followed up on this suggestion by examining the winter ecology of various components of the bighorn sheep population in Banff National Park during the winters of

data collected were utilized to determine whether the sexes are ecologically distinct during winter, to determine the extent of any differences noted, to discuss how any such differences might have evolved, and to suggest what implications these findings may have to the practice of wildlife management.

II. THE STUDY AREA AND POPULATION

All observations were made on the Cascade Valley bighorn population located on the Palliser Range in the southeast corner of Banff National Park (Figure 1). This population has been the subject of a succession of studies by several workers (Geist 1966, 1968, 1971; Petocz 1973; Shackleton 1973; Stelfox 1975, 1976; Geist and Petocz 1977) whose publications include full descriptions of the study area. Only those features of the area relevant to the present study are given here.

The study area lies on the westerly facing slopes of the 7 km segment of the Palliser Range from Stoney Creek in the southwest to the level of Grassy Mountain in the northeast (Figure 2). The altitude of the valley floor is 1650 m above sea level with the ridge-top reaching an elevation of 2850 m. The bedrock of the lower slopes of the Palliser Range, up to 2135-2285 m, consists of Triassic siltstones, mudstones, and shales of the Spray River Group while the higher and steeper cliff areas are comprised of more resistant Mississippian limestones of the Etherington, Mount Head, and Livingstone Formations (Geological Survey of Canada 1972). The lower slopes, corresponding to the soft, productive Triassic sedimentaries, are vegetated by disclimax Elymus innovatus-Festuca subalpine meadows. Bighorn sheep tend to concentrate their activities in the upper portions of this meadow zone and consequently their



Figure 1. The location of the study area in Banff National Park, Canada (used by permission of S. Herrero).

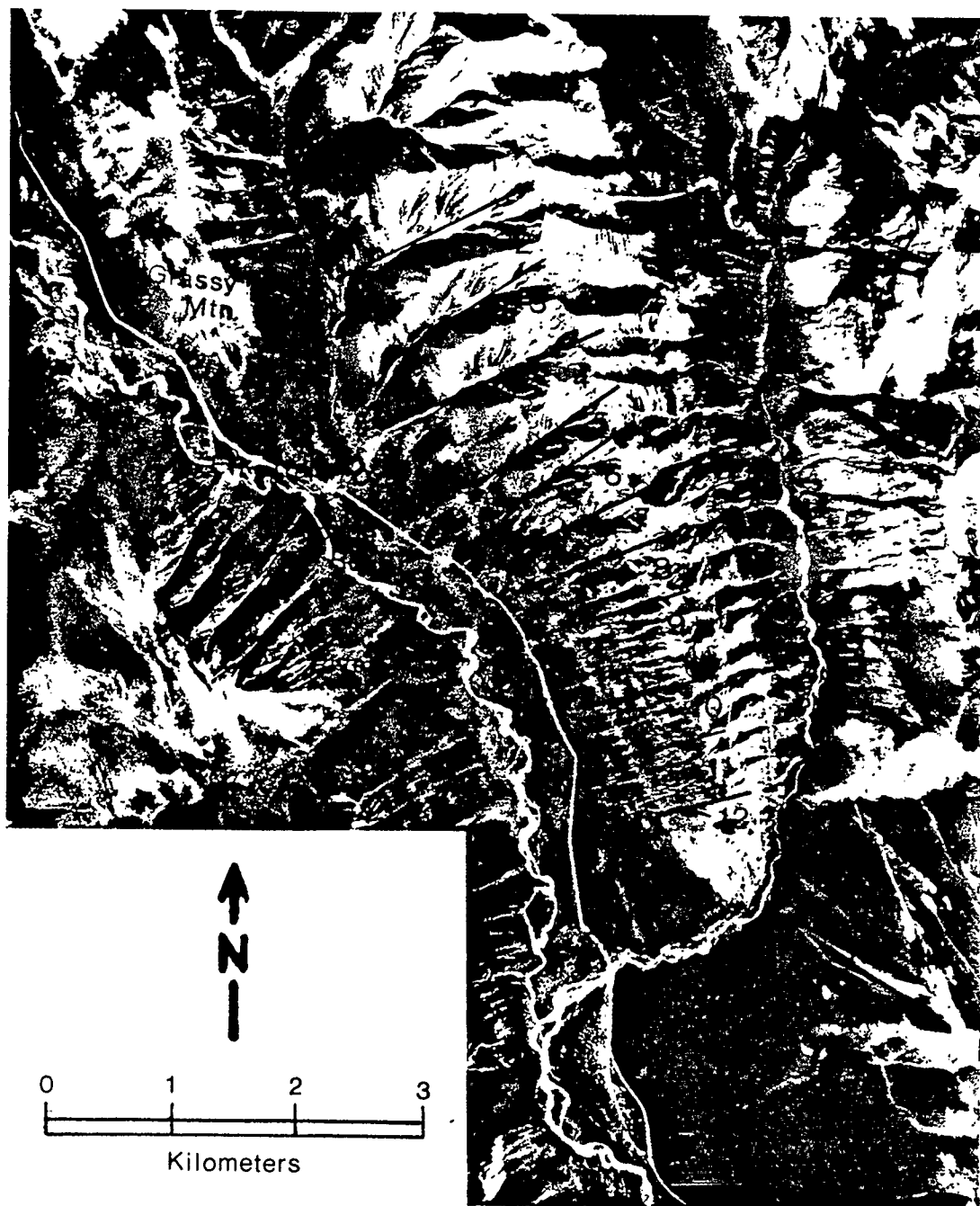


Figure 2. Aerial photograph of the Palliser Range study area. Numbers 1-12 indicate spatial units used in censuses.

distribution is ultimately determined by the bedrock. The meadow zone is sharply dissected resulting in exposed spurs which are rapidly blown clear of snow during the winter.

In recent years, the Cascade Fire Road (Figure 2), which runs the length of the Cascade Valley, has remained uncleared throughout the winter. Consequently, access to the sheep range may only be gained by skiing 20 km from the road-head.

The winter weather of the Cascade Valley is harsh (recorded low of -44°C during the winter of 1975-1976) but is occasionally moderated by warm, gusty chinook winds. Snow begins to accumulate in mid-November and remains until May. Winter snowfall for the winter of 1975-1976 was 1.85 m in Banff townsite (Table 7).

The sheep population has been stable in number for at least a decade (Shackleton 1973). Using different sets of criteria, the quality of the population has been characterized by Shackleton (1973) as "poor" and by Stelfox (1975, 1976) as "medium". The Palliser Range is primarily a rutting and winter range with the rams and ewes arriving from various surrounding areas in the fall and departing in the late spring (Geist 1971). The mean numbers of adult rams and non-rams (i.e., adult ewes, lambs, and yearlings) observed in each bi-weekly period in 1975-1976 are presented as Figure 3.

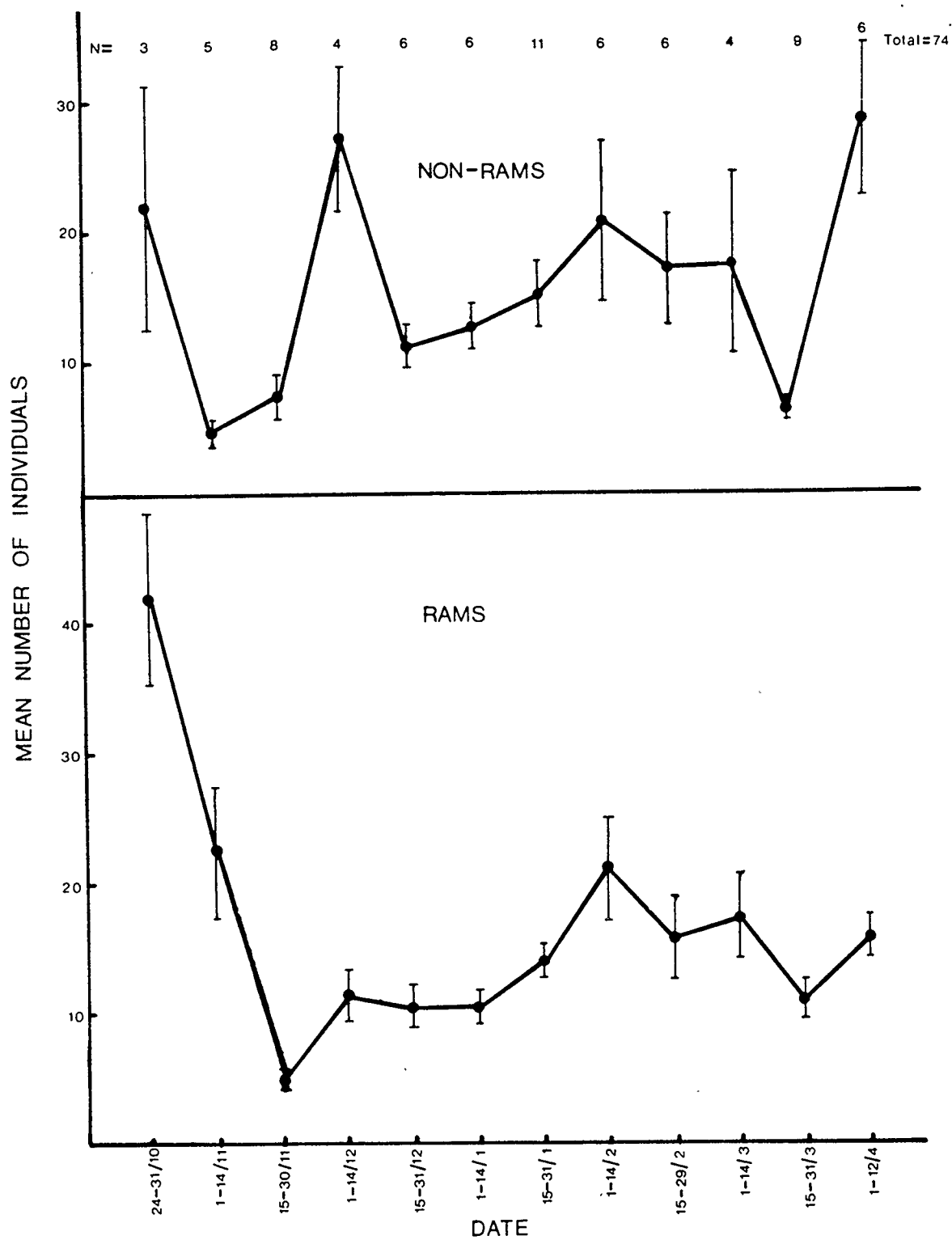


Figure 3. Mean bi-weekly numbers of rams and non-rams observed per census trip during the winter of 1975-1976. N = number of censuses.

III. THE CONCEPTUAL FRAMEWORK AND METHODS OF DATA COLLECTION

A. THE NICHE CONCEPT

The term "niche" has been used in such a variety of contexts and continues to be such a problematic concept that even in the 1970's, when the number of niche studies is increasing more than four times as fast as typical scientific studies (Schoener 1974), some authors prefer not to use the term (e.g., Williamson 1972). Since I wish to use the niche concept in a manner differing from the usual one, I feel it necessary to briefly describe how the term will be used. I have found this to be by no means easy and the description offered here has many inadequacies. Robert MacArthur, in one of his last publications (MacArthur 1972), stated that a precise definition is probably still premature so my failure is in some respects understandable. I have prefaced the discussion of the way in which I propose to use the term with a brief review of the concept so that my useage can be considered in a historical perspective.

1. Historical Review of the Niche Concept

It is impossible to determine when the general notion of the "ecological niche" was first recognized. Certainly Darwin had some inkling of the idea when he wrote "We can dimly see why the competition should be most severe between allied life forms, which fill nearly the same place in the

economy of nature..." (1970 p.127, first published in 1859). Cody (1974) cites examples of an implicit niche concept in the work of several Victorian naturalists and a thorough examination of that literature would doubtlessly exhumate other instances.

The term "niche" was apparently first used in an ecological sense by Johnson (1910 in Gaffney 1975) but went unnoticed. Joseph Grinnell is generally credited with introducing the idea into ecological thinking. He first hinted at the idea in a paper of 1904 and elaborated the term without definition in 1917 and 1924. In 1928 he defined the niche as "the ultimate distributional unit, within which each species is held by its structural and instinctive limitations, these being subject only to exceedingly slow modification through time." (Grinnell 1928 in Vandermeer 1972).

A number of aspects are evident in Grinnell's idea of the niche. This is primarily a "habitat" concept in that it is most concerned with those factors causing and allowing a species to occur where it does. There is, however, some ambiguity in the way Grinnell used the term "distribution" as is suggested by the following quote: "...we can usefully recognize as measures of distributional behaviour, the realm, the region, the life-zone, the fauna, the sub-fauna, the association and the ecologic or environmental niche" (Grinnell 1924 p.226-227). The terms "realm", "region", and

"life-zone" are unequivocally distributional, spatially defined and construable as habitats. But "fauna", "subfauna" and "association" are clearly not measures of habitat. To say that an animal is distributed in relation to a fauna is to make a functional niche statement. Grinnell's definition is therefore probably not restricted to a pure habitat concept. Another point is that the definition is autecological in focus. Grinnell was interested in single species, not communities.

During the first two decades of this century, ecology was involved in a phase of primarily autecological studies with heavy emphasis on the "conditions of existence" (Allee et al. 1949). Grinnell's definition was therefore located directly within the mainstream of ecological thinking at the time by representing a useful schema for typifying and classifying species primarily by their habitat requirements.

In 1927, Charles Elton presented his "functional" niche concept. He defined an animal's niche as "...its place in the biotic environment, its relation to food and enemies" (Elton 1927 p.64, his italics). In reality Elton's examples of the niche were all formulated in terms of food.

The operative terms in this definition, "place" and "relation", are ambiguous rendering the entire definition vague. Nothing is said of the criteria by which places or relations are to be defined or described. The term "place" itself has connotations of "rightful position" implying that

community processes are teleological; e.g., the place of the rabbit is as prey to the fox. In context, it is obvious that the definition was meant primarily to refer to position within a separately derived trophic model. The great strength of the concept, and the reason that it continues to be useful, is that it represents a dynamic description of the species interactions with, and adaptation to, the biotic environment (I am indebted to V. Geist for this insight).

Following the late 1920's, ecological thinking entered into consideration of synecological relationships with emphasis on community description and analysis of their temporal development. Very little quantification or theorizing was done during this period although progress was made in recognizing organizational principles and natural patterns (Allee et al. 1949). Elton's (1927 p.17) definition was firmly entrenched into this phase of ecological development. This is evident in Elton's consideration of his niche concept as a "powerful digestive juice" used to assimilate "masses of interesting but unrelated facts" about communities.

By the mid-1930's, the mainstream of ecology had shifted more toward a population focus which continued until the 1950's. During this period, the niche concept had no unequivocal public meaning as can be seen by the varied definitions offered in standard texts (e.g., Allee et al. 1949, Dice 1952, Clarke 1954). Consequently, the term

"niche" rarely occurred in the literature of the period. In 1953, Odum (1953) suggested that the niche be viewed as an animal's "profession". This analogy served as a "handle" to the elusive functional concept and effectively fixed the popular conception of the niche into the Eltonian sense.

Significantly, in their history of ecology, Allee et al. (1949) do not mention the body of theory and experiment concerned with ecological competition which was developing during this period in a line separate from, but converging on, the mainstream of ecology. The principle that two species with identical ecologies cannot coexist indefinitely, which has become known as the "competitive exclusion principle" (Hardin 1960), has a history interwoven with that of the niche concept. Darwin clearly appreciated the importance of interspecific competition (Hardin 1960, Diamond 1978) as did several naturalists of the late 19th and early 20th centuries (Hutchinson 1975). Grinnell stated the principle in 1917 but it was only when Haldane (1924) and Volterra (1926, translated in Whittaker and Levin 1975) developed mathematical formulations and when Gauss (1934) presented his evidence from laboratory experiments that the principle attracted attention and was considered by some as being of potential interest (Hutchinson 1975). Gauss (1934 p.17) initially stated his formulations in terms of Elton's niche definition and the concept of the niche thereafter became tightly integrated into competition theory as the

abstract entity within which two species cannot coexist. On the other hand, the importance of competition in molding niches was not generally recognized.

Until Huxley's (1942) evolutionary synthesis, the ecological determinants of evolution were not clearly perceived. Robson and Richards (1936 in Lack 1947), for example, expressed the commonly held opinion that variation between closely related species is of no adaptive significance. Those evolutionists who felt all characters to be in some way adaptive sought to interpret these differences as reproductive isolating mechanisms (Mayr 1973). Huxley (1942 p.280-284) was the first to suggest that such differences arose as a means of resource partitioning made necessary by competition. In 1944, David Lack independently came to the same conclusion during the reanalysis of his data on Darwin's finches (Lack 1973). Lack presented these views at a now-famous 1944 meeting of the British Ecological Society attended by C. Elton, G.C. Varley, J.B.S. Haldane, C. Diver, and my thesis supervisor, J.B. Cragg (Harvey 1945). Lack was, in his own words, "widely disbelieved" (Lack 1973). This general reluctance to accept the competitive exclusion principle as an ecological force was not unreasonably based on the principle's unfalsifiability, its inherent tautological nature, the unreality of some parameters in the mathematical formulation, the lack of direct evidence from nature, and

the numerous known instances of apparent niche identity. Lack argued that the principle should be accepted because it is such a powerful device for explaining natural patterns of communities. He continued to champion this interpretation until his death in 1972 (Lack 1944, 1945, 1947, 1971).

In the late 1940's and 1950's, evidence for ecological differences in sympatric species began to accumulate (review in DeBach 1966). Vaurie (1951) compared body sizes of two Asian nuthatches (Sitta) and showed that whereas there are no significant interspecific differences when allopatric populations are compared, sympatric populations of the species exhibit no overlap in size. This led to Brown and Wilson's (1956) definition of "character displacement". Numerous studies showed the introduction of exotic species to be coupled with decreases in populations of native ones (Andrewartha and Birch 1954 p.457-458). MacArthur (1958) showed that an entire group of apparently ecologically identical warblers (Dendroica) in reality subtly partition their foraging space. By the time of Andrewartha and Birch's (1954) influential book, it was generally conceded that sympatric species almost always differ ecologically but the causal role of competition was commonly rejected due to lack of direct evidence (Andrewartha and Birch 1954 p.463).

Because the concept of the niche is central to the competitive exclusion principle, being the abstract entity in which two species cannot coexist indefinitely, semantic

or logical ambiguities in the niche are of necessity reflected in the principle itself. As previously argued, the Grinellian and Eltonian niches were defined for purposes relevant to problems of their day and, as such, cannot reasonably be expected to function adequately in logical or mathematical formulations of the exclusion principle. What was required was a niche concept, defined independently from the exclusion principle, which was sufficiently precise to render the principle testable. Hutchinson (1957) attempted to do this with his hypervolume model of the niche. He proposed that a niche be characterized as the hypervolume resulting from the projection of the regions of a population's positive fitness along each of the potentially infinite number of independent and continuously varying environmental dimensions which affect fitness. This definition, by describing how the niche can be precisely delineated, allows a precise enough statement of the niche that competitive exclusion is, in principle, falsifiable. Operationally, of course, it is not so because of the niche's infinite dimensionality which makes it impossible ever to characterize the compared niches completely.

Hutchinson's treatment attracted considerable attention to the principle. Hardin (1960) suggested that since the principle is not falsifiable but useful, it should be accepted so long as its predictions are valid. Cole (1960) promptly accused Hardin of advocating dogmatism. MacArthur

and Levins (1964) and Rescigno and Richardson (1965) reformulated the exclusion principle to read that n species can have no fewer than n limiting resources. Levin (1970) replaced "limiting resources" with "limiting factors" thereby admitting the force of predation in affecting communities.

With these developments, ecology entered a new phase. The exclusion principle was consecrated as ecology's only law of nature (Vandermeer 1972). Therefore, simple determination of niche differences between species became a problem of little intrinsic interest. The realm of interest became analysis of the manner in which competition acts in structuring communities. Led by the work of MacArthur, Levins, Levin, May, and others, a large body of theory began to develop. Coupled with this was the initiation in the late 1960's of niche quantification whereby the ecological relationships of species could be precisely measured and compared. With the reformulation of the exclusion principle, it became generally recognized that reference to a very few dimensions was adequate to describe the population's niche in all aspects pertinent to coexistence. By limiting niche descriptions to only those dimensions capable of separating species, the complexity of the infinitely dimensional niche was stripped away. Because survival or fitness is so difficult to determine, especially in the field, these axes of the Hutchinsonian niche were

replaced by utilization or occurrence axes. This schema allows an empirically delimited geometric model of a species' niche the shape and position of which can be compared with other species' niches in terms of breadth, dimensionality, and overlap (Levins 1968). This served to alter the Hutchinsonian niche from a static concept describing populations tolerances, to a more dynamic model describing populations responses to environmental conditions. Hence, the Hutchinsonian niche, developed as a logical device designed to lend precision to the competitive exclusion principle, evolved into an empirical construct designed to lend precision to field observations.

2. Working Definition of the Niche

This study is characterized by sexes, rather than species, being treated as the "operational taxonomic units" in Vandermeer's (1972) sense. Since the sexes are reproductively interdependent, the competitive exclusion principle does not apply; i.e., there may be only one factor limiting both sexes. Establishing the existence of significant niche differences between the sexes is therefore not a trivial problem but addresses questions about the nature of intraspecific competition.

As Hutchinson (1957) realized, limiting relevant niche axes to continuous environmental variables ignores the whole class of typological variables. Hespenheide (1975) shows how translation of nomological variables into continuous

ones can confuse niche relations. In practice, I found it impossible to consider continuous niche dimensions and retain any realism. This disallows any attempts to compare niche shapes.

The great usefulness of Hutchinson's niche model lies in the geometric visualization of the niche such that species' niches of different shapes may be compared. These attributes have been useful in the development of a unified theory of community structure and development. However, for merely documenting the existence of niche differences, the hypervolume model is unnecessary; a simple determination of significant utilization differences is adequate. This approach is clearly illustrated by Lack's (1971) work wherein niche differences are catalogued and discussed for many bird genera with no reference to utilization distributions.

The niche is herein considered as the sum of all environmental attributes used by or acting on the organism. This concept is static and descriptive but provides the experiential basis from which more dynamic Eltonian niche statements may be inferred. It emphasises purposiveness on the part of the animal in the choice of certain environmental attributes from amongst a larger array. It is infinitely-dimensional but not spatial since the niche axes are not necessarily continuous variables. It represents a reversion to the type of definition offered by Elton and

Grinnell wherein the niche is offered as an aid in organizing thoughts and labelling imprecisely defined but suggestive categories. Such a definition is adequate for the problems to be investigated.

B. HYPOTHESIS TESTING

As Levins (1968) has suggested, only those niche axes which actually separate species need be investigated. Unfortunately, it is never known prior to investigation which dimensions will prove to be actually separating. Lizard investigators (Rand 1964, Schoener 1968, Lister 1976) have shown that the niche dimensions they term "structural", "thermal", and "food" are the aggregate niche dimensions most efficacious in separating sympatric species. My investigations were organized under these broad categories. The data collection methods employed and the arguments for these three aggregate niche categories, and a single non-niche category, are described below. Figure 4 represents the test components of these determinations and their interrelationships.

Macfadyen (1975) has argued persuasively that ecologists should spend less time in amassing field data and more time testing specific hypotheses. Throughout this study emphasis was placed on testing the null hypothesis that no niche related differences exist between social classes of bighorn sheep. The data gathered were derived for the sole purpose of hypothesis testing. Therefore,

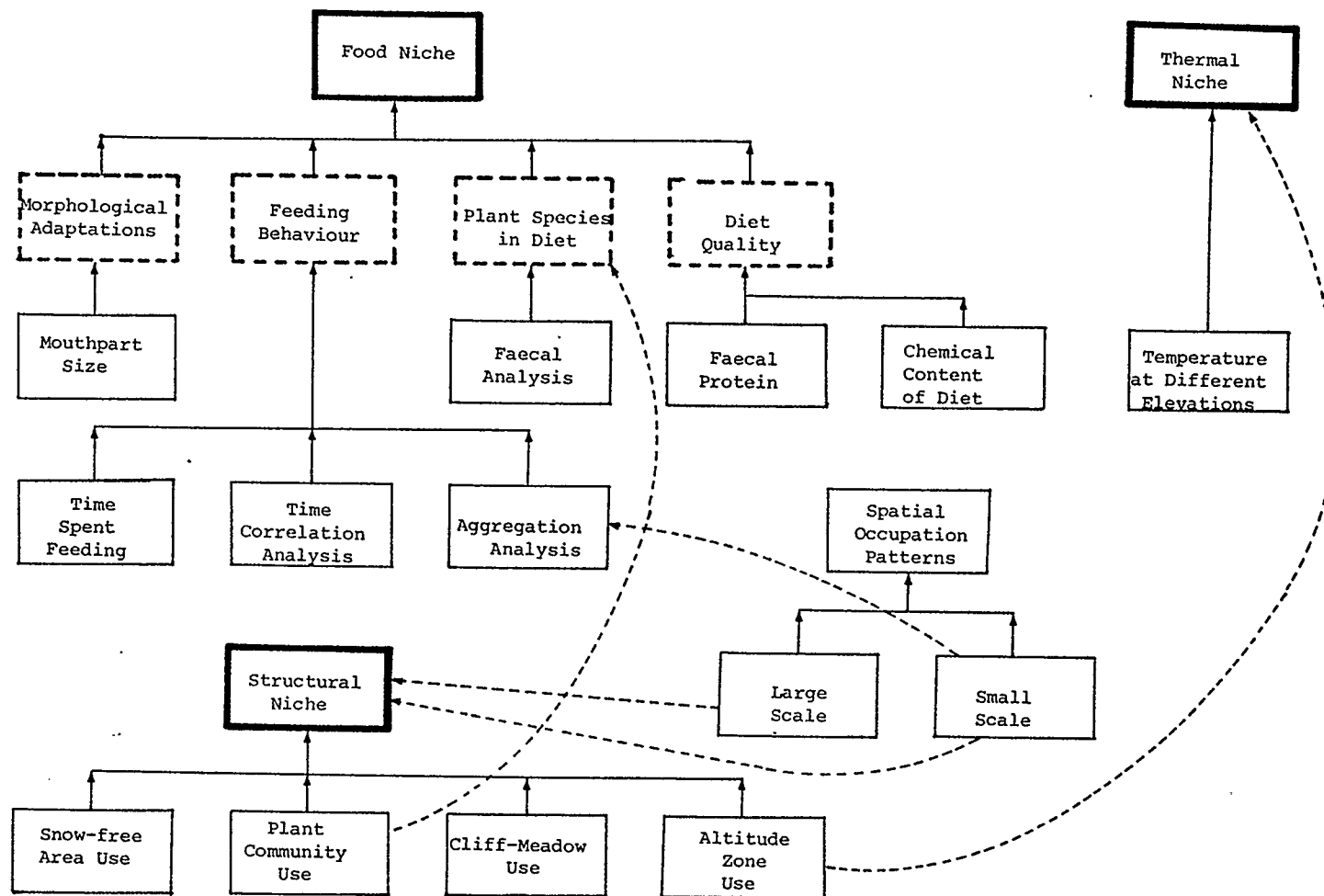


Figure 4. Schematic representation of the hypothesis network.

other sheep biologists will find some of the data presented (e.g., use of snow-free areas) to be of limited applicability to other populations. In all cases, the 5 percent level of probability was used.

1. Spatial Occupation Patterns

Patterning of spatial occupation in itself does not represent a niche dimension but is necessary for the determination of the abundance axis of idealized abundance vs resource curves. Spatial occupation patterns were determined by censusing the animals on the range much as did Geist and Petocz (1977). Census data were gathered one to four times weekly by recording all sheep on the 7 km range from four standardized observation points. Sheep were classified according to age-sex class (Geist 1971) and position on any of 12 spatial units labelled U1 to U12 (Figure 2). These spatial units correspond roughly with those of Geist and Petocz (1977). Between 24 October 1975 and 12 April 1976, 74 census trips were completed yielding 2153 sightings. Small-scale spatial distribution or "micro-distribution", was determined during the collection of "activity" observations. Activity observations were taken throughout the winter from the same four standardized observation points. Every five minutes, each individual was classified according to age-sex class, activity type, and location on one of eight coded grids. These grids consisted of a photograph of the range from the observation points

with an arbitrary grid superimposed over it. The series of grids covered the entire range and in sum comprised about 50 000 possible locations. Depending on distance, perspective, and proximity of landmarks, an individual could usually be located on the grid to a mean distance of approximately ± 5 m in real space. Between November 1975 and April 1976, 15 871 such observations were gathered. All behavioural observations were made from the valley floor with a 20X spotting scope at distances usually exceeding one kilometre in straight-line distance. It was often difficult to separate age-sex classes according to Geist's (1971) criteria because of the rapidity of sequential observations and the frequently poor observation conditions. Therefore, aggregate classes of rams and non-rams (ewes, lambs, yearlings) were used. This proved to be an acceptable level of resolution for most of the analyses employed.

2. The Structural Niche

The structural niche is regarded as the manner in which an animal utilizes the physical patterning of its environment. Four structure types were analyzed; cliff use, snow depth, altitude, and plant community use. Utilization was considered as spatial occupation of particular subdivisions in the structure type.

i. Cliff Use--As described earlier (Section II), the Palliser Range has a distinct subalpine meadow zone under the cliff zone. Differences between rams and non-rams in

use of these two zones were determined by delineating a cliff-meadow interface on the small-scale location grids and determining from each record of the activity data which zone was being inhabited.

ii. Use of Snow-free Areas--To determine whether rams and non-rams were differentially sensitive to snow depth during feeding, an attempt was made to measure the actual snow depth of the feeding sites. It was discovered that the method contains a built-in bias. Feeding areas themselves are trampled down and cannot be measured for snow depth while the edges of the feeding site can be construed as representing the interface where snow characteristics are no longer favourable for feeding. I therefore defined standardized "snow-free areas" and determined the proportion of time spent within and outside of these zones. Snow-free areas were defined as bare areas on photographs of the range taken on 20 January 1976 when snow depths were at a mid-winter low (Table 7). Bare areas were delineated on the photographs and spatial occupation patterns determined from the activity data were compared to arrive at the proportions of rams and non-rams occupying these standardized snow-free areas. This method results only in an index of snow-free area use since at any time before or after 20 January more or fewer grid locations were bare. At no time, including the limiting cases of completely bare or completely snow-covered range, would a defined snow-free location be

covered with more snow than a standardized snow-covered area. The index therefore conveys information suitable for hypothesis testing but does not indicate the proportion of real time that bighorn sheep fed on areas actually snow-covered or bare.

The effect of snow depth and hardness on cliff use and use of snow-free areas was investigated by determining mean snow characteristics and relating these to the relevant simultaneous behaviours. At weekly intervals from 1 December 1975 to 12 April 1976, depth and hardness were measured along a vertical transect on Unit 4 (Figure 2) consisting of the following 12 stations:

7500-1-- ridge-top; elevation 7500 ft (2285 m); aspect 242° ; slope 27° . This station was on a narrow part of the ridge near the north side and therefore collected considerable snow.

7500-2-- ridge-top; elevation 7500 ft (2285 m); aspect 242° ; slope 27° . Located 8 m south of 7500-1 and therefore not subjected to cornice formation.

7500-3-- south side; elevation 7500 ft (2285 m); aspect 207° ; slope 37° . A heavy snow collection and compaction area.

7500-4-- south side; elevation 7500 ft (2285 m); aspect 187° ; slope 33° .

LD-1-- ridge-top; elevation 7250 ft (2210 m); aspect 242° ; slope 35° . A broad, snow-free top which represents the single best indicator of snow conditions in relation to foraging.

LD-2-- north side; elevation 7250 ft (2210 m); aspect 282° ; slope 35° .

LD-3-- south side; elevation 7250 ft (2210 m); aspect 197°; slope 36°.

M-1-- south side; elevation 7000 ft (2135 m); aspect 202°; slope 37°.

M-2-- south side; elevation 7000 ft (2135 m); aspect 227°; slope 37°.

M-3-- ridge-top; elevation 7000 ft (2135 m); aspect 257°; slope 37°.

M-4-- north side; elevation 7000 ft (2135 m); aspect 272°; slope 37°.

Stump-- ridge-top; elevation 6750 ft (2055 m); aspect 247°; slope 36°.

Both depth and hardness were determined with a Swiss Ramsonde Penetrometer (Geotest Instr. Corp., Wheeling Illinois) equipped with a 60° cone. Lent and Knutson (1971) present a description of the apparatus, its use, and its desirability as a biological tool.

iii. Elevation of Occupation--Differences between rams and non-rams in the altitude of their range occupation was investigated by defining 100 ft (30 m) contour intervals on the location grids from reference points determined with a hand altimeter. Numbers of sheep occupying each elevation zone were calculated from all the activity data excluding that gathered for Grids 5 and 1.

iv. Plant Community Use--An important aspect of feeding behaviour is the actual species spectrum of forage plants available on the chosen feeding areas. To determine if rams and non-rams spent different proportions of time feeding on different plant communities, I originally planned

to map the communities of the Palliser Range and then, from the activity observations, determine if feeding locations used by rams and non-rams differed with respect to plant communities. The extremely homogeneous nature of the vegetation did not, however, allow differentiation of the associations. A continuum analysis of the vegetation would have entailed more work and a greater level of precision than was warranted by other aspects of the study.

Instead, I chose the less desirable method of characterizing the vegetation on the specific areas most highly favoured by rams and non-rams as determined from activity data. On each of the north, south, and middle parts of the range, the two most favoured ram and non-ram feeding areas (accurate to ± 5 m) were selected. With respect to the southern part of the range, the most highly favoured feeding areas were identical. In total, the vegetation on 10 separate areas was characterized.

Vegetation analyses were done in late August 1978 when most of the year's growth had been completed. The data presented are therefore a good estimate of available winter forage prior to alteration by winter grazing.

Daubenmire's (1959) canopy-cover method was selected since, barring actual clipping and weighing, this method yields a better estimate of available forage than any other vegetation parameter (Daubenmire 1970 in Shepherd 1975). Stelfox (1976), after using a point-intercept technique on

the Palliser, recommended the use of the canopy-cover method. Shepherd (1975) also used this technique on Colorado bighorn ranges after testing the point-intercept method. Following Shepherd (1975), actual percentage cover was recorded rather than the six-point scale advocated by Daubenmire (1959).

Eddleman et al. (1964) recommended a plot-frame of 20 x 40 cm for alpine vegetation, however, I followed Shepherd (1975) in choosing a 20 x 50 cm size. The transect configuration consisted of three 10 m lines following the contour and located two metres apart vertically. Quadrats were placed at one metre intervals yielding a total of 30 quadrats per transect. This close configuration of quadrats was necessitated by the restricted areas defined as favoured feeding areas.

The standard technique for determining the minimum acceptable number of quadrats per transect is to plot the cumulative number of species found against the number of quadrats. The point at which the curve levels off indicates the optimal number of quadrats (Mueller-Dombois and Ellenburg 1974). This technique was considered inappropriate for the present study since the interest is in the relative covers of the major taxa present; actual numbers of species is irrelevant. The number of quadrats needed for a valid estimation of species cover can be determined by the number of quadrats at which the running

mean of cover reaches a steady state. Figure 5 shows the relationship of running mean to number of quadrats for three taxa on Transect 1. It shows that 30 quadrats/transect are sufficient for a reasonable estimation of percentage cover.

The grassland vegetation of Banff, Jasper, and Waterton Lakes National Parks has been described by Stringer (1972). The vegetation of the Palliser Range itself has been investigated by Ogilvy (pers. comm.), Stelfox (1975,1976), and Hamer et al. (1977). Because the vegetation of the Palliser Range is so well-known and because corresponding identifications in the faecal analysis (Section IV.C.1.) were rarely made to the species level, field identifications during the vegetation analysis were made at the generic level while rare and some non-flowering forbs were combined into a single class. This method leaves open a possible confounding factor. If, for example, the same genera were found on both ram and non-ram feeding areas, this would not necessarily mean that the two areas were vegetatively identical since different congeneric species might be present on the two areas. If however, different genera were found in the two areas, the areas would be unequivocally different. This technique is adequate for demonstrating major differences between areas but degree of similarity in the vegetation of the two areas cannot be well documented.

3. The Food Niche

The food niche is the niche axis usually implicated by

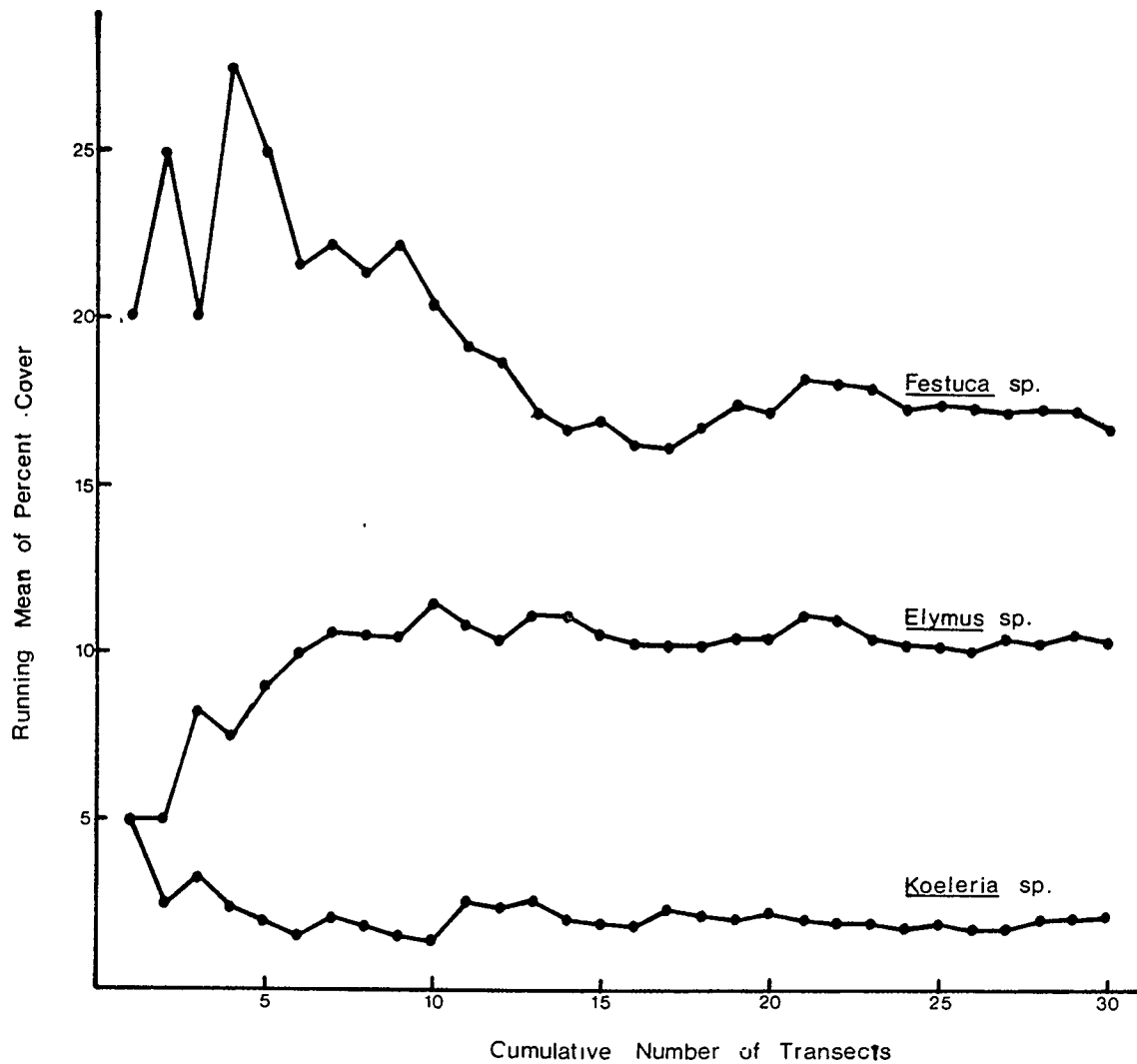


Figure 5. Running mean of percent cover against number of quadrats for three grass genera on Transect 1.

vertebrate ecologists as exercising the greatest separating effect between sympatric species. Accordingly, this dimension was investigated in greater detail than other dimensions. Four sub-questions were asked and are represented as the boxes outlined by dotted lines in in Figure 4. These sub-questions are (a) do different age-sex classes eat different forage species?, (b) does the quality of the forage ingested vary between classes?, (c) are there differences in the feeding behaviour of different classes?, and (d) are there morphological differences between classes which would affect feeding behaviour?

i. Forage Species in Diet--Differences in the forage species spectrum in the diets of the age-sex classes were examined by analysis of plant fragments in the faeces. Although this technique has been in use since 1939 (Baumgartner and Martin 1939), there is still considerable controversy concerning its validity. The degree to which plant fragments in the faeces are digested is largely dependent on the content in the plant of indigestible lignin and cutin (Storr 1961). Consequently, some authors infer that this means that the remains of digestible species are not as recognizable as those of less digestible ones thereby introducing a bias (Stewart 1967, Casebeer and Koss 1970, Free et al. 1970). In contrast, Hansen et al. (1973) state that digestibility has a greater effect on the mean weight of fragments than on their discernability and should

therefore enter very little bias into the determinations. Using the faecal technique, Anthony and Smith (1974) found higher than expected values for evergreens and lower than expected values for herbs. Vavra et al. (1978) showed that grass fragments occurred significantly more frequently in faecal samples as compared with esophageal samples while forbs showed the opposite tendency. The only test of the faecal analysis technique as applied to bighorn sheep was by Todd and Hansen (1973) who found no significant differences between faecal and rumenal samples.

These objections are fundamental enough to raise questions as to how closely the results obtainable from the faecal analysis reflect the actual diets of sheep on the Palliser Range. Vavra et al. (1978), while stating that the esophageal fistula method is the technique of choice in the absence of constraints, state that the faecal method can be properly employed when (a) wild animals are being studied, (b) when all individuals occupy the same range, and (c) where relative values are important. Since this study is concerned with a comparison between diets of components of a single population of wild animals on a single range, the faecal analysis technique would seem to be appropriate.

Faecal samples were collected between 16 November 1975 and 6 April 1976 and between 26 January and 16 April 1978. Samples were collected by two methods. In the first, sheep were followed as they fed and pellets were collected from

observed defecations by animals of known age and sex. In the second, faeces were collected from bed sites less than 24 hr old as determined by snow melt, pellet characteristics, and sheep occupation. The mean weight of all samples (dried for 24 hr at 85-90°C) was determined to the nearest 0.01 g on an analytical balance. Figure 6 shows the frequency distributions of mean pellet weight for lambs, yearling, ewes, and rams. It shows that about 93% of all pellets weighing 0.10 g or less are from lambs while 100% of all pellets of more than 0.22 g are from rams. Using these criteria, certain of the unknown faecal samples could be determined as being from rams and lambs. All other unknown samples were left unanalyzed. In total, 448 samples were collected of which 272 were analyzed.

Analysis was done by the Composition Analysis Laboratory of Colorado State University and followed the method of Sparks and Malechek (1968). One slide was made per sample and 20 fields per slide were examined under a 100X binocular microscope. Species presence was expressed in terms of relative density (Hansen and Reid 1975).

ii. Diet Quality--Between-class differences in quality of diet were examined by two methods; the faecal nitrogen index and estimated digestible energy based on content of acid detergent fibre (ADF).

The faecal nitrogen index of digestibility was first proposed by Lancaster (1949) who suggested that the nitrogen

content of ruminant faeces is directly proportional to the nitrogen content of the diet which is, in turn, directly proportional to dry matter and energy digestibility. High quality forage is primarily attributable to high contents of protein and digestible carbohydrates and low fibre contents. At any point in time, different plant species and various parts of a single plant may both differ in quality. Diet quality then depends not only on species selectivity but also on plant part selectivity (Gwynne and Bell 1968, Jarman 1974). The faecal nitrogen index of digestibility is a particularly suitable technique for estimating diet quality since it measures the combined effect of both types of grazing selectivity.

The quantitative relationships between faecal nitrogen and digestibility which have been reported in the literature are reviewed by Van Dyne (1969). Several authors have discussed the shortcomings of the technique (see Van Dyne 1969) the most significant of which is that herbage of the same organic matter digestibility often exhibit different nitrogen digestibilities.

Subsamples of 86 faecal samples collected in the winter of 1975-1976 were stored frozen, air-dried, and analyzed for nitrogen content by micro-Kjeldahl digestion (Association of Agricultural Chemists 1960) by R. Beames of the Department of Animal Science, University of British Columbia.

To determine if the major forage species differ in a

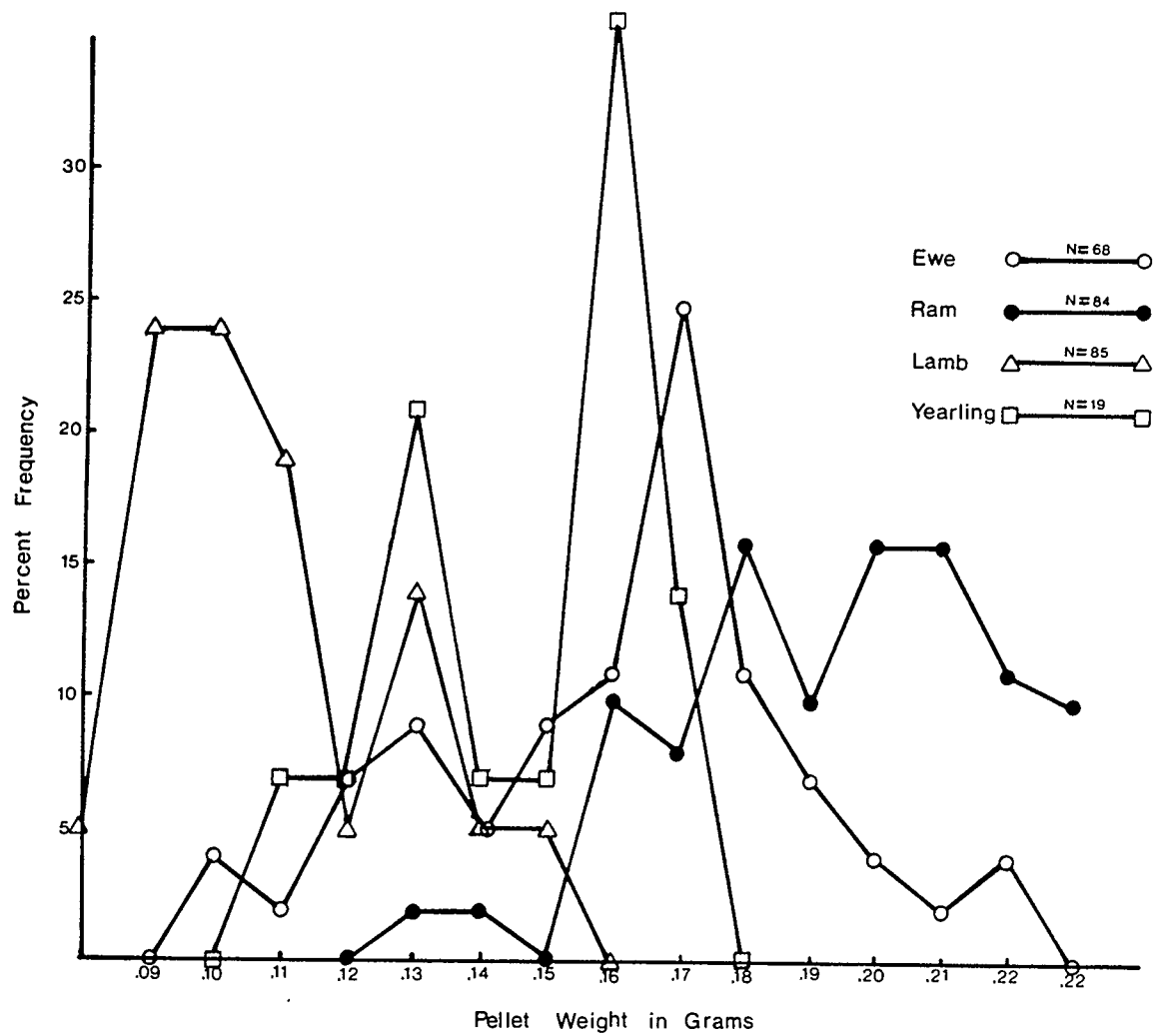


Figure 6. Mean faecal pellet weights for known samples from rams, lambs, yearlings, and ewes.

qualitative manner, weathered samples of Carex, Agropyron, Bromus, Poa, Festuca, and Koeleria were collected from various areas of the range on 23 March 1978. The collection procedure simulated actual grazing as nearly as possible. The plant was grasped close to the ground with the thumb and forefinger and pulled sharply upwards thereby producing the distinctive, squeaky pop which is heard as sheep are grazing. Samples weighed 6-9 g after being dried for 24 hr at 60°C. These samples were then analyzed by the Soil and Feed Testing Laboratory of the Alberta Department of Agriculture for moisture-free content of crude protein, acid detergent fibre (ADF), calcium, and phosphorus. Estimated digestible energy was calculated as $-1.921 \times \%ADF + 124.78$ (E.S. Redshaw, pers. comm.).

iii. Feeding Behaviour--If two individuals were feeding on different plant types, one might reasonably expect to observe a difference in the manner in which they were feeding. Conversely, an observed difference in feeding behaviour is presumptive evidence for a difference in diet. Feeding behaviour as it relates to diet was examined in two manners which can be termed "time correlation analysis" and "aggregation analysis".

If we consider the habitat to contain two or more forage species of differing quality (i.e., palatability, digestibility, mineral content) and that the quality density is greater in some areas than in others, several grazing

strategies (A, B, C) can be envisaged. In Strategy A, the animal specializes on only the very highest quality individual items (species or plant parts) which in an exploited environment, can be expected to have a dispersed distribution. Such a strategy would entail short feed states followed by short walk states and considerable movement. Strategy B is that of a patch specialist wherein the animal moves from one high quality patch to the next and feeds nonselectively within the patch. The strategy would be characterized by long feed states interspersed with long walk states and a reasonably sedentary spatial occupation pattern. Strategy C is a combination of Strategies A and B and entails choosing high quality patches but feeding somewhat selectively within the patch. This strategy would be characterized by moderately long mean feed and walk states both with a high variance and moderate sedentariness.

Time correlation analysis represents an attempt to deduce the feeding strategies of bighorn sheep from the temporal organization of feeding behaviour. The data for these analyses were obtained from "focal animal observations" (J. Altmann 1974) on individuals actively engaged in feeding. Each behavioural state-to-state transition was recorded with the time (accurate to about a second) of transition. An observation period was initiated on a feed state and terminated if the animal laid down, was no longer visible, or after 20 minutes of continuous

observation. In total, 38.9 hrs of such data were recorded comprising 8275 transitions. A feed state was considered as terminated when the animal raised its head to the level of its withers. These data were then analyzed using the time correlation function approach advocated by S.A. Altmann (1974), Slatkin (1975), and Slatkin and Hausfater (1976).

It should be clearly recognized that these analyses of feeding behaviour are not direct evidence for differences or similarities in the nature of forage consumption. It is entirely possible that unrelated factors (nervousness, social behaviour) might influence the pattern of feeding but not the diet itself. These analyses are however a) presumptive evidence for diet differences, b) supplementary to other analyses, and c) suggestive of the behavioural mechanisms proximally resulting in class specific diets.

Aggregation analysis represents an attempt to deduce the feeding strategies from a combination of spatial and temporal aspects of feeding behaviour. The locations of feeding animals recorded in the activity data at five-minute intervals were accumulated over time to generate a grid representing the density in space and time of feeding observations. The development of this final aggregation pattern through time was analyzed using a modification of Iwao and Kuno's (1971) adaptation of Lloyd's index of patchiness (Lloyd 1967). The results suggest the sedentary nature of feeding activity which, as described above, can be

related to the tendency of patch feeders to remain for long periods of time within a relatively restricted area.

iv. Morphological Correlates--Lack (1971) attributes to Huxley (1942) the idea that differences in size of closely related species imply ecological differences. This relationship has become nearly axiomatic in avian studies. Cody (1968) considered bill size to be a better measure of interspecific diet overlap than analysis of stomach contents. Significant differences in mouthpart size between classes of bighorn sheep would be presumptive evidence for diet differences or might allow interpretation of diet differences noted. Data for such analyses were obtained from skull measurements of a large sample of Rocky Mountain and California bighorns (O. c. californiana) from the collections of The Cowan Vertebrate Museum of the University of British Columbia and from unpublished data gathered by D.M. Shackleton, Department of Animal Science, University of British Columbia.

4. The Thermal Niche

To determine if sheep occupying different elevations are subject to different temperature regimes, a vertical series of thermographs was monitored on Unit 4 (Figure 2). Thermographs were mounted 1.5 m above the ground on tripods. They were not enclosed in a Stevenson screen and hence were subjected to radiative heat loss at night and solar insolation during the day. The temperatures were not

true air temperatures. This is not of great importance for the purposes of this study as what is required are only comparative values and because temperatures recorded in the open more nearly reflect the temperatures experienced by sheep.

Stations were maintained and serviced weekly from 1 December 1975 until 12 April 1976 at elevations of 5600 ft (1707 m), 6250 ft (1905 m), 7000 ft (2135 m), 7500 ft (2285 m), and 8000 ft (2440 m). Few useable records were obtained due to the unreliability of the clock-drives in the extreme cold and various mishaps (avalanches, high winds, aggressive rams) which periodically took out one or another of the stations.

IV. RESULTS

A. SPATIAL DISTRIBUTION PATTERNS

Geist and Petocz (1977) demonstrated conclusively that rams and non-rams concentrated on separate portions of the Palliser Range during winter. The discussion will therefore be limited to a very brief description of the spatial occupation patterns observed during the winter of 1975-1976.

Table 2 presents the number of non-rams, small rams (i.e., the classes I and II of Geist 1971), and large rams (i.e., the classes III and IV of Geist 1971) seen on the 12 range units over the entire winter. The spatial distributions of large rams, small rams, and non-rams all differ significantly from each other (large rams vs non-rams, $\chi^2=218.1$, 11 d.f.; large rams vs rams, $\chi^2= 47.9$, 11 d.f.); small rams vs non-rams, 61.5, 11 d.f.). Figure 7 shows the relative deviation from the expected number of observations ($\{\text{observed}-\text{expected}\} \cdot \text{expected}^{-1}$) on any unit if dispersion over the range were uniform. It shows that large rams prefer the more northerly end of the Palliser while non-rams highly prefer the extreme southern end of the range. If Units 1 through 6, 6 through 11, and Unit 12 are respectively aggregated into three combined spatial units and if large rams are combined with small rams, the numbers of rams and non-rams on the North (1-6), South (12), and Middle (7-11) aggregated spatial units form a very nearly

Table 2. Spatial occupation patterns of large rams, small rams, and non-rams (ewes, lambs, yearlings) on the 12 spatial units of the Palliser Range for the entire winter of 1975 to 1976.

		Spatial Unit Number												Total
		1	2	3	4	5	6	7	8	9	10	11	12	
Non-rams	No.	4	14	37	14	57	120	9	55	99	127	53	522	1111
	%	0.4	1.3	3.3	1.3	5.1	10.8	0.8	5.0	8.9	11.4	4.8	47.0	
Small Rams	No.	5	5	7	3	32	51	1	21	22	48	41	54	290
	%	1.7	1.7	2.4	1.0	11.0	17.6	0.3	7.2	7.6	16.6	15.9	18.6	
Large Rams	No.	27	30	84	74	77	166	9	29	57	58	80	61	752
	%	3.6	4.0	11.2	9.8	10.2	22.1	1.2	3.9	7.6	7.7	10.6	8.1	
Total	No.	36	49	128	91	166	337	19	105	178	233	174	637	2153
	%	1.7	2.3	5.9	4.2	7.7	15.7	.9	4.9	8.3	10.8	8.1	29.6	

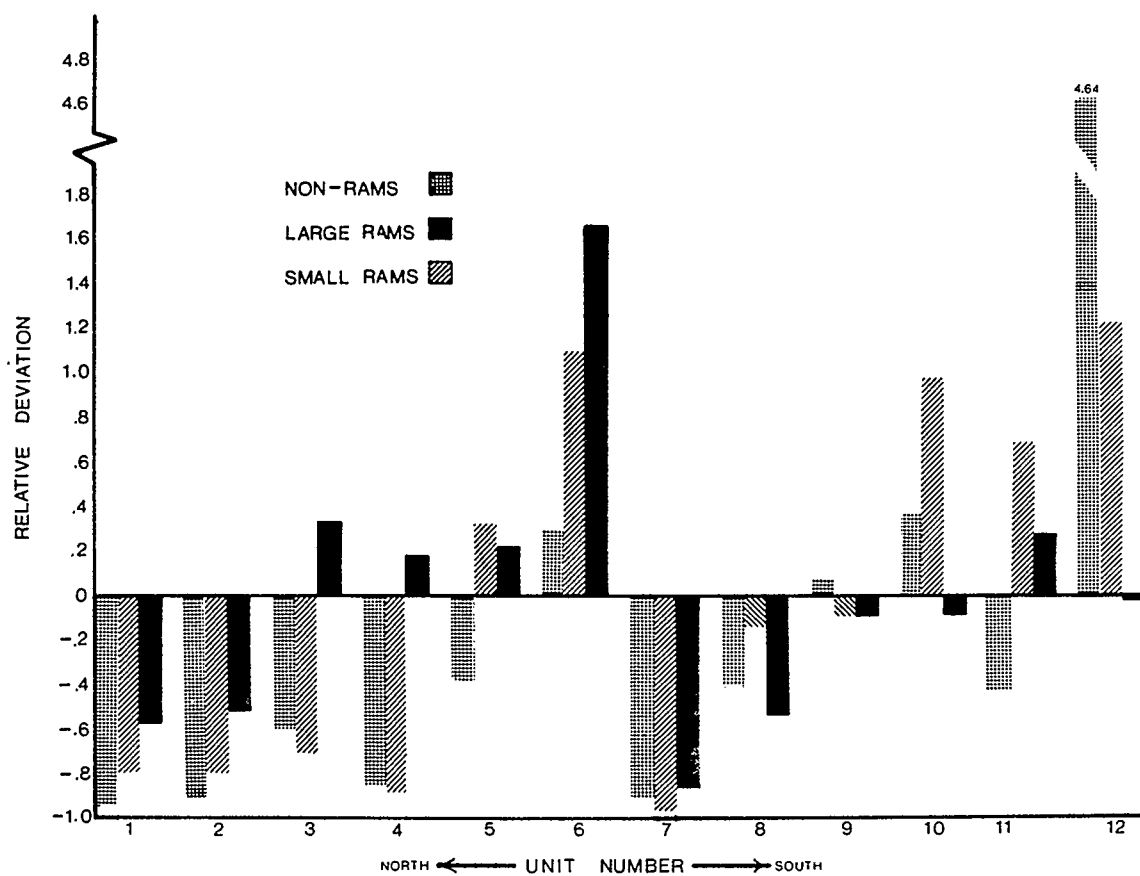


Figure 7. Relative deviation from the expected number of large rams, small rams, and non-rams on the 12 spatial units. Relative deviation expressed in arbitrary units from -1 to +infinity.

inverse relationship (Figure 8). The distributions are significantly different ($\chi^2=137.0$, 2 d.f.). In future discussions, these combined units will be termed "aggregate spatial units" (abbreviated "ASU") and be designated as North (ASU N) South (ASU S), and Middle (ASU M).

Geist and Petocz (1977) determined spatial overlap of sheep classes on the Palliser Range by calculating an overlap value for each unit as the number of the class in lesser abundance divided by the number of the class in greater abundance with the result multiplied by 100. They then determined a total value for the range as the mean of the individual unit overlaps. This method contains the bias that relatively uninhabited spatial units influence the total range overlap as much as do heavily occupied units. A more appropriate measure of spatial overlap is provided by Pianka's (1974) symmetrical formulation of Levins' (1968) niche overlap index:

$$O_{ij} = \frac{\sum_k^n p_{ik} \cdot p_{jk}}{\sum_k^n p_{ik}^2 \cdot \sum_k^n p_{jk}^2}$$

where O_{ij} is the overlap between classes i and j and where p_{ik} is the proportion of class i in the k^{th} spatial unit. Monthly overlap values were calculated as the mean of individual census values. This formulation has the advantage of providing an overlap coefficient of 1.0 when overlap is complete even when the numbers of i are not equal to the numbers of j . Monthly overlap values are depicted in

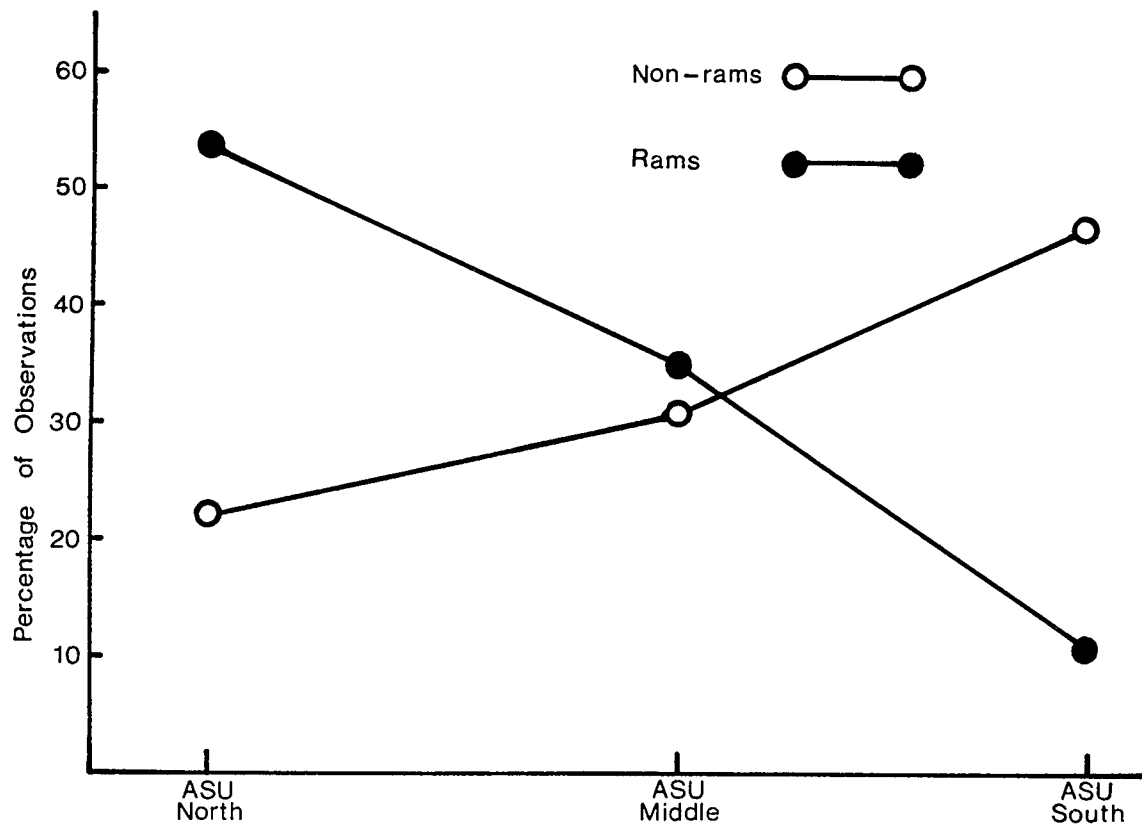


Figure 8. Percentage occupation by rams and non-rams on the north, south, and middle portions of the Palliser Range over the entire winter of 1975-1976.

Figure 9. The figure shows that prior to the rut, large rams joined non-rams and afterwards again became dissociated from them. Following the rut, small rams tended to leave the non-ram groups as well and became associated to a moderate degree with both large rams and non-rams. These findings are essentially the same as those of Geist and Petocz (1977).

Since rams and non-rams occupy different portions of the range and overlap little, the range has in effect been spatially partitioned. It is of some interest to examine whether this division is equal or whether one class is getting more than an equal share of space. One manner of approaching this problem is through the use of the Shannon-Weaver information index of diversity (Poole 1974). In this case, spatial units are substituted for resource states. However, a real problem is encountered in scaling this measure. If the relative areas of the spatial units of the Palliser Range are hypothetically characterized as the x-axis in Figure 10 and the distribution of sheep over the range as the accompanying curves, the calculated breadth would be dependent upon how the range was broken up into spatial units. If each unit represented an equal area, as in the x-axis labelled A, spatial occupation breadth would be equal for rams and non-rams in the example given. If the x-axis is altered to form axis B, where the units in the northern part of the range are small as compared to the

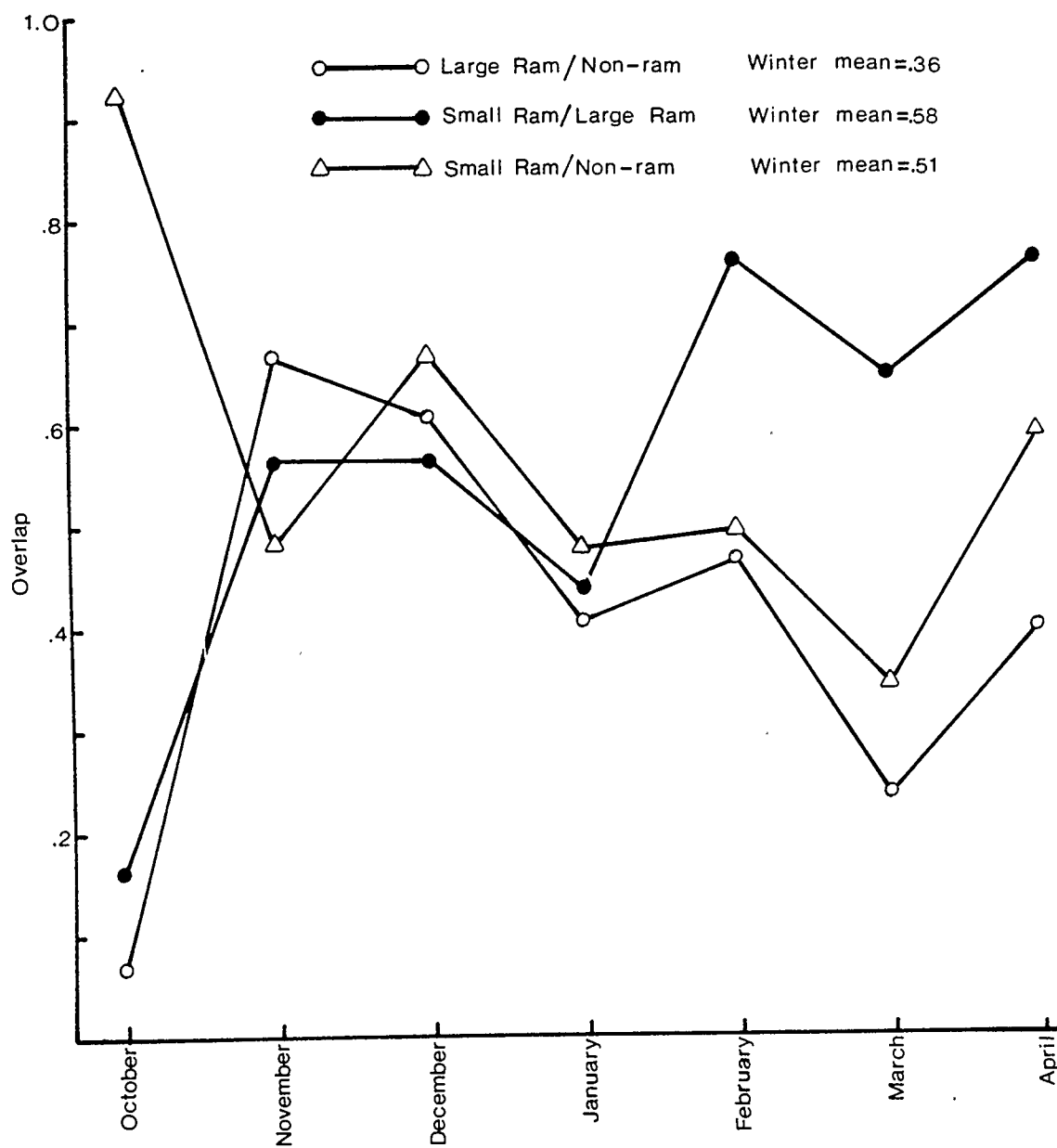
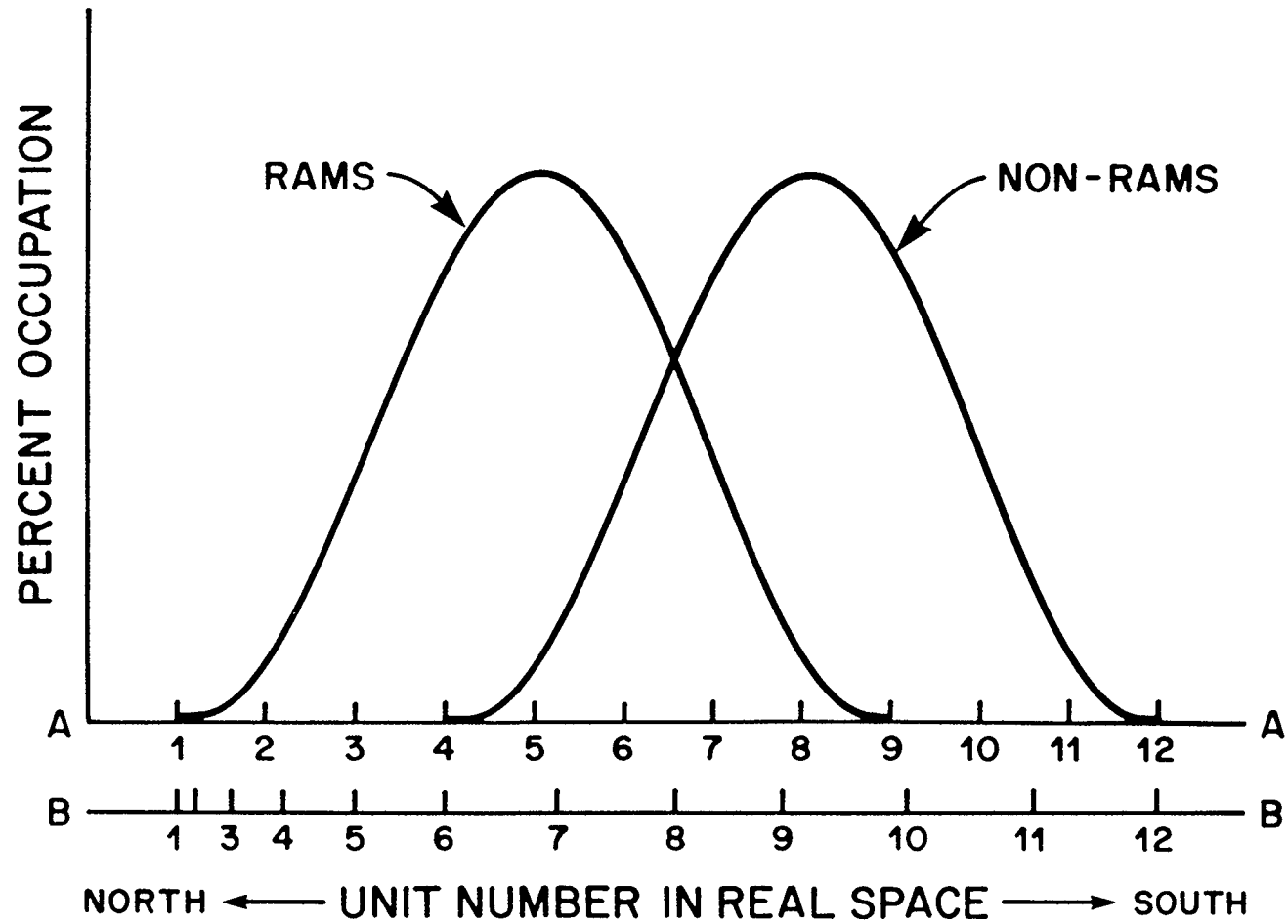


Figure 9. Mean monthly spatial overlap between large rams, small rams, and non-rams.

Figure 10. Hypothetical representation of spatial occupation patterns of rams and non-rams exhibiting the effect of different spatial divisions on determination of occupation breadth.



units in the southern part, rams would extend over 10 units as compared with the non-rams 7 units. This would give the appearance of rams exhibiting a greater occupation breadth than non-rams when they are actually equal in real spatial terms.

One way around this problem is to scale the range into units of equal size. This is, however, not only difficult but there is, as well, no assurance that the sheep actually perceive and react to the spatial aspects of their environment in such a simplistic manner. Colwell and Futuyma (1971) have suggested a scaling factor based on actual occupation patterns of animals present. Translated into terms used herein, their method consists of partitioning the total heterogeneity of the occupation matrix and then determining the contribution of each of the spatial units to the total heterogeneity. This contribution then becomes a weighting factor in the calculation of spatial breadth. Since the factor is determined by the animals' behaviour, it ensures that some arbitrary spatial division has not been imposed. To avoid a circular argument, the weighting factor for a class (non-ram, small ram, large ram) was determined as a function of the other two classes. The relative spatial breadth, homologous to Colwell and Futuyma's "relative niche breadth", was determined as 0.92 for non-rams, 0.97 for small rams, and 0.99 for large rams. This can be interpreted as meaning

that large rams are less spatially restricted on the Palliser Range than are non-rams and small rams.

B. THE STRUCTURAL NICHE

1. Cliff use

Geist and Petocz (1977) showed that rams on the range spend considerably less time in the cliff zone than do non-rams. This conclusion was based on census data without reference to behaviour type. If census data were collected at particular times of day when particular behaviours were more likely to occur, and if cliff use were more commonly associated with certain behaviours, then a potential bias might be entered.

Table 3 presents the numbers of activity data records for rams and non-rams in the cliff and meadow zones grouped according to activity type and portion of the range. It shows that both rams and non-rams spend more time in the cliffs during resting and more time in the meadows during feeding. It also shows that both rams and non-rams occupy the cliff zone to a greater extent in the Middle portion of the range than in the North or in the South. A paired t-test (Sokal and Rohlf 1969 p.331-332) shows that non-rams in general spend a greater proportion of time in the cliffs than do rams regardless of the activity type or the area ($t=3.16$, 8 d.f.).

Because the South, North, and Middle portions of the

Table 3. Number and percentage of observations in the meadow and cliff zones grouped by activity, class, and area.

Area	Non-Rams			Rams		
	No. Meadow Obs.	No. Cliff Obs.	% Cliff Obs.	No. Meadow Obs.	No. Cliff Obs.	% Cliff Obs.
Feeding						
ASU S	2749	551	16.70	569	96	14.43
ASU N	166	1024	86.05	492	529	51.81
ASU M	<u>1231</u>	<u>606</u>	<u>32.99</u>	<u>2714</u>	<u>663</u>	<u>19.63</u>
Total	4146	2181	34.47	3775	1288	25.44
Resting						
ASU S	122	163	57.19	277	71	20.40
ASU N	2	183	98.92	28	423	93.79
ASU M	<u>64</u>	<u>85</u>	<u>57.05</u>	<u>537</u>	<u>521</u>	<u>49.24</u>
Total	188	431	69.63	842	1015	54.66
Other Activities						
ASU S	141	58	29.15	149	48	24.37
ASU N	40	289	87.84	95	203	68.12
ASU M	<u>147</u>	<u>134</u>	<u>47.69</u>	<u>482</u>	<u>219</u>	<u>45.45</u>
Total	328	481	59.46	726	470	39.30
Total						
ASU S	3012	772	20.40	995	215	17.77
ASU N	208	1496	87.79	615	1155	65.25
ASU M	<u>1442</u>	<u>825</u>	<u>36.39</u>	<u>3733</u>	<u>1403</u>	<u>27.32</u>
Total	4662	3093	39.88	5343	2773	34.17

range were occupied differentially by rams and non-rams (Figure 8), the total cliff/meadow occupation figures in Table 3 tell us little about the actual percentages of time spent in the cliff zone by the population as a whole. Such an estimate can be determined by weighting the percentage of cliff occupation on any ASU by the percentage of rams and non-rams utilizing that ASU as calculated from the census data (Figure 8). Table 4 presents these derived figures and shows that, for the entire range, non-ram and ram use of the cliff zone varies by 11% for feeding, 8% for resting, 0% for all other activities and 5% for all activities combined. These figures can be compared with those of Geist and Petocz (1977).

If the data from Geist and Petocz's (1977) Table 3 are reworked, they reveal a total winter (November-April) cliff occupation of 46% for non-rams and 24% for rams. The value for non-rams differs little from that determined in this study (Table 4), however their data indicate a 16% lesser cliff occupation by rams than herein noted.

In summary, non-rams on the Palliser Range spend a larger proportion of their time in the cliff zone than do rams no matter what the area or the activity type. The greatest difference in cliff occupation occurs during feeding periods.

2. Reaction to Snow

The number of feeding observations on standardized

Table 4. Percentage of cliff occupation for rams and non-rams grouped by activity and weighted by percentage occupation of the ASU. This represents an estimate of total cliff occupation throughout the winter on the entire Palliser Range.

	Non-rams	Rams
Feeding	42%	30%
Resting	70%	62%
Other	51%	51%
Total	45%	40%

snow-free or clear areas are presented in Table 5. It shows that on all grids (except Number 2) and on all ASU's, non-rams fed more often on clear areas than did rams. A paired t-test over the 8 grids shows that this intersexual difference is significant ($t=3.04$, 7 d.f.). The relatively low percentage of snow-free feeding noted for both rams and non-rams on Grid 6 (ASU S) arises largely from a single observation period on 3 March 1976 when the largest group of individuals observed all winter fed on a snow-covered area. If the data for this atypical day are removed from the data set, a winter total of snow-free area use can be set at 9 % for non-rams and 82% for rams. Non-rams then would appear to be significantly more careful in choosing feeding areas where snow depth is minimal. Lent and Knutsen (1971) showed the same for musk oxen. Pruitt (1960) suggested that sexual differences in sensitivity to snow was sufficient to explain spatial segregation of the sexes in caribou.

To determine whether snow conditions affect rams and non-rams differently in their use of snow-free areas and the cliff zone, percentage occupation in these areas were correlated with snow parameters of the week previous to data collection. These parameters consisted of mean integrated hardness, mean hardness, mean depth, and depth at Station LD-1. Mean integrated hardness (Table 6) is the mean over all 12 stations of the amount of force required to drive the 60° Ramsonde cone through the entire snowpack. Lent and

Table 5. Use of snow-covered and snow-free areas grouped by class and area.

	Grid No.	Non-Ram		Ram	
		No.	% Clear	No.	% Clear
ASU N	1	79	100.0	87	77.2
	2	293	90.4	538	96.1
	3	475	88.8	1077	77.7
	4	<u>441</u>	<u>89.6</u>	<u>1205</u>	<u>87.5</u>
ASU Total		1288	90.1	2907	88.6
ASU M	5	375	95.2	261	77.3
	7	99	100.0	504	77.2
	8	<u>562</u>	<u>96.6</u>	<u>223</u>	<u>87.4</u>
ASU Total		1036	96.4	988	79.5
ASU S	6	<u>3193</u>	<u>41.9</u>	<u>469</u>	<u>35.6</u>
ASU Total		3193	41.9	364	35.6

Knutson (1971) suggested that integrated hardness represents a useful index of the amount of work expended by a feeding animal as it digs through the snow layer. Mean hardness per cm (Table 6) is the average over all 12 stations of the integrated hardnesses divided by the snow depths.

Therefore, it is a measure of snow hardness per se without reference to snow depth. Mean snow depth (Table 7) is the average over all 12 stations of snow depth in centimeters. Since several of the stations were in snow accumulation areas where sheep never fed, mean depth is a poor indication of snow depth as it relates to feeding conditions. Snow depth at Station LD-1 (Table 7), which was located on a ridge-top on which snow blew clear quickly, represents a better indication of snow depth experienced by sheep during feeding.

Table 8 shows that snow characteristics are poorly correlated with both snow-free area and cliff use in both rams and non-rams and that, with the exception of two cases, the correlations are not significantly different from zero. The two exceptions are that rams tended to occupy snow-free areas significantly less and the cliff zone significantly more during periods of high integrated hardness.

Geist and Petocz (1977) suggest that the greater occupation of cliffs by the non-rams may be as a response to unfavourable snow conditions in the meadow zone. My findings indicate that snow characteristics are certainly

Table 6. Integrated hardness of snow layer in kg-cm. Asterisks (*) indicate less than 100% snow cover.

Station	DATE																			
	12-1	12-8	12-15	12-22	12-29	1-5	1-12	1-19	1-26	2-2	2-9	2-16	2-23	3-1	3-8	3-15	3-22	3-29	4-5	4-12
7500-1	251.6	587.8	285.8	373.4	245.8	245.5	651.0	309.4	235.4	537.2	204.5	225.0	313.0	134.4	226.5	281.4	151.0	92.0	259.8	*
7500-2	45.2	74.3	56.4	69.0	33.4	112.0	138.0	126.0	80.8	*	27.8	2.6	36.4	144.8	223.8	140.6	100.6	187.6	333.2	*
7500-3	577.3	622.1	1000.4	1162.8	1226.7	1436.5	2076.0	1839.2	1888.6	1774.7	1627.4	1902.2	1220.4	1633.2	1686.0	1680.8	1680.8	1983.4	578.2	407.4
7500-4	--	--	231.6	252.2	512.6	180.4	199.4	183.8	210.4	163.0	200.4	196.4	199.4	217.6	198.6	257.6	427.2	222.0	348.6	98.0
LD-1	<31.2	<33.8	*	*	<15.6	<39.0	<28.6	*	*	*	<7.8	<13.0	<54.6	<72.8	<46.8	<26.0	<26.0	<13	*	*
LD-2	<26.0	48.8	<39.2	<18.2	<15.6	<30.6	114.6	<18.2	68.2	<5.2	<15.6	<26.0	<72.8	<80.6	<78.0	<33.8	*	*	*	*
LD-3	<40.7	178.2	517.4	399.5	376.0	803.4	513.6	594.0	358.0	312.4	477.4	276.8	610.6	465.8	751.0	410.6	340.2	455.2	333.8	116.8
M-1	--	156.4	308.3	?	473.4	1716.0	959.2	1051.0	832.2	682.8	677.6	608.0	563.6	767.8	1100.1	760.0	513.2	799.6	539.2	174.4
M-2	<51.5	196.9	352.9	379.4	378.6	405.6	651.4	1023.6	483.4	569.0	645.2	565.4	824.9	697.0	819.4	1062.6	528.8	91.6	671.0	174.4
M-3	--	<46.8	<39.0	<32.0	<18.2	<39.0	54.7	25.6	140.8	*	<15.6	<15.6	<52.0	<72.8	<75.4	<62.4	<46.8	<46.8	129.0	*
M-4	--	<70.2	<85.8	<54.6	112.0	<96.2	<80.6	114.6	<39.0	<13.0	<20.8	<20.8	<67.6	<98.8	<96.2	100.6	93.2	<78	112.8	*
Stump	<31.2	<75.4	<80.6	<71.2	<46.8	<96.2	119.2	<75.4	77.2	<36.4	51.2	<44.2	<80.6	<111.8	<91.0	<91.0	<72.6	<72.6	155.0	*
Mean	131.8	190.1	190.7	281.2	309.6	433.4	465.5	487.4	401.2	454.6	330.9	324.7	341.7	374.8	449.3	409.0	331.7	336.8	371.7	80.9
Hardness/ cm	6.8	5.1	4.8	8.4	9.2	8.0	8.8	11.5	9.4	12.4	9.3	8.9	6.9	6.2	8.0	5.6	5.1	5.3	8.5	4.0

Table 7. Snow cover in centimeters. Snowfall data refer to previous week at Banff townsite (elevation 1418 m). (Courtesy of the Banff Weather Office)

Station	DATE																			
	12-1	12-8	12-15	12-22	12-29	1-5	1-12	1-19	1-26	2-2	2-9	2-16	2-23	3-1	3-8	3-15	3-22	3-29	4-5	4-12
7500-1	16	53	39	40	33	40	35	19	29	22	17	25	30	44	45	39	35	20	23	0
7500-2	17	17	18	15	9	20	30	10	8	0	3	7	14	48	35	31	31	26	32	0
7500-3	51	74	89	75	72	122	113	110	111	103	96	98	104	108	108	112	110	109	108	99
7500-4	--	--	43	43	51	69	69	58	65	55	54	59	69	76	68	76	72	70	68	30
LD-1	12	13	0	0	6	15	11	0	0	0	3	5	21	28	18	10	10	5	0	0
LD-2	10	15	15	7	6	12	21	7	7	2	6	10	28	31	30	10	0	0	0	0
LD-3	16	53	67	61	60	95	86	90	83	76	71	68	81	83	85	81	77	77	63	28
M-1	--	49	52	?	59	106	92	84	85	79	75	79	88	103	93	99	82	96	92	42
M-2	20	61	70	69	61	79	89	85	82	83	75	80	84	95	88	100	89	88	86	42
M-3	--	18	15	12	7	15	19	6	8	0	6	6	20	28	29	24	18	18	15	0
M-4	--	27	33	21	20	37	31	12	15	5	8	8	26	38	37	31	30	30	28	0
Stump	12	29	31	27	18	37	42	29	22	14	12	17	31	43	35	35	28	28	25	0
Mean	19.3	37.2	39.4	33.6	33.5	53.9	53.2	42.5	42.9	36.6	35.5	38.5	49.7	60.4	55.9	54.0	48.5	47.3	45.0	20.1
Snowfall	2.9	43.4	35.3	0.3	0.8	24.2	9.1	1.0	2.3	0.0	3.6	3.2	.6	29.5	tr	21.9	0.8	5.4	1.5	0.0

Table 8. Snow-free area and cliff zone use correlated with snow characteristics for rams and non-rams.

	Mean Integrated <u>Hardness</u>	Mean Hardness <u>per cm</u>	Mean Snow Depth	Snow depth at LD-1
Non-Rams (N = 43)				
Snow-free Area Use	r = -0.025 t = -0.159	r = -0.035 t = -0.227	r = -0.126 t = -0.814	r = -0.164 t = -0.064
Cliff Use	r = +0.089 t = +0.572	r = -0.165 t = -1.088	r = -0.004 t = -0.026	r = -0.249 t = -1.648
Rams (N = 53)				
Snow-free Area Use	r = -0.333 t = -2.527*	r = +0.045 t = +0.322	r = -1.978 t = -1.441	r = -0.069 t = -0.492
Cliff Use	r = +0.238 t = +1.751*	r = -0.195 t = -0.417	r = +0.152 t = +1.099	r = -0.177 t = -1.286

* indicates statistically significant difference

not a singular causal factor in cliff occupation. The factors influencing cliff and snow-free area useage would appear to be complex and only partially, if at all, related to snow conditions.

3. Elevation of Occupation

Geist (1971) demonstrated that the Palliser Range experiences a temperature inversion and suggested that occupation of the warmer elevations might entail profound bioenergetic benefits to sheep. As a first step toward determining whether rams and non-rams benefit differentially from the inversion zone, the elevations favoured by rams and non-rams were determined from the activity data.

Figure 11 presents elevation occupation curves for rams and non-rams on the three ASU's. Figure 11 shows no striking differences between rams and non-rams in elevation occupation on any of the three ASU's. It does show, however, that both rams and non-rams on ASU S occupy much lower elevations than on the other two ASU's as would be expected due to the altogether lower elevation of ASU S as it drops off into the Stoney Creek valley (Figure 2).

Since rams and non-rams differentially occupy the ASU's (Section IV.A.), an indication of their elevation occupation patterns of the range as a whole can be gained by determining the mean percentage occupation of each elevation zone weighted by the percentage of total time spent on that ASU (Figure 8). Figure 12 presents the results of such a

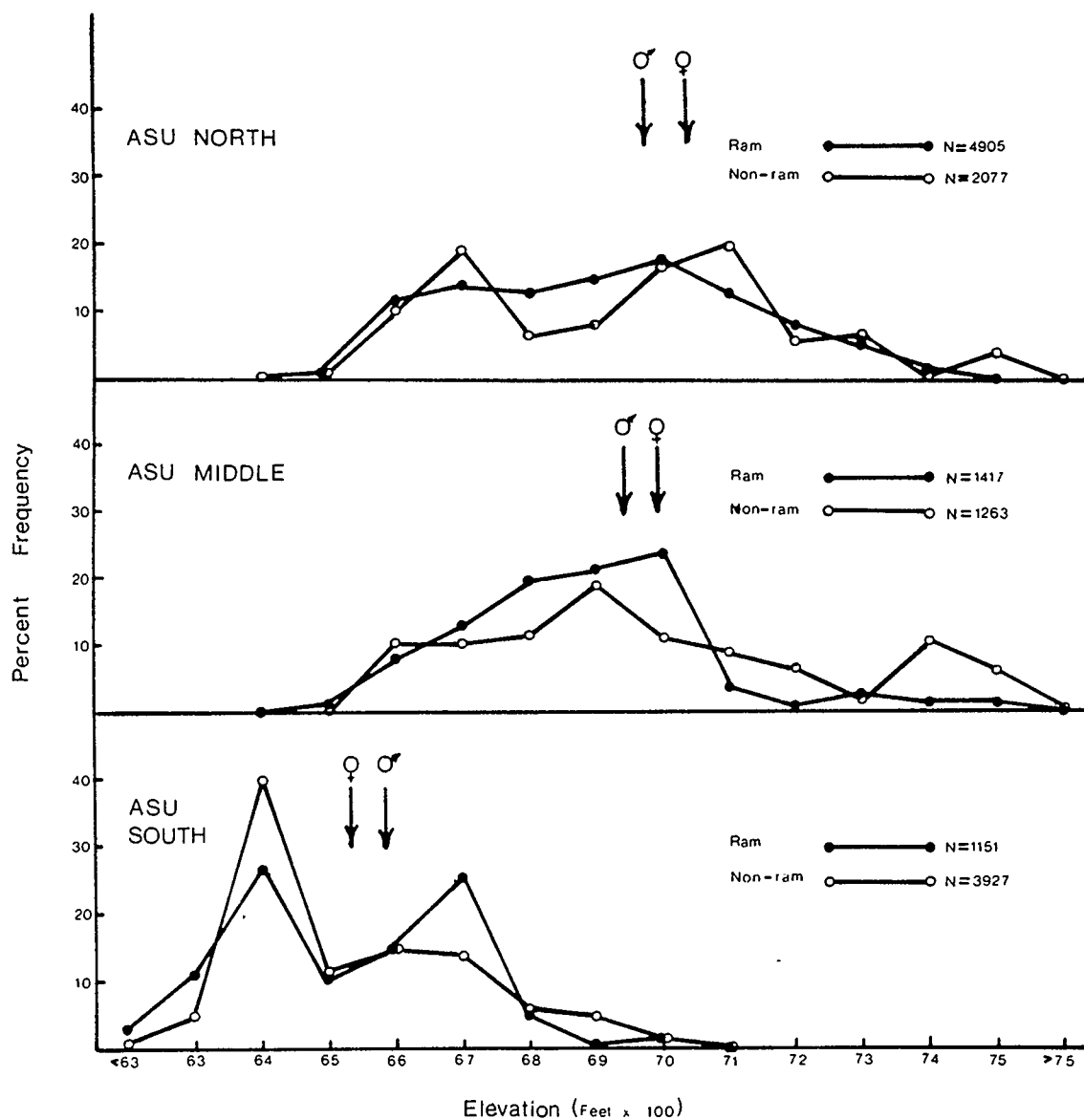


Figure 11. Percent frequency distributions of occupation of elevation zones on the three ASU's by rams and non-rams. Vertical arrows represent medians.

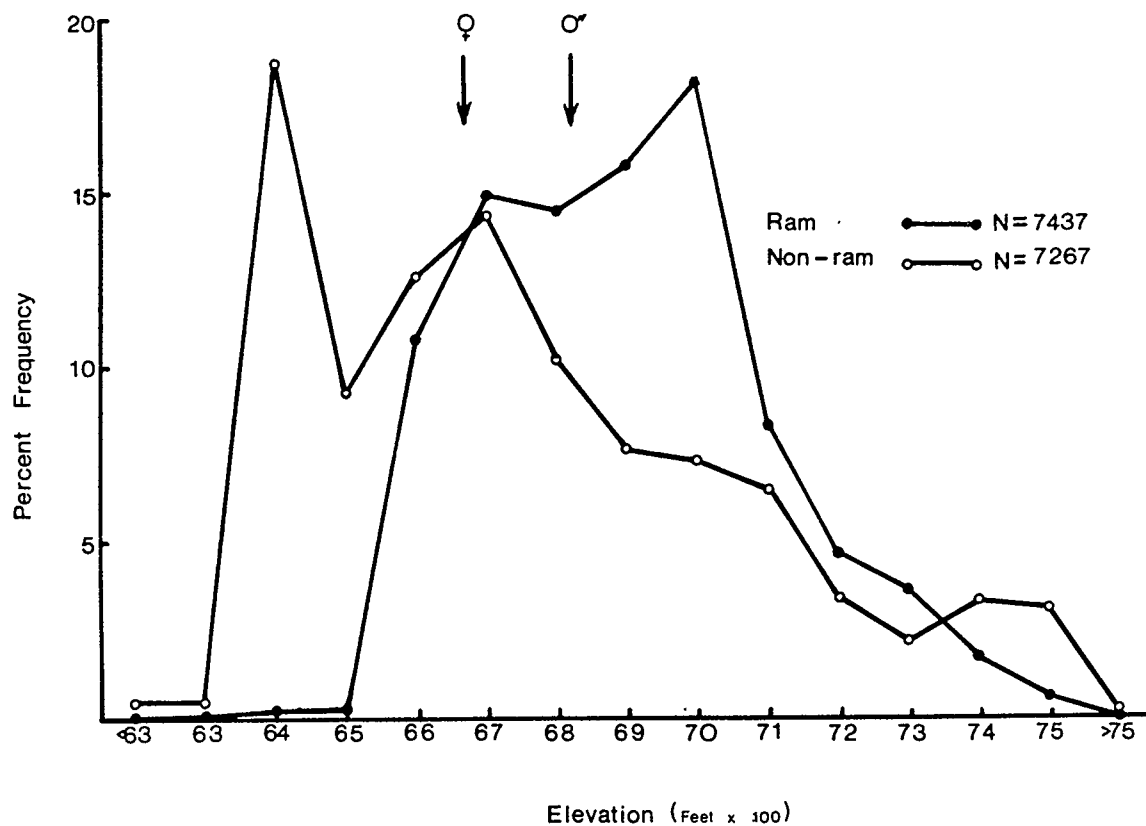


Figure 12. Percent frequency distribution of occupation of elevation zones by rams and non-rams over the entire Palliser Range as determined by weighting the occupation of elevation zones by occupation of the spatial units.

calculation and indicates that rams as a whole tend to occupy higher elevations than do non-rams. The calculated median occupation elevation for rams is about 6820 ft (2079 m) whereas for non-rams it is about 6650 ft (2027 m); a difference of nearly 200 vertical ft (60 m).

4. Use of Plant Communities

The meadow zone of the Palliser Range is a very uniform Elymus innovatus-Festuca Grassland (Stelfox 1976). The dominant species are Elymus innovatus, Festuca scabrella, Bromus pumpellianus, Poa rupicola, Cerastium arvense, Hedysarum sulphurescens, and Solidago multiradiata (Stelfox 1976). Tables 9 and 10 present the frequencies and canopy covers of the plant taxa on the six ram and the six non-ram feeding areas as determined by this study. Percent cover for graminoids was between 5-32%, for forbs between 6-30%, and for shrubs between a trace and 22%.

To determine if there were complexes of taxa which tended to occur together, associations were sought through ordination using principle-component analysis based on correlations between genera (Q-type analysis in Pielou 1977). Three factors were calculated using the Statistical Package for the Social Sciences (SPSS) factor analysis library programme (Kim 1975).

Table 11 presents the factor matrix and the proportion of the total variance accounted for by the three factor values. The three factors account for most of the variance

Table 9. Percentage frequency, canopy coverage, and composition of major plant taxa on favoured ram feeding areas. All values are rounded to the nearest 1%. Plus (+) symbols refer to values of 0.5% or less. Summations of percentage frequencies represent only an index of relative graminoid, forb, and shrub frequencies.

ASU	North	North	South	South	Middle	Middle
<u>Dryas</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0
<u>Achillea</u> sp.	70-1-1	40-+-+	83-1-2	70-1-3	80-2-4	80-+-1
<u>Cerastium</u> sp.	73-2-3	83-1-2	97-3-6	93-1-1	80-2-4	63-1-1
<u>Agoseris</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	7-+-+
<u>Cirsium</u> sp.	23-3-4	0-0-0	3-+-+	3-1-1	0-0-0	0-0-0
<u>Fragaria</u> sp.	77-6-8	77-4-10	3-+-1	0-0-0	87-3-6	7-+-1
<u>Hedysarum</u> sp.	90-12-17	83-6-13	37-3-6	13-1-3	60-5-10	90-11-19
<u>Penstemon</u> sp.	13-+-+	57-1-3	7-+-+	0-0-0	0-0-0	13-+-+
<u>Potentilla</u> sp.	7-+-+	0-0-0	0-0-0	27-1-2	0-0-0	0-0-0
<u>Solidago</u> sp.	0-0-0	7-+-+	3-+-1	0-0-0	0-0-0	3-+-+
<u>Oxytropis</u> sp.	0-0-0	7-+-+	50-4-7	97-6-14	3-+-+	10-+-+
<u>Artemisia</u> sp.	0-0-0	3-+-+	0-0-0	3-+-1	0-0-0	10-1-1
<u>Antennaria</u> sp.	3-+-+	0-0-0	13-1-1	13-+-+	7-+-+	0-0-0
<u>Campanula</u> sp.	7-+-+	10-+-+	77-1-2	40-+-1	23-+-+	0-0-0
<u>Alium</u> sp.	0-0-0	3-+-+	0-0-0	10-+-+	0-0-0	0-0-0
<u>Saxifraga</u> sp.	0-0-0	27-1-1	0-0-0	0-0-0	0-0-0	0-0-0
Others	77-6-8	87-5-12	93-6-12	70-3-8	90-10-19	90-8-15
Total Forbs	440-30-41	403-18-41	497-20-40	440-13-33	450-22-43	373-22-39
<u>Juniperus</u> sp.	0-0-0	3-1-1	0-0-0	47-8-21	0-0-0	0-0-0
<u>Arctostaphylos</u> sp.	50-10-13	63-10-23	0-0-0	0-0-0	50-6-11	20-3-4
<u>Salix</u> sp.	0-0-0	3-+-+	0-0-0	0-0-0	0-0-0	0-0-0
<u>Potentilla</u> sp.	3-+-+	0-0-0	3-+-+	13-1-3	0-0-0	0-0-0
<u>Rosa</u> sp.	33-2-2	27-2-5	0-0-0	0-0-0	0-0-0	27-2-3
<u>Shepherdia</u> sp.	0-0-0	3-+-+	0-0-0	0-0-0	0-0-0	3-+-+
Total Shrubs	87-11-15	97-13-30	3-+-+	60-10-24	50-6-11	50-5-8

Table 9--Continued

ASU	North	North	South	South	Middle	Middle
Location	4/RMI8	3/RML35	6/LMF24	6/RMC34	7/BMH11	8/BLI3
% Bare	8 ^b	13 ^b	10 ^b	27 ^b	8 ^b	9 ^b
% Scree & rock	1	15	17	29	6	4
% Litter	17	25	24	4	24	31
% Non-vascular	1	4	1	1	1	1
% Vascular	73	44	49	40	52	56
Slope	35 ^o	35 ^o	40 ^o	30 ^o	30 ^o	30 ^o
Elevation (ft)	6700	6800	6400	6700	6700	6600
Aspect	WSW	NW	WSW	SW	WSW	WSW
Taxa						
<u>Agropyron</u> sp.	0 ^a -0 ^b -0 ^c	0 ^a -0 ^b -0 ^c	10 ^a -+ ^b -1 ^c	0 ^a -0 ^b -0 ^c	3 ^a -+ ^b -+ ^c	0 ^a -0 ^b -0 ^c
<u>Bromus</u> sp.	13-1-1	0-0-0	77-5-10	87-4-9	97+4-7	87-9-15
<u>Carex</u> sp.	0-0-0	7-+-+	3-+-+	67-4-11	60-4-8	3-+-+
<u>Danthonia</u> sp.	0-0-0	0-0-0	0-0-0	3-+-+	17-1-2	0-0-0
<u>Elymus</u> sp.	97-10-14	100-6-15	100-14-29	93-3-8	80-5-9	97-11-19
<u>Festuca</u> sp.	100-17-23	87-4-9	7-+-+	0-0-0	93-9-17	67-9-16
<u>Koeleria</u> sp.	50-2-3	33-+-1	90-4-8	77-2-6	3-1-1	7-+-+
<u>Trisetum</u> sp.	17-+-+	0-0-0	3-+-+	0-0-0	3-+-+	10-+-1
<u>Juncus</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	3-+-+	0-0-0
<u>Poa</u> sp.	53-2-2	80-2-5	17-5-11	80-2-6	50-1	57-2-3
<u>Deschampsia</u> sp.	0-0-0	0-0-0	0-0-0	60-2-4	0-0-0	0-0-0
Total Graminoids	330-32-44	307-13-29	387-29-60	467-17-43	440-24-47	327-30-53

(a) percentage of quadrats in which taxon occurred.

(b) mean percentage cover. (c) percentage of total vegetative cover.

Table 10. Percentage frequency, canopy coverage, and composition of major plant taxa on favoured non-ram feeding areas. All values are rounded to the nearest 1%. Plus (+) symbols refer to values of 0.5% or less. Summation of percentage frequencies represent only an index of relative graminoid, forb, and shrub frequencies.

Taxa	North	North	South	South	Middle	Middle
<u>Dryas</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	17-2-10	0-0-0
<u>Achillea</u> sp.	53-1-2	65-2-4	83-1-2	70-1-3	10-+-+	57-+-1
<u>Cerastium</u> sp.	93-2-5	85-1-2	97-3-6	93-1-1	47-+-1	37-+-+
<u>Agoseris</u> sp.	3-+-1	5-+-+	10-1-1	0-0-0	0-0-0	1-+-+
<u>Cirsium</u> sp.	0-0-0	0-0-0	3-+-+	3-1-1	0-0-0	0-0-0
<u>Fragaria</u> sp.	0-0-0	30-2-2	3-+-1	0-0-0	0-0-0	87-4-7
<u>Hedysarum</u> sp.	17-3-6	65-7-12	37-3-6	13-1-3	17-1-4	93-12-18
<u>Penitemon</u> sp.	0-0-0	5-+-+	7-+-+	0-0-0	0-0-0	60-1-2
<u>Potentilla</u> sp.	7-+-1	0-0-0	2-+-1	27-1-2	0-0-0	27-+-+
<u>Solidago</u> sp.	0-0-0	5-+-+	3-+-1	0-0-0	0-0-0	7-+-+
<u>Oxytropis</u> sp.	90-12-28	5-+-+	50-4-7	97-6-14	17-1-2	0-0-0
<u>Artemisia</u> sp.	13-1-2	0-0-0	0-0-0	3-+-1	0-0-0	3-+-+
<u>Antennaria</u> sp.	0-0-0	0-0-0	13-1-1	13-+-1	0-0-0	23-+-+
<u>Campanula</u> sp.	0-0-0	20-+-+	77-1-2	40-+-1	23-+-1	3-+-+
<u>Alium</u> sp.	0-0-0	0-0-0	0-0-0	10-+-+	7-1-2	27-1-1
<u>Saxifraga</u> sp.	0-0-0	15-1-1	0-0-0	0-0-0	27-1-3	0-0-0
Others	90-7-15	100-8-13	93-6-12	70-3-8	30-1-3	93-6-10
Total Forbs	367-26-59	400-20-34	497-20-40	440-13-33	193-6-27	520-26-18
<u>Juniperus</u> sp.	0-0-0	0-0-0	0-0-0	47-8-21	13-2-7	3-1-1
<u>Arctostaphylos</u> sp.	0-0-0	10-2-2	0-0-0	0-0-0	37-7-29	80-19-28
<u>Salix</u> sp.	0-0-0	5-3-4	0-0-0	0-0-0	0-0-0	0-0-0
<u>Potentilla</u> sp.	3-+-+	5-1-2	3-+-+	3-1-3	43-4-17	0-0-0
<u>Rosa</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	37-2-4
<u>Sheperdia</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0
Total shrubs	3-+-+	20-5-8	3-+-+	60-10-24	21-13-54	120-22-33

Table 10--Continued

ASU	North	North	South	South	Middle	Middle
Location	4/LMJ11	3/LMI33	6/LMF24	6/RMC34	7/RMJ33	8/BRH4
% Bare	18 ^b	7 ^b	10 ^b	27 ^b	13 ^b	2 ^b
% Scree & rock	29	15	17	29	57	9
% Litter	3	16	24	4	6	18
% Non-vascular	7	2	1	1	1	6
% Vascular	43	60	49	40	24	66
Slope	40 ^o	--	40 ^o	30 ^o	45 ^o	30 ^o
Elevation (ft.)	6600	7100	6400	6700	6900	6700
Aspect	NW	W	WSW	SW	WSW	WSW
Taxa						
<u>Agropyron</u> sp.	50 ^{a-3b-6c}	0 ^{a-0b-0c}	10 ^{a-+b-1c}	0 ^{a-0b-0c}	17 ^{a-+b-1c}	0 ^{a-0b-0c}
<u>Bromus</u> sp.	20-1-2	45-1-2	77-5-10	87-4-9	30-1-2	17-+-1
<u>Carex</u> sp.	0-0-0	5-+-+	3-+-+	67-4-11	50-1-6	3-+-+
<u>Danthonia</u> sp.	0-0-0	0-0-0	0-0-0	3-+-+	0-0-0	0-0-0
<u>Elymus</u> sp.	57-3-7	100-19-31	100-14-29	93-3-8	23-1-4	100-11-17
<u>Festuca</u> sp.	90-6-14	90-14-22	7-+-+	0-0-0	3-+-1	90-7-10
<u>Koeleria</u> sp.	93-3-8	0-0-0	90-4-8	77-2-6	7-+-+	13-+-+
<u>Trisetum</u> sp.	0-0-0	0-0-0	3-+-+	0-0-0	0-0-0	0-0-0
<u>Juncus</u> sp.	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0
<u>Poa</u> sp.	50-2-3	65-2-2	97-5-11	80-2-6	37-1-3	47-1-1
<u>Deschampsia</u> sp.	7-+-+	0-0-0	0-0-0	60-2-4	33-1-3	0-0-0
Total Graminoids	367-17-40	305-35-38	387-29-60	467-17-43	200-5-20	270-19-28

(a) percentage of quadrats in which taxon occurred.

(b) mean percentage cover. (c) percentage of total vegetative cover.

Table 11. Factor matrix for principle-component analysis. Tabulated values indicate the proportion of variance accounted for by each factor.

Genus	Factor 1	Factor 2	Factor 3	Proportion of Explained Variance
<u>Bromus</u>	.464	.061	-.012	.219
<u>Carex</u>	-.125	-.393	.765	.756
<u>Elymus</u>	.158	.772	-.164	.648
<u>Festura</u>	-.360	.811	.128	.804
<u>Koeleria</u>	.805	-.001	.179	.681
<u>Poa</u>	.868	.190	-.200	.829
<u>Achillea</u>	.211	.421	.864	.968
<u>Cerastium</u>	.737	.417	.273	.791
<u>Fragaria</u>	-.627	.546	-.060	.694
<u>Hedysarum</u>	-.433	.706	-.427	.868
<u>Oxytropis</u>	.603	-.396	.184	.555
Other Forbs	.290	.738	.143	.647
<u>Arctostaphylos</u>	.771	.162	-.406	.785
<u>Juniperus</u>	-.073	-.734	.252	.608
<u>Rosa</u>	-.457	.338	-.692	.802

in all cases except that of Bromus. Figure 13 plots the factor values in 3-dimensional factor space. To make the spatial relations more obvious, Table 12 presents the distance in 3-space between each combination of two points as calculated by the Pythagorean Theorem. Utilizing a distance of 0.70 units as an arbitrary division between association and disassociation, lines are drawn in Figure 13 joining together the associated taxa. Three unambiguous groupings are present; one comprised of Juniperus and Carex, one containing Oxytropis, Koeleria, Poa, and Bromus, and the last comprised of Festuca, Rosa, Hedysarum, Fragaria, and Arctostaphylos. The ubiquitous taxa (Cerastium, Achillea, Other Forbs, and Elymus) form a bridge between the latter two groups but are fully integrated into neither.

Environmental parameters were not quantified but subjectively the three groupings have rather clear ecological relationships. The Festuca type is associated with high biomass, sheltered conditions indicating winter snow cover, good soil formation, and mesic conditions. By contrast, the Koeleria type is associated with exposed slopes, much scree and little soil, low biomass, and more xeric conditions. The Carex type is similar to the Koeleria type but on rockier, more exposed locations.

Smoliak (1974) discovered that under conditions of heavy grazing by domestic sheep, Festuca decreased or disappeared while Koeleria increased in abundance. Stelfox

(1976) found overgrazed bighorn sheep ranges to carry more Koeleria and less Festuca than more lightly grazed areas. On the Palliser Range, then, the Festuca type might well be indicative of light grazing and the Koeleria type of over-grazing. The above-mentioned environmental correlates of the Koeleria type (little soil, low biomass, xeric conditions) may be a result of overgrazing as well.

To determine whether there are differences in the vegetation of the areas favoured for feeding by rams and non-rams on the three ASU's, a two-way multivariate analysis of variance was performed using the SPSS MANOVA library programme (Cohen and Burns 1977). Data consisting of percent cover for the 15 most common taxa were arc-sin transformed and entered quadrat-wise to form 360 separate cover vectors. Table 13 presents the mean covers of the 15 taxa grouped by area and by sex. Wilks' lambda criterion (Morrison 1976) (with parameters $S=2$, $M=6$, $N=168.5$) indicates that there are significant sex ($\Lambda=0.859$, $p=0.0001$), area ($\Lambda=0.241$, $p=0.0001$), and area-sex interaction ($\Lambda=0.545$, $p=0.0001$) effects. We can conclude then that rams and non-rams on any ASU choose feeding areas comprised of different proportions of forage on offer, that preferred feeding areas differ on various portions of the range, and that these two main effects interact.

A caveat must be added here. Cochran's C test (Dixon and Massey 1957) shows that many of the variances utilized

Figure 13. Representation of the spatial relations of plant taxa in 3-dimensional factor space as determined by principle component analysis.

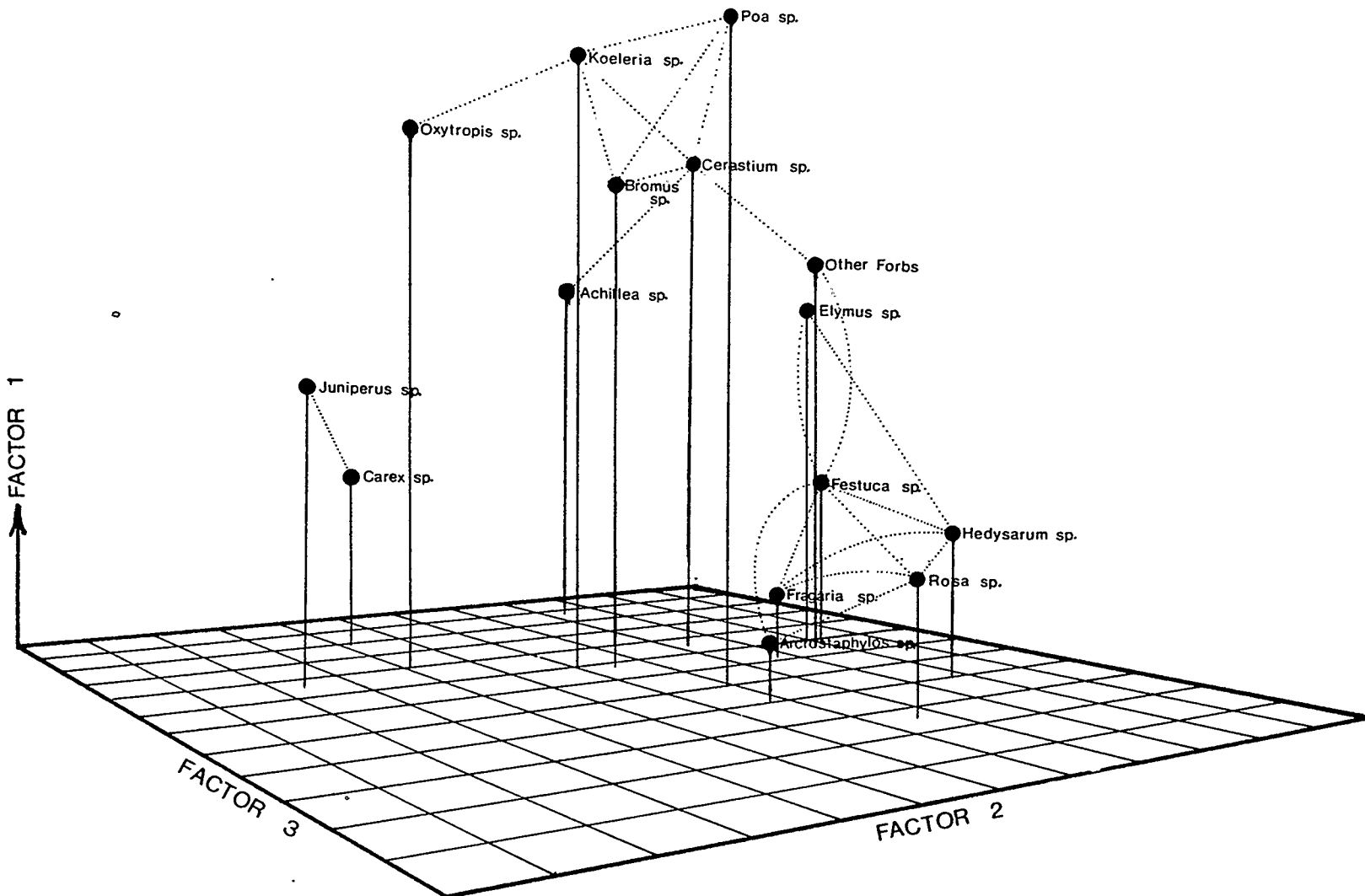


Table 12. Distance in arbitrary units separating species points in 3-dimensional factor space.

	<u>Carex</u>	<u>Elymus</u>	<u>Festuca</u>	<u>Koeleria</u>	<u>Poa</u>	<u>Achillea</u>	<u>Cerastium</u>	<u>Fragaria</u>	<u>Hedysarum</u>	<u>Oxytropis</u>	Other Forbs	<u>Arctostaphylos</u>	<u>Juniperus</u>	<u>Rosa</u>
<u>Bromus</u>	1.08	0.79	1.12	0.40	0.46	0.98	0.53	1.20	1.18	0.52	0.72	1.30	1.00	1.18
<u>Carex</u>		1.52	1.38	1.17	1.50	0.88	1.28	1.35	1.65	0.93	1.36	1.45	0.62	1.66
<u>Elymus</u>			0.60	1.07	0.90	1.06	0.81	0.82	0.65	1.32	0.34	1.14	1.58	0.92
<u>Festuca</u>				1.42	1.42	1.01	1.18	0.42	0.57	1.55	0.65	0.94	1.58	0.95
<u>Koeleria</u>					0.43	1.00	0.43	1.55	1.55	0.44	0.90	1.69	1.15	1.57
<u>Poa</u>						1.27	0.54	1.54	1.42	0.75	0.87	1.65	1.39	1.42
<u>Achillea</u>							0.28	1.25	1.47	1.13	0.79	1.63	1.34	1.70
<u>Cerastium</u>								1.41	1.39	0.83	0.57	1.67	1.41	1.54
<u>Fragaria</u>									0.45	1.57	0.96	0.54	1.43	0.69
<u>Hedysarum</u>										1.63	0.92	0.64	1.63	0.45
<u>Oxytropis</u>											1.18	1.60	0.76	1.56
Other Forbs												1.32	1.52	1.19
<u>Arctostaphylos</u>													1.31	1.31
<u>Juniperus</u>														1.48

in the MANOVA programme are not homogeneous. Homogeneity of the variances is a fundamental assumption in analysis of variance and, strictly speaking, the test should not be performed. In view of the fact that the calculated significances of both main effects and the interaction effect are 500 times higher than the 5% level previously defined as the acceptable level of probability (Section III.B.), I suggest that these very general conclusions can be accepted with caution.

Determination of which particular taxa differ between areas and between sexes was carried out by univariate analysis of variance. Again, not all samples exhibit equal variances. Cochran's C test is extremely restrictive when the sample sizes are large. In the case of the between-sex differences, Cochran's C test requires that the sample variances be identical to five decimal places (Appendix A-17 in Dixon and Massey 1957). Clearly, this could rarely occur in practice. The taxa marked by an asterisk (*) in Table 13 exhibit significant differences. It can be seen that few purely sex effects exist. Rams are seen to utilize areas containing more Bromus, Festuca, Cerastium, Hedysarum, and Rosa than do non-rams. Similarly, it can be seen that in comparison to ASU S, ASU N feeding areas contain more Festuca, Fragaria, Hedysarum, Arctostaphylos, and Rosa and less Bromus, Carex, Koeleria, Poa, Oxytropis, and Juniperus. These taxa fall out quite clearly into the groupings

Table 13. Mean cover ($\pm$ SD) of the 15 most common taxa grouped by area and by class. Expressed in standard numerical form; statistical tests were based on arc-sin transformed data. Asterisks (*) indicate significant differences.

	ASU						Sex					
	N		M		S		F		M			
<u>Bromus</u>	.63 $\pm$	1.69	3.29 $\pm$	5.29	4.67 $\pm$	4.75	*a	2.03 $\pm$	3.62	3.69 $\pm$	5.16	*b *c
<u>Carex</u>	.04 $\pm$	.45	1.41 $\pm$	4.06	3.23 $\pm$	8.63	*	1.33 $\pm$	5.37	1.80 $\pm$	5.92	
<u>Elymus</u>	9.54 $\pm$	9.96	6.79 $\pm$	7.24	10.08 $\pm$	12.95	*	9.00 $\pm$	11.52	8.61 $\pm$	9.14	
<u>Festuca</u>	10.21 $\pm$	9.41	6.16 $\pm$	9.54	.92 $\pm$	6.45	*	4.72 $\pm$	7.86	6.81 $\pm$	10.59	* *
<u>Koeleria</u>	1.45 $\pm$	2.70	.21 $\pm$	1.00	2.91 $\pm$	3.47	*	1.55 $\pm$	2.76	1.50 $\pm$	2.89	
<u>Poa</u>	1.70 $\pm$	2.78	.83 $\pm$	2.18	4.58 $\pm$	6.94	*	2.25 $\pm$	4.76	2.50 $\pm$	4.77	
<u>Achillea</u>	1.04 $\pm$	2.12	.63 $\pm$	2.00	1.75 $\pm$	6.60		1.17 $\pm$	4.16	1.11 $\pm$	4.21	*
<u>Cerastium</u>	1.41 $\pm$	2.37	.75 $\pm$	2.01	1.67 $\pm$	2.70	*	1.14 $\pm$	2.31	1.42 $\pm$	2.49	* *
<u>Fragaria</u>	2.88 $\pm$	4.27	2.00 $\pm$	3.91	1.08 $\pm$	6.55	*	1.37 $\pm$	4.77	2.61 $\pm$	5.32	* *
<u>Hedysarum</u>	6.87 $\pm$	7.61	7.08 $\pm$	7.29	2.08 $\pm$	4.13	*	4.47 $\pm$	6.41	6.22 $\pm$	7.30	* *
<u>Oxytropis</u>	3.00 $\pm$	6.50	.25 $\pm$	1.26	4.41 $\pm$	5.51	*	3.58 $\pm$	6.21	1.52 $\pm$	3.81	*
Other Forbs	7.92 $\pm$	5.18	8.12 $\pm$	6.21	7.58 $\pm$	7.30		7.47 $\pm$	6.16	8.28 $\pm$	6.39	*
<u>Arctostaphylos</u>	5.38 $\pm$	11.39	8.42 $\pm$	13.35	.83 $\pm$	6.43	*	4.83 $\pm$	11.48	4.92 $\pm$	10.96	*
<u>Juniperus</u>	0 $\pm$	0	.63 $\pm$	3.34	3.78 $\pm$	7.96	*	1.68 $\pm$	5.54	1.26 $\pm$	4.93	
<u>Rosa</u>	.96 $\pm$	2.77	1.04 $\pm$	2.89	.83 $\pm$	6.43	*	0.67 $\pm$	4.14	1.22 $\pm$	4.57	* *

a indicates significant between-area effect

b indicates significant between-sex effect

c indicates significant interaction effect

separated out by the principle-component analysis (Figure 13). Since rams primarily occupy ASU N while non-rams spend most of the winter on ASU S (Figure 8), it follows that rams are concentrating on more productive, mesic and probably lightly grazed areas characterized by the Festuca type while non-rams are more limited to the drier and probably overgrazed Koeleria type.

C. THE FOOD NICHE

1. Forage Species in Diet

To determine whether class differences exist in the diets of bighorn sheep, plant epidermal remains were analyzed in 272 faecal samples collected from 4 known age-sex classes (ewes, lambs, yearlings, rams) during 2 winters of 6 months duration. Table 14 presents a breakdown of sample numbers by class, month, and year. It should be noted that cell frequencies differ greatly.

Table 15 presents the means ($\pm$ SE) of the percentage presence of 32 forage types in the diets of the four classes for the entire data set. A useful index in comparative diet studies is a measure of "similarity" of two or more diets. For this purpose, most diet studies (e.g., Vavra et al. 1978, Hansen and Reid 1975, Shank et al. 1978) have employed Kulczynski's similarity index (Oosting 1956, Gauch 1973). This measure treats only those diet components which are shared in the compared diets. For example, in the case

Table 14. Breakdown of the 272 faecal samples by month and year of collection and by age-sex class of individuals from which the samples were collected.

		Nov.	Dec.	Jan.	Feb.	March	April	Total
Ewes	1975-1976	5	8	6	3	0	8	30
	1978	0	0	12	10	19	14	55
	Total	5	5	18	13	19	22	85
Lambs	1975-1976	3	2	5	2	0	1	13
	1978	0	0	13	12	22	18	65
	Total	3	2	18	14	22	19	78
Yearlings	1975-1976	3	1	4	2	0	0	10
	1978	0	0	1	3	3	1	8
	Total	3	1	5	5	3	1	18
Rams	1975-1976	6	4	4	11	5	3	33
	1978	0	0	14	8	17	19	58
	Total	6	4	18	19	22	22	91
Total	1975-1976	17	15	19	18	5	12	86
	1978	0	0	40	33	61	52	186
	Total	17	15	59	51	67	64	272

Table 15. Summary of the percentages of 32 forage taxa ingested by ewes, lambs, yearlings, and rams during the winters of 1975-1976 and 1978. Asterisks(*) indicate those taxa utilized in subsequent statistical analyses. Parenthetical values are SE's.

Taxon		Ewe N = 85	Lamb N = 78	Yearling N = 18	Ram N = 91	Total N = 272
<u>Agropyron</u> sp.		0.0 (0.0)	0.04 (0.04)	0.15 (0.15)	0.07 (0.05)	0.04 (0.02)
<u>Bromus</u> sp.	*	4.14 (0.62)	4.63 (0.60)	3.73 (1.30)	3.78 (0.51)	4.13 (0.32)
<u>Carex</u> sp.	*	11.94 (1.34)	11.73 (1.75)	12.38 (2.60)	3.71 (0.49)	9.16 (0.73)
<u>Danthonia</u> sp.		0.0 (0.0)	0.02 (0.02)	0.0 (0.0)	0.14 (0.07)	0.05 (0.02)
<u>Elymus</u> sp.	*	2.16 (0.48)	3.29 (0.84)	1.28 (0.84)	3.16 (0.81)	2.76 (0.40)
<u>Festuca</u> sp.	*	68.70 (2.24)	68.56 (2.62)	68.02 (3.76)	77.18 (2.03)	71.45 (1.28)
<u>Kobresia myosuroides</u>		0.11 (0.06)	0.17 (0.08)	0.26 (0.25)	0.11 (0.06)	0.14 (0.04)
<u>Koeleria cristata</u>	*	4.83 (0.77)	5.47 (0.72)	3.55 (1.18)	3.96 (0.66)	4.64 (0.41)
<u>Poa</u> sp.	*	2.37 (0.37)	1.72 (0.36)	3.36 (1.36)	1.27 (0.27)	1.88 (0.20)
<u>Trisetum spicatum</u>		0.67 (0.20)	0.79 (0.27)	0.65 (0.47)	0.44 (0.14)	0.63 (0.11)
<u>Androsace carinata</u>		0.0 (0.0)	0.09 (0.07)	0.45 (0.31)	0.07 (0.05)	0.08 (0.03)
<u>Antennaria</u> sp.		0.0 (0.0)	0.06 (0.06)	0.48 (0.26)	0.08 (0.08)	0.08 (0.04)
<u>Astragalus</u> sp.	*	0.75 (0.27)	1.00 (0.28)	0.96 (0.50)	0.14 (0.06)	0.63 (0.12)
<u>Descurainia</u> sp.		0.54 (0.14)	0.50 (0.16)	0.64 (0.37)	0.40 (0.13)	0.49 (0.08)
<u>Dryas</u> sp.		0.07 (0.05)	0.03 (0.03)	0.0 (0.0)	0.27 (0.20)	0.12 (0.07)
<u>Juniperus</u> sp.		0.09 (0.06)	0.30 (0.16)	0.0 (0.0)	0.81 (0.31)	0.39 (0.12)
<u>Picea</u> sp.	*	0.27 (0.25)	0.0 (0.0)	0.12 (0.12)	1.54 (0.67)	0.61 (0.21)
<u>Potentilla</u> sp.		0.0 (0.0)	0.11 (0.06)	0.14 (0.14)	0.07 (0.07)	0.07 (0.03)
<u>Rhus</u> sp.		0.0 (0.0)	0.00 (0.00)	0.0 (0.0)	0.02 (0.02)	0.01 (0.01)
<u>Saxifraga</u> sp.		0.11 (0.06)	0.14 (0.07)	0.0 (0.0)	0.23 (0.09)	0.15 (0.04)
<u>Shepherdia canadensis</u>		0.12 (0.07)	0.06 (0.04)	0.0 (0.0)	0.03 (0.03)	0.06 (0.03)
<u>Sphaeralcea</u> sp.		0.0 (0.0)	0.01 (0.01)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Unknown borage		0.06 (0.06)	0.00 (0.00)	0.0 (0.0)	0.04 (0.04)	0.03 (0.02)
Unknown composite	*	0.85 (0.26)	0.39 (0.17)	1.56 (0.60)	0.64 (0.20)	0.69 (0.12)
Unknown forb	*	1.35 (0.29)	0.69 (0.26)	1.89 (0.75)	1.26 (0.30)	1.17 (0.16)
<u>Draba</u> sp.		0.05 (0.05)	0.00 (0.00)	0.19 (0.19)	0.02 (0.02)	0.04 (0.02)
<u>Cladonia</u> (type)		0.04 (0.04)	0.03 (0.03)	0.0 (0.0)	0.0 (0.0)	0.02 (0.01)

Table 15--Continued

Taxon	Ewe N = 85		Lamb N = 78		Yearling N = 18		Ram N = 91		Total N = 272	
Lichen	0.13	(0.10)	0.00	(0.00)	0.0	(0.0)	0.02	(0.02)	0.05	(0.03)
Moss	0.59	(0.25)	0.17	(0.07)	0.21	(0.21)	0.38	(0.11)	0.38	(0.04)
<u>Lupinus</u> sp.	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.04	(0.04)	0.01	(0.01)
Seed	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.08	(0.06)	0.03	(0.02)
<u>Salix</u> sp.	0.07	(0.05)	0.0	(0.0)	0.0	(0.0)	0.05	(0.05)	0.04	(0.02)

of two diets each containing 10 forage species of which one and only one is shared in some negligible amount (say, 5%), then Kulczynski's index would indicate complete diet overlap. Clearly, a more robust similarity index would be desirable.

A more appropriate index is provided by Cavalli-Sforza and Edwards' (1967) measure of "genetic distance" as described in Batschelet (1976). Modified for diet analysis, this method views each diet as a "unit vector" comprised of n possible forage species which are expressed as a proportion of the total diet. These n elements in concert define a unique point in n -dimensional hyperspace. Diet similarity is expressed then simply as the cosine of the angle between the lines connecting the origin with the points defining the compared diets. Greater values of this index indicate lesser similarities.

$$\text{Similarity} = \cos \theta = \underline{a}_1' \cdot \underline{a}_2$$

where $\underline{a}_1$ and $\underline{a}_2$ are the unit vectors of the two diets. Table 16 presents these measures which indicate that ewes, lambs, and yearlings (i.e., non-rams) represent a close cluster of high diet similarity as opposed to rams which differ from each of the non-ram classes.

This is a non-statistical measure of similarity; it must be demonstrated statistically that class differences in diet are significant. For the sake of economy in the subsequent analyses, I treated only those 10 forage taxa

Table 16. Cavalli-Sforza's index of similarity comparing mean diets of ewes, lambs, yearlings and rams.

	Lamb	Yearling	Ram
Ewe	7.1	9.2	12.7
Lamb		7.0	13.4
Yearling			15.7

which comprise 1% or more of the total diet of any sheep class. These 10 taxa are marked with an asterisk in Table 15 and together comprise 97.4% of the diet of ewes, 97.5% of the lambs' diet, 96.9% of the yearlings' diet, and 96.6% of the rams' diet. Clearly, little accuracy is lost in failing to treat the other 22 taxa which together make up only 2.5-3.4% of any single class diet. Of these 10 taxa, Carex and Festuca are by far the most important, together comprising about 83% of the total.

The investigation of statistically significant diet differences requires resolution of two questions; (a) do the unitary diets of the classes differ?, and (b) what single forage types contribute most to observed differences? To consider diet as a unit, the 10 taxa were treated as a diet vector and analyzed using multivariate techniques. The contributions of the various forage types were analyzed through univariate tests. Throughout, the SPSS MANOVA programme (Cohen and Burns 1977) was employed. In the case of non-orthogonal designs, this programme performs analysis of variance based on cell means. In all cases, the significance of the effect in question was tested using the combined within- and residual-error terms as the denominator of the F-value. Wilks' lambda criterion was chosen for the multivariate test of significance.

To examine the effects of year, month, and class

variance were performed. Because no samples were collected in November or December of 1978, the year by month interaction could not be calculated. Therefore, the not unreasonable assumption was made that the seasonal intakes of forage did not vary from one year to the other. The multivariate interactions were discovered to be significant (class x month, $S=10$, $M=2$, $N=118$, $\Lambda = .4778$) (class x year, $S=3$, $M=3$, $N=124$, $\Lambda = .8199$) as were all the main effects (class x month/class; $S=3$, $M=3$, $N=118$, $\Lambda = .7858$ /month; $S=5$, $M=2$, $n=118$, $\Lambda = .4335$ / year; $S=1$, $M=4$, $N=118$, $\Lambda = .5098$) (class x year/class; $S=3$, $M=3$, $N=124$, $\Lambda = .8029$ / month; $S=5$, $M=2$, $N=124$, $\Lambda = .4503$ /year; $S=1$, $M=4$, $N=124$, $\Lambda = .5191$).

In summary, it would appear that although year and month affect diet composition significantly, real class differences exist as well. This can be seen in Figure 14A and 14B where the presence of Festuca and Carex in class diets are broken down by year and by month. Figure 14A shows that little difference exists between years in terms of the mean percentage of Festuca (Table 17) and that in both years the rams ingested more Festuca than did each of the non-ram classes. Figure 14A shows as well that Festuca consumption drops off in the middle of winter in all classes but not to such a great extent in rams. This is undoubtedly attributable to Festuca's occurrence primarily in sheltered areas where snow tends to accumulate. The rams lesser response to this effect is probably due to their greater

Figure 14. Festuca (A) and Carex (B) contents of age-sex class diets broken down by month and by year.

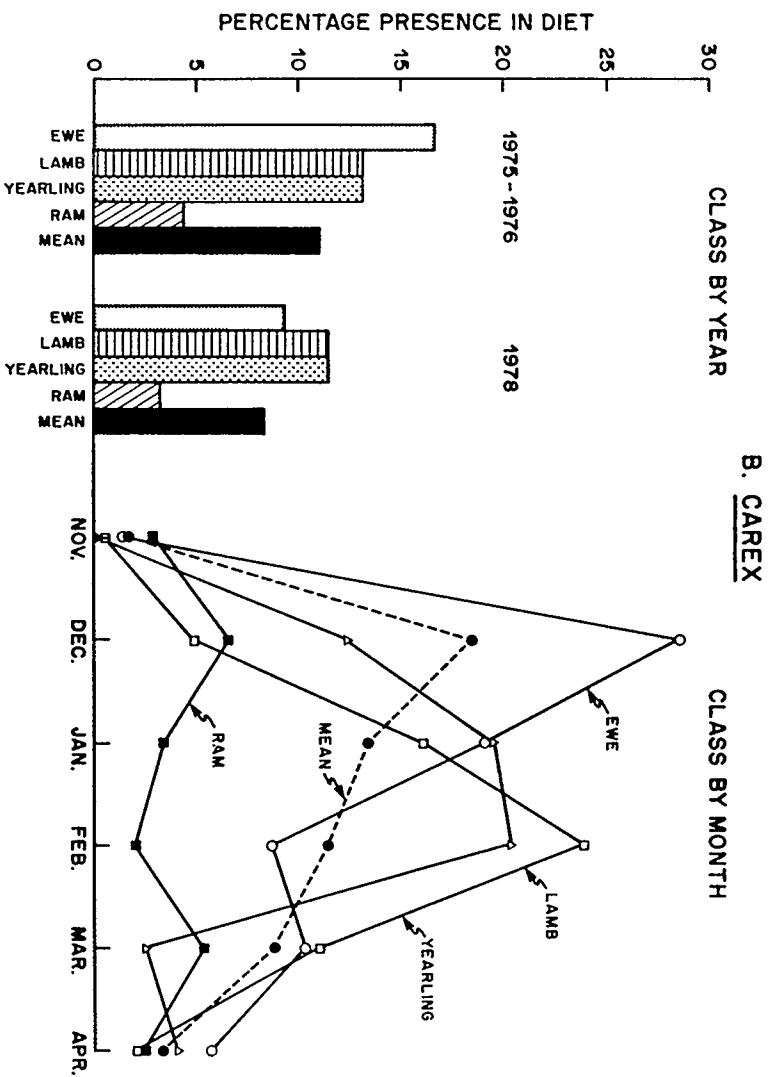
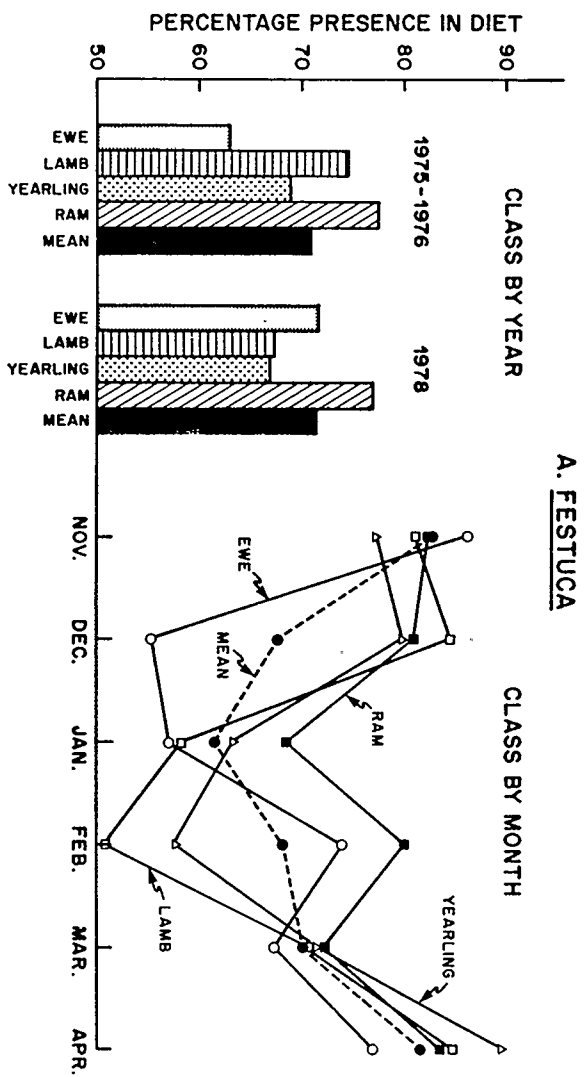


Table 17. Breakdown of the 10 most common forage types by year, month, and class. Parenthetical values are SE's. Asterisks (*) indicate significant differences as univariate main effects in 3-way analysis of variance.

Primary Division	Secondary Division		<u>Bromus</u> sp.		<u>Carex</u> sp.		<u>Elymus</u> sp.		<u>Festuca</u> sp.		<u>Koeleria</u> sp.		<u>Poa</u> sp.		<u>Astragalus</u> sp.		<u>Picea</u> sp.		Unknown Composite		Unknown Forb	
Year	1975-1976	N = 86	2.98	(0.48)*	11.01	(1.43)*	0.02	(0.02)*	70.97	(2.11)	0.95	(0.20)*	3.55	(0.45)	0.43	(0.12)	1.83	(0.74)*	1.79	(0.33)*	2.99	(0.40)*
	1979	N = 186	4.67	(0.41)	8.29	(0.83)	4.02	(0.56)	71.67	(1.59)	6.34	(0.52)	1.11	(0.18)	0.72	(0.17)	0.04	(0.03)	0.19	(0.07)	0.32	(0.10)
Month	November	N = 17	0.88	(0.32)	1.54	(0.35)*	0.0	(0.0)*	82.32	(3.35)*	1.81	(0.73)*	5.21	(1.54)*	0.41	(0.28)	0.09	(0.08)	2.60	(0.95)*	2.69	(1.06)*
	December	N = 15	5.42	(1.62)	18.48	(4.34)	0.0	(0.0)	67.87	(5.35)	1.15	(0.45)	2.31	(0.50)	0.29	(0.20)	0.0	(0.0)	0.33	(0.25)	1.00	(0.35)
	January	N = 59	3.64	(0.77)	13.41	(1.80)	7.37	(1.55)	61.61	(2.79)	4.51	(0.76)	2.47	(0.43)	0.50	(0.18)	0.07	(0.05)	0.56	(0.18)	1.19	(0.32)
	February	N = 51	4.10	(0.79)	11.49	(1.94)	2.27	(0.50)	68.29	(2.79)	4.76	(0.89)	1.98	(0.37)	0.57	(0.23)	0.51	(0.26)	1.19	(0.36)	1.88	(0.26)
	March	N = 66	4.69	(0.65)	8.89	(1.29)	2.08	(0.28)	70.53	(2.56)	8.49	(1.05)	1.11	(0.34)	1.28	(0.42)	0.25	(0.17)	0.30	(0.14)	0.38	(0.20)
	April	N = 64	4.60	(0.57)	3.49	(0.66)	0.98	(0.24)	81.93	(2.27)	2.24	(0.44)	1.06	(0.35)	0.27	(0.11)	1.83	(0.97)	0.41	(0.23)	1.01	(0.38)
Class	Ewe	N = 85	4.14	(0.61)	11.94	(1.34)*	2.16	(0.48)	68.70	(2.24)*	4.83	(0.77)	2.37	(0.37)*	0.75	(0.27)*	0.27	(0.25)	0.85	(0.26)	1.35	(0.29)
	Lamb	N = 78	4.63	(0.60)	11.73	(1.75)	3.29	(0.84)	68.56	(2.62)	5.47	(0.72)	1.72	(0.36)	1.00	(0.28)	0.0	(0.0)	0.39	(0.17)	0.69	(0.26)
	Yearling	N = 18	3.73	(1.30)	12.38	(2.60)	1.28	(0.84)	68.02	(3.76)	3.55	(1.18)	3.36	(1.36)	0.96	(0.50)	0.12	(0.12)	1.56	(0.60)	1.89	(0.75)
	Ram	N = 91	3.78	(0.51)	3.71	(0.49)	3.15	(0.81)	77.18	(2.03)	3.96	(0.66)	1.27	(0.27)	0.14	(0.06)	1.54	(0.67)	0.64	(0.20)	1.25	(0.30)

propensity to utilize snow-covered areas (Section IV.B.2.). Carex (Figure 14B) shows significant between-year differences but during both years rams consumed less Carex than did the non-rams. Carex also exhibits a significant month effect (see Table 17) but one which is inverse to that of Festuca ($r = -.86$). Carex consumption is greater in mid-winter undoubtedly due to its occurrence on high, windswept areas where snow is blown clear quickly. Rams, with their greater ability to use snow-covered areas, maintain a steady but low intake of Carex throughout the winter.

The qualitative conclusions of Cavalli-Sforza's similarity analysis would seem to have been upheld statistically; rams and non-rams consume diets containing different proportions of plant taxa. The most significant differences, from the standpoint of percentage occurrence, are that rams eat more Festuca and less Carex than do each of the non-ram classes.

However, one problem does exist. It was noted in Section IV.A. that rams tend to concentrate on ASU N while non-rams occur predominantly on ASU S. Consequently, most ram faecal samples were collected on ASU N while most non-rams samples were taken from ASU S. Table 18 presents the breakdown of sample number by area and class. It was further noted in Section IV.B.4. that the favoured feeding areas on the different ASU's differ significantly in forage

Table 18. Breakdown of 272 faecal samples by area on which they were collected and by age-sex class of the individuals from which they were taken.

	Ewe	Lamb	Yearling	Ram	Total
ASU S	68	53	16	7	144
ASU M	13	16	1	7	37
ASU N	4	9	1	77	91

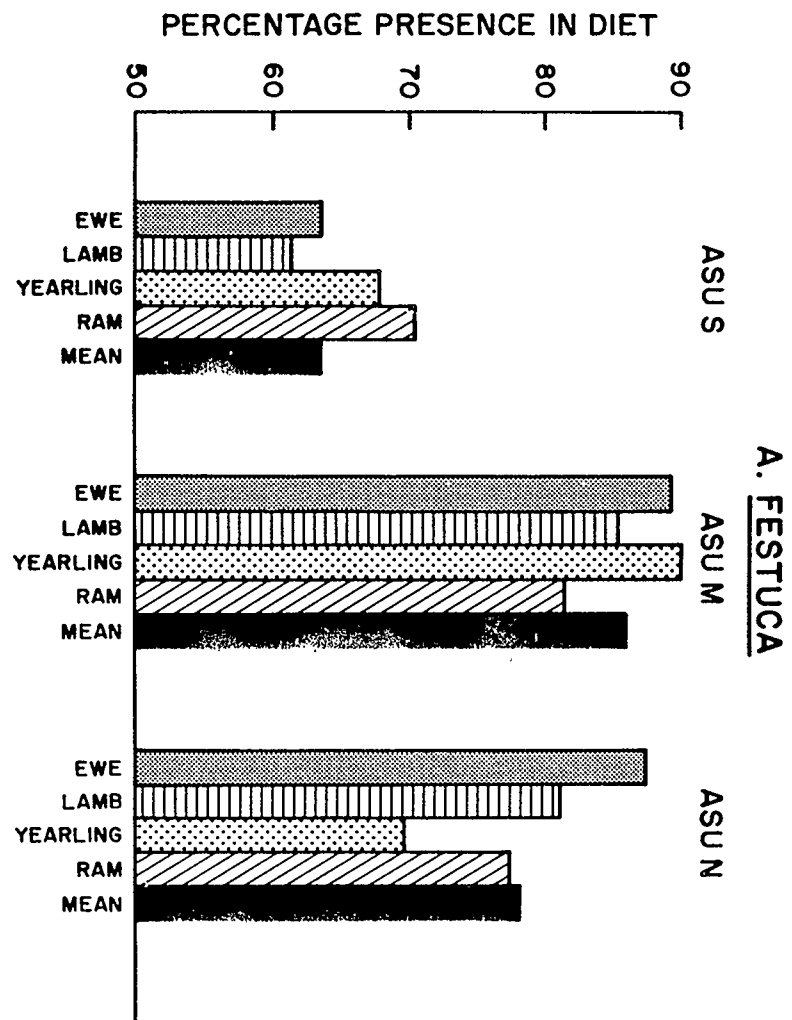
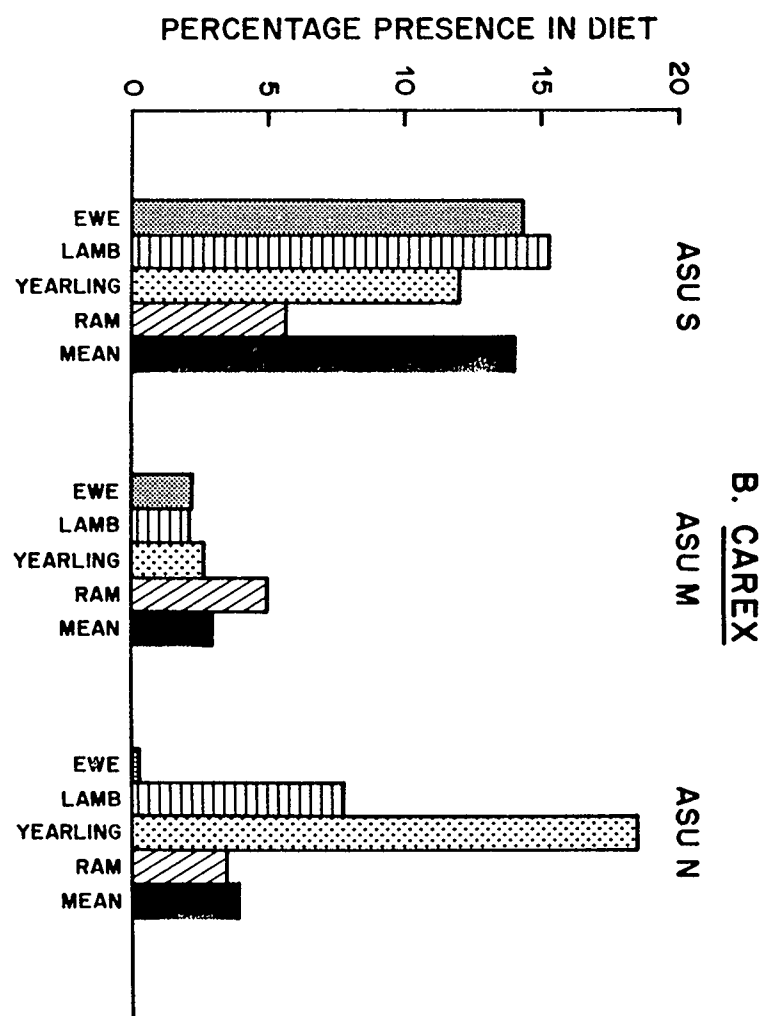
availability with ASU S (the preferred non-ram range) being characterized by the Koeleria type and ASU N (the preferred ram range) being characterized by the Festuca type. Are the class differences observed above actually due to class diet preferences or are they an artifact of an area effect on diet expressed as a class effect through unequal sample sizes? This is tantamount to the biological question of whether sheep diet is determined more by preference or more by availability.

Accordingly, class and area effects were tested in 4-way incomplete multi- and univariate designs. No area x class interaction effect was noted ($S=6$, $M=1$, $N=121.5$, $\Lambda = .8868$) nor was there any class effect ($S=3$, $M=3$, $N=121.5$, $\Lambda = .9364$). There were, however, significant effects by year ($S=1$, $M=4$, $N=121.5$, $\Lambda = .5170$), month ($S=5$, $M=2$, $N=121.5$, $\Lambda = .4447$), and area ($S=2$, $M=3.5$, $N=121.5$, $\Lambda = .7295$). Table 19 presents the mean presence of the 10 most common taxa broken down by area of collection. Figure 15A and 15B show the effect of area on class for consumption of Festuca and Carex respectively. It shows quite clearly that on ASU S all classes ate little Festuca while on ASU M and ASU N this genus was consumed in large quantities by all classes. In fact, on ASU M and ASU N ewes and lambs ate more Festuca than did rams. By contrast, all classes ate more Carex on ASU S than on the other two areas. These conclusions are fully understandable in relation to the findings of Section

Table 19. Breakdown of means of the 10 most common forage types by area of collection. Parenthetical values are SE's. Asterisks (*) indicate significant univariate effects.

		ASU S	ASU M	ASU N
N =		145	36	91
<u>Bromus</u> sp.		4.53 (0.49)	4.45 (0.73)	3.37 (0.48)
<u>Carex</u> sp.	*	14.07 (1.14)	2.70 (0.65)	3.88 (0.68)
<u>Elymus</u> sp.		3.11 (0.55)	1.00 (0.33)	2.90 (0.77)
<u>Festuca</u> sp.	*	63.63 (1.73)	86.02 (1.59)	78.15 (2.02)
<u>Koeleria</u> sp.		5.71 (0.58)	2.52 (0.61)	3.76 (0.65)
<u>Poa</u> sp.	*	2.65 (0.32)	0.53 (0.19)	1.20 (0.25)
<u>Astragalus</u> sp.	*	1.00 (0.22)	0.23 (0.13)	0.22 (0.09)
<u>Picea</u> sp.	*	0.21 (0.15)	0.00 (0.00)	1.48 (0.67)
Unknown Composite		0.86 (0.19)	0.07 (0.07)	0.68 (0.20)
Unknown Forb		1.26 (0.23)	0.31 (0.15)	1.35 (0.30)

Figure 15. Festuca (A) and Carex (B) contents of age-sex class diets broken down by area of collection.



IV.B.4. which showed that Carex is common on ASU S and rare on ASU N while Festuca shows the opposite trend.

It can be concluded from these analyses that availability of forage affects diet more than does class-specific preference. Therefore, whatever factors are causing rams and non-rams to segregate onto separate ranges are also causing, as a secondary effect, significant between-class diet differences.

2. Diet Quality

A first attempt at determining whether the age-sex classes ingest diets of different qualities was made using the faecal nitrogen index. Crude protein, conventionally defined as $6.25 \times \text{nitrogen content}$, decreases in forage plants with increasing maturity and weathering (Bezeau and Johnston 1962, Johnston and Bezeau 1962) and consequently any combination of faecal samples collected at different dates will contain an inherent, time-related bias. To remove this bias, faecal protein was plotted against the number of days after 1 November that the sample was collected. Figure 16 is a scattergram of faecal protein against date of collection with the fitted regression line for all data points. This regression equation explains a significant proportion of the variability (Table 20) and exhibits a negative slope as would be expected with decreasing forage quality through the winter.

Between-class differences in faecal protein, and hence

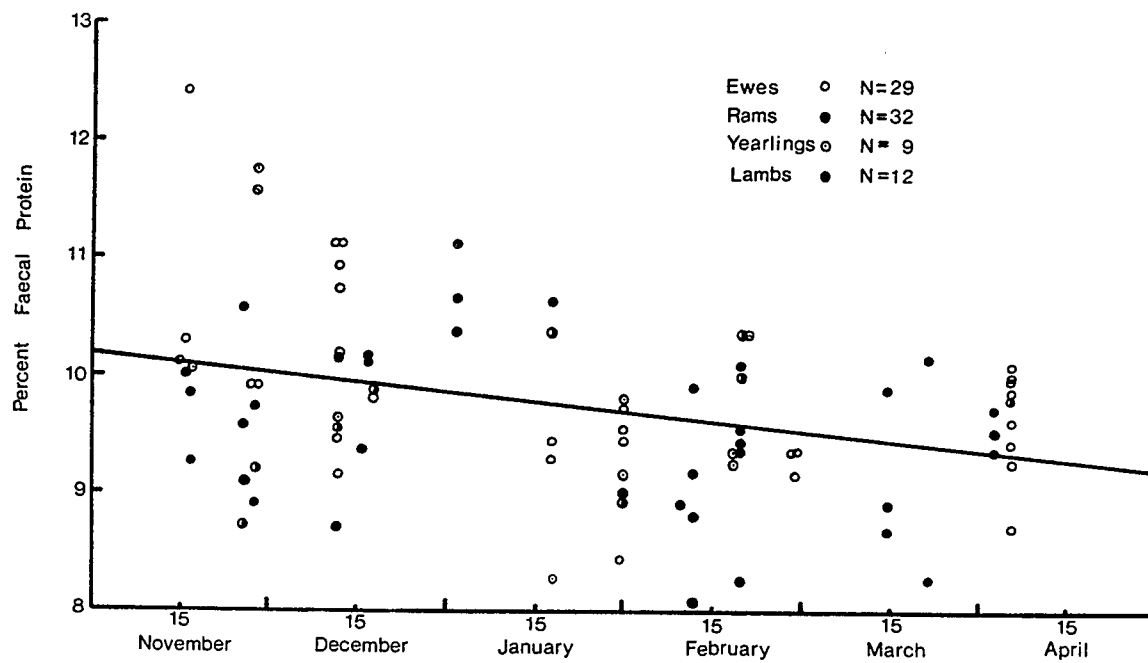


Figure 16. Scattergram of faecal protein contents of samples versus date of collection for six months of winter 1975-1976.

Table 20. Linear regression equations relating faecal protein to month of collection for ewes, lambs, yearlings, and rams. Based on 86 samples collected during winter 1975-1976.

Class	Regression Equation	Calculated F	df	
Ewe	$P^{\dagger} = 10.433 - .007 D^{\S}$	5.816	1,28	X*
Lamb	$P = 9.363 + .004 D$	0.557	1,11	
Yearling	$P = 11.080 - 0.163 D$	3.784	1, 8	
Ram	$P = 9.959 - .005 D$	3.413	1,31	
Total	$P = 10.165 - .006 D$	3.96	1,81	X

† = % faecal protein

§ = date of collection in number of days after 1 November

* = statistically significant difference

diet quality, can be demonstrated by showing that the regression equations for each age-sex class are significantly different. However, Table 20 shows that only the regression equation for adult ewes explains a significant proportion of the observed variability; therefore no between-class comparisons can be made.

The faecal protein analysis yields no information about class differences in forage quality. This failure may be attributed to the following factors acting singly or together: (a) The sample size may simply be inadequate to overcome the effect of high variance, (b) the index itself may not reflect real quality differences, (c) inadequate standardization of sample handling, storage and drying may have resulted in differential nitrogen decomposition, or (d) diets may vary greatly in quality within a single class.

Table 21 presents, in descending order of quality, the results of the analyses for chemical content, fibre content, and estimated digestible energy for six common forage genera. It shows that Agropyron is the most favourable forage plant in all categories followed by Poa and Festuca. In terms of protein and digestible energy content, Bromus, Koeleria, and Carex are all of obviously lesser quality.

Johnston et al. (1968) commented upon the high quality of alpine vegetation in comparison to similar associations at lower elevations. Although some of the species analyzed in this study are different than those treated by Johnston

Table 21. Analysis of chemical content, acid detergent fibre content (ADF), and estimated digestible energy for six major forage genera collected in weathered condition from the Palliser Range on 23 March 1978.

	% Protein	% ADF	% Calcium	% Phosphorus	Estimated Digestible Energy
<u>Agropyron</u> sp.	9.8	35.1	1.09	0.17	2.52
<u>Poa</u> sp.	7.0	35.4	0.92	0.15	2.50
<u>Festuca</u> sp.	6.4	35.5	1.17	0.11	2.49
<u>Bromus</u> sp.	5.6	38.5	1.36	0.09	2.24
<u>Koeleria</u> sp.	5.5	39.8	1.04	0.11	2.13
<u>Carex</u> sp.	4.3	40.4	0.92	0.04	2.08

et al. (1968), generic comparisons may still be made. In a comparable stage of maturity, the protein and phosphorus contents listed in Table 21 are higher than those obtained by Johnston et al. (1968) for all cases except that of Carex. Johnston et al. (1968) did not include Koeleria samples in their analyses. Observed calcium contents in all samples were higher than those reported by Johnston et al. (1968) by a factor of 2-3 times. Fibre and digestibility cannot be compared because different analytic procedures were followed.

The estimated digestible energy of Agropyron is only marginally below the $2.56 \text{ Mcals} \cdot \text{kg}^{-1}$ of average brome hay (E.S. Redshaw, pers. comm.) yet Agropyron occurs as only 0.04% of the total diet of Palliser bighorns (Table 15). This cannot be attributed solely to rarity on the range since Stelfox (1976) found it to represent 0.09% of the total range cover. However, Agropyron samples were collected near bed-sites where dung concentrations may have resulted in highly favourable growing conditions not representative of the rest of the range. Johnston et al. (1968) show the same species of Agropyron to be only of moderate quality.

Carex is clearly the poorest forage listed in Table 21 and, in terms of digestible energy, is less favourable than oat straw which averages $2.29 \text{ Mcals} \cdot \text{kg}^{-1}$ (E.S. Redshaw, pers. comm.). Yet, it comprises 11% of the non-rams' diet.

Stelfox (1976) lists four Carex species on the Palliser Range and it is possible that I collected a species not utilized by sheep although traces of grazing on the tussocks sampled suggest that this was not the case.

It is clear why Festuca is so highly preferred by all classes. It is obviously superior in quality to Bromus, Koeleria, and Carex and is not much inferior to either Agropyron or Poa. Festuca occurs commonly on the range in large, dense patches which are easily exploited and therefore probably represents the optimal compromise between availability and quality.

Some indication of class specific diet quality can be obtained by calculating the average digestible energy content of the diet weighted by percentage presence of the genus in the class diet (Table 15). The weighted means representing class-specific diet quality are presented as Table 22 which shows clearly that rams are ingesting a better quality diet than are non-rams. It is unlikely that the 7.9-11.1% of the total diets not utilized in these calculations will alter these general results. Of the five common forage taxa not used in this analysis (Astragalus, Picea, Unknown Composites, Unknown Forbs, and Elymus), only Astragalus exhibits statistically significant class differences (Table 15) and is present in the diets only in negligible amounts.

3. Feeding Behaviour

Table 22. Digestible energy content of class diets estimated as digestible energy ($\text{Mcal} \cdot \text{kg}^{-1}$) of six forage genera weighted by percentage presence of the six genera in the class diets.

	Ewes	Lamb	Yearling	Rams
Digestible energy Content ($\text{Mcal} \cdot \text{kg}^{-1}$)	2.4	2.4	2.4	2.5
% of diet represented	91.98	92.11	91.04	89.90

i. Time Correlation Analysis-- As discussed earlier (Section III.B.3.iii.), animals feeding on plants with different spatial characteristics should exhibit differences in the temporal organization of their feeding activity (S.A. Altmann 1974). Table 23 presents descriptive statistics for the time course data. It shows that lambs spent the greatest proportion of time actually feeding followed by ewes and rams. Rams and ewes had approximately equal walking and feed state lengths while both the feeding and walking states of lambs were shorter in mean duration than those of rams and ewes. The sample distributions were normalized by a common log transformation and tested for differences between the means by a one-way analysis of variance (Sokal and Rohlf 1969 p.208-209). There were no differences between rams and ewes in mean walking or feed state lengths ($F = 0.15$; $F = 2.57$; d.f.=1, ∞) but both mean state lengths of lambs were significantly shorter than those of both ewes and rams (ewe vs lamb-- $F = 13.32$, $F = 59.31$, d.f.=1, ∞ ; ram vs lamb-- $F = 19.22$, $F = 94.95$, d.f.=1, ∞). This suggests that lambs conform to Strategy A while rams and ewes tend to exhibit the characteristics of Strategies B or C.

The distribution of feed state lengths are very highly skewed toward the lower end of the distribution for lambs, rams, and ewes. The coefficients of skewness (Simpson et al. 1960 p. 143) is +0.88 for ewes, +0.82 for lambs, and

Table 23. Statistics describing the duration of walk and feed bouts of lambs, ewes, and rams.

	No. of transitions	No. of seconds	No. of feeds	No. of walks	$\bar{x}$ feed $\pm$ SD	$\bar{x}$ walk $\pm$ SD	proportion of time spent feeding
Ewe	2814	51 821	1264	522	31.9 $\pm$ 56.7	5.2 $\pm$ 6.8	.78
Lamb	2525	29 047	1146	505	20.6 $\pm$ 29.7	3.9 $\pm$ 4.2	.82
Ram	2936	59 162	1257	555	30.4 $\pm$ 47.4	5.5 $\pm$ 6.3	.65

+0.78 for rams indicating more of the ewes' feed state observations were further below the mean than was the case for rams and lambs. As well, the variance of the ewes' feed state sample (Table 23) was significantly greater than for lambs and rams (Sokal and Rohlf 1969 p.186) (ewe vs lamb- $F=3.64$; ewe vs ram-- $F=1.43$; d.f.=1, ∞). These differences suggest that ewes are tending toward Strategy C wherein the long feed-long walk sequence is broken by short feed states which result in a larger occurrence of short feed states and a higher variance of feed state lengths.

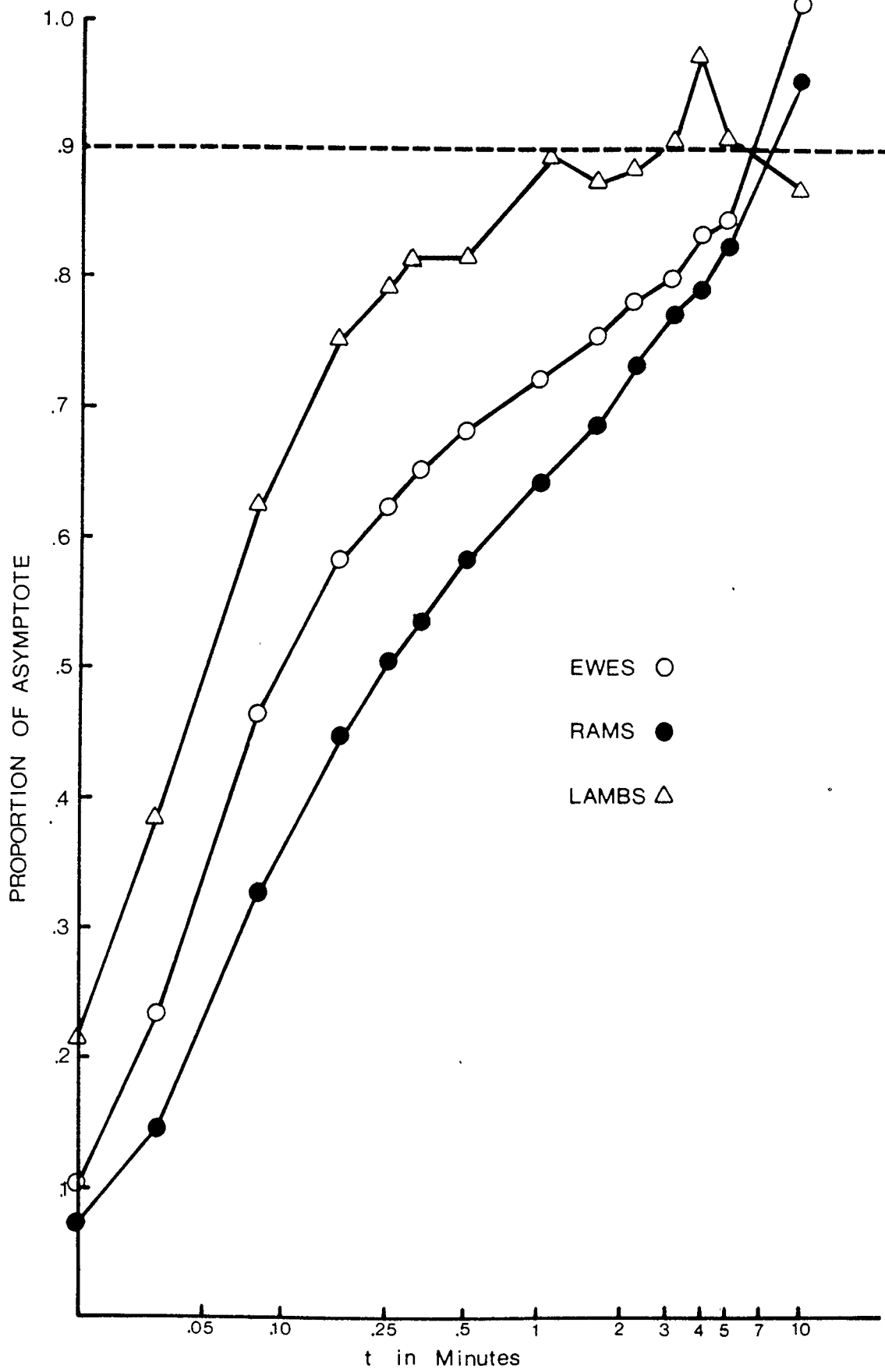
S.A. Altmann (1974), Slatkin (1975), and Slatkin and Hausfater (1976) have suggested the use of "time correlation functions" or autocorrelations for relating the temporal aspects of feeding activity to the distribution of resources. The time correlation function is defined as the conditional probability that if an animal is feeding at any time T , it will be feeding at a sequence of times $T+t$ thereafter regardless of whether the feed state was continuous or not. Such a function decays to an asymptote which is the proportion of time in the observation actually spent feeding. The length of time required to closely approach this limit (t_c) is the time following which the effect of the initial feed state is no longer influencing the probability of the animal being in a feed state; that is, when $t > t_c$, the sample is effectively being randomly sampled.

The value t_c is determined by the feed state duration and the rapidity of the return to the feed state (Slatkin and Hausfater 1976). Slatkin (in S.A. Altmann 1974) suggests that long time correlation functions (high t_c) are associated with utilization of patchy food resources while low t_c values indicate utilization of more homogeneously dispersed food items.

Figure 17 depicts the cumulative frequency function of the approach to the asymptote of the proportion of time spent feeding based on a sample of 209 249 points. The value of t_c is considered as the point of the x-axis at which the cumulative frequency function intersects the line representing 90% of the asymptotic value. It will be noted that the lamb curve tends to oscillate about the 90% line. This is due to the low variance of the lamb feed state sample (Table 23). The t_c for lambs falls at about one minute while those of rams and ewes differ little and fall within the range of 6-7 minutes.

These results suggest that rams and non-rams feed in a nearly identical manner. However, the greater variance and skewness of the ewes' feed state distribution and the greater proportion of time they spend feeding suggest a marginally greater degree of forage selectivity by ewes. The obviously smaller t_c value exhibited by lambs suggests strongly that they specialize on small, dispersed and evenly distributed food items. This sort of feeding is what would

Figure 17. The decay of the feeding time correlation function in lambs, ewes, and rams. The time correlation function is the proportion of all observations that are feeds t seconds after an initial feed state at time T . This function decays to the total proportion of time spent feeding. The dotted line represents 90% of the proportion of time spent feeding by each class. The y-axis is the proportion of the asymptote reached t minutes after T (i.e., the proportion of observations at each time t that were feeds divided by the proportion of total observations that were feeds).



be expected if the lamb were following its mother and selecting only the very highest quality food items. In terms of the strategies defined in Section III.B.3.iii., lambs most nearly approximate Strategy A, while ewes and rams tend toward Strategies C and B respectively.

ii. Feeding Mobility-- As discussed earlier (Section III.B.3.iii.), animals feeding on plants with different spatial patterns should exhibit differences in the sedentariness of their grazing activity. If the food resource occurs in localized, dense patches, considerable time should be spent in one location before moving to another patch. If the food resource is, however, evenly distributed, the animal should move more or less continuously. The net result of these different foraging techniques should be differences in the patchiness of the grid representing the location of all feeding sites observed throughout the winter.

Unfortunately, this cumulative grid develops under the influence of two interrelated factors; gregariousness and sedentariness. Assume that one derived a cumulative grid from three "slice-of-time" observations at 5 minute intervals as depicted in Figure 18. The cumulative grid representing 60 observations in each of three different spatial cells could be generated in two distinct manners; either as 20 individuals in three different cells remaining sedentary over three observations (Figure 18A) or as 60

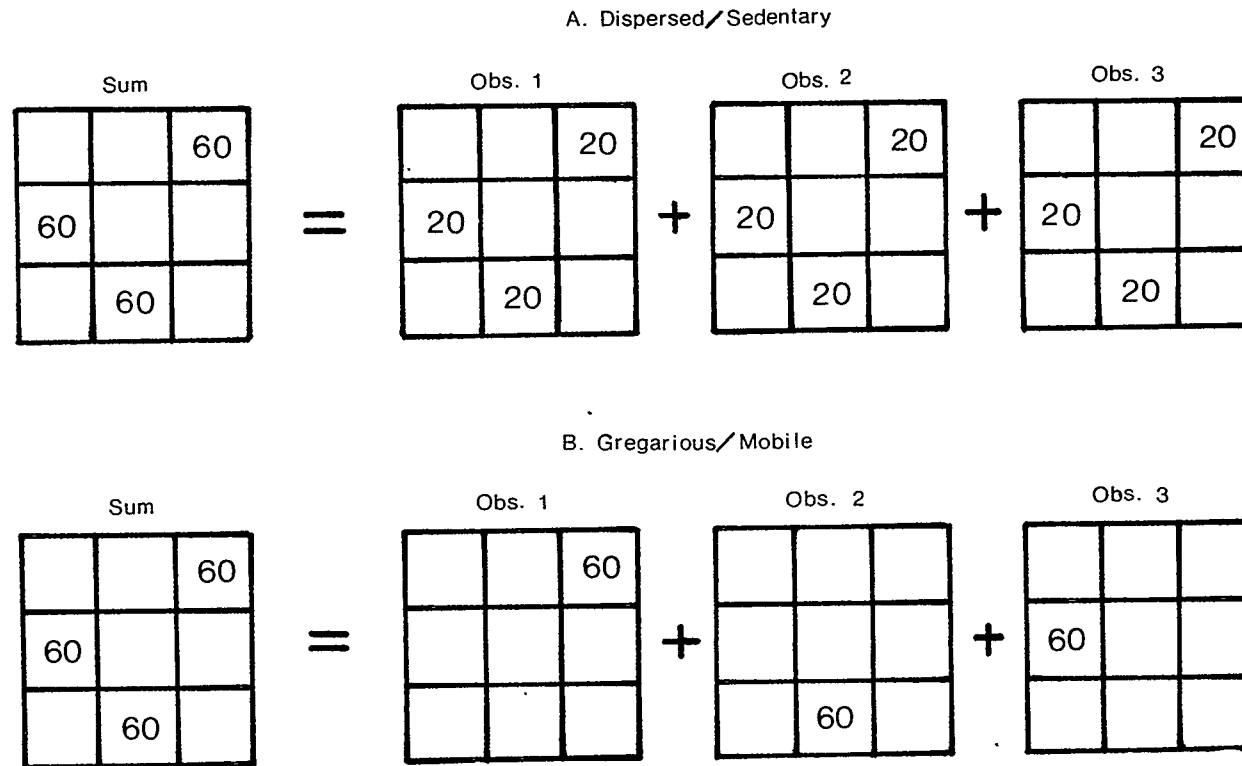


Figure 18. A hypothetical example of how differing degrees of mobility and gregariousness can lead to identical cumulative feeding location grids. In A, three groups of 20 individuals remain stationary over three observations. In B, one group of 60 individuals changes location between each observation.

individuals in three different cells remaining sedentary over three observations (Figure 18A) or as 60 individuals moving as a group between each observation (Figure 18B). In the first case, the animals are spatially dispersed but sedentary through time while in the second case, the animals are gregarious but mobile. An adequate measure of feeding mobility must factor out the gregariousness element from the sedentariness factor. This can be accomplished using a modification of Iwao and Kuno's (1971) adaptation of Lloyd's index of patchiness (Lloyd 1967). Lloyd's index is one of the more intuitively comprehensible and mathematically tractable indices of aggregation available. The technique consists of first calculating an "index of mean crowding", m' , defined as the mean number of other individuals per individual per occupied cell:

$$m' = \frac{\sum_{i=1}^N x_i (x_i - 1)}{\sum_{i=1}^N x_i}$$

where x_i is the number of individuals in the i th quadrat and N is the total number of quadrats. The index of patchiness is then calculated by dividing mean crowding, m' , by mean density, m , the mean number of individuals per cell. Patchiness, defined in this manner, can remain unchanged as mean crowding increases with increasing density.

Iwao and Kuno (1967) developed an extension of Lloyd's index to generate conclusions about species-specific spatial

aggregation patterns. They show that if the index of mean crowding, m' , is graphed against the mean density, m , for several independent populations, the y-intercept of the regression equation is an estimate of the intrinsic gregariousness (my term) of the species while the slope represents the intrinsic species-specific patchiness of distribution.

This method can be accordingly modified for use in separating the gregariousness and sedentariness factors in the sheep activity data. At each 5-minute interval in the accumulation of a feeding spatial grid, m' and m were calculated. The relationship between these values was expressed in a regression equation. The y-intercept represents an index of gregariousness during feeding while the slope indicates the amount of feeding mobility. A singular m'/m value can arise either from a high y-intercept value and a low slope indicating great gregariousness and low mobility or from a low y-intercept and a steep slope indicating little gregariousness but great mobility.

Because patterns of spatial occupation can be expected to vary with such imponderable factors as time of day, weather, snow cover, and month, I compared rams and non-rams only in those situations in which both simultaneously occurred on one grid in substantial numbers. Sixteen separate data sets were compared representing 23 hours of observation and 4306 sightings. The regression coefficients

are presented in Table 24. Paired t-tests show no significant differences in slope ($t=0.041$, d.f.=15) nor y-intercept ($t=1.276$, d.f.=15). It can be concluded that no differences in the spatial and mobility patterns of feeding were observable between rams and non-rams. This lends no support to the hypothesis that rams and non-rams feed in different manners.

4. Morphological Correlates

The relationship between mouthpart size and feeding behaviour has never been extensively analyzed in large herbivores. Anecdotal references do exist such as the difference between the wide-lipped white rhinoceros (Ceratotherium simim), a grazer, and the narrow-lipped black rhinoceros (Diceros bicornis), which is a browser (Hutchinson 1965 p.33-35). Part of the problem lies in the difficulty in serially arraying forage types along a continuous niche axis such as size as is possible with discrete prey like insects, seeds, and small mammals. Intuitively, it would seem likely that herbivores with small mouthparts would be better adapted to a specialist existence wherein they could gather particular items from amongst a larger array.

Given that such a relationship does exist, a significant difference between the mouthpart size of male and female bighorn sheep might be indirect evidence for sexual difference in the specialization of diet or might

Table 24. Regression coefficients relating mean density to mean number of other individuals per spatial location.

Date	No. Obs.	Non-Rams				Rams			
		No. Indivs.	y intercept	slope	r	No. Indivs.	y intercept	slope	r
13 December	9	123	.21	.12	.99	69	1.18	.22	.96
17 December	45	215	2.34	.24	.99	93	-.03	.17	.99
21 December	25	219	1.68	.06	.98	86	.19	.07	.98
3 January	25	121	6.94	.30	.96	49	-.95	.44	.99
7 January	36	220	2.62	.18	.87	62	-4.28	.59	.99
20 January	43	139	2.75	.25	.95	43	-.19	.30	.99
28 January	19	50	-.98	.69	1.00	23	.75	.21	.94
29 January	22	91	.40	.12	.99	38	-.57	.15	.97
3 February	30	87	.49	.17	.99	119	.67	.15	.98
17 February	25	139	.78	.17	.98	328	1.07	.11	.97
21 February	31	148	.83	.25	1.0	264	2.86	.10	.98
2 March	22	631	4.28	.13	.99	85	-.24	.15	.99
3 March	59	164	.28	.10	.98	248	2.65	.13	.99
23 March	27	74	.62	.09	.98	108	3.86	.09	.95
23 March	27	71	.24	.06	.95	42	-.09	.10	.92
31 March	27	75	-.41	.15	.99	82	-.23	.07	.99

help to explain differences in class-specific diet preferences. Skull measurements, following Cowan (1940), for Rocky Mountain and California bighorns, are summarized in Table 25. It shows that in both sub-species, male premaxillary widths exceed those of adult ewes. In canadensis, the ewe:ram ratio is 1.00:1.21 while in californiana it amounts to 1.00:1.17. These differences are significant (Table 25). The width of the base of the incisor row shows lesser but still statistically significant differences (Table 25).

Selander (1972) pointed out the difficulties in determining the ultimate causation of sexual dimorphism since sexual selection for body size differences will also produce differences in the size of the feeding apparatus. For example, Darwin (1888, first published in 1872) attributed the longer beak of male European goldfinches (Carduelis carduelis) to sexual differences in feeding behaviour. Newton (1967) showed that Darwin was incorrect in this conclusion since sexual dimorphism in bill size is no greater than in body size and therefore the observed niche shift is probably a secondary effect.

If the muzzle width differential is solely a function of body size difference, the ratio of muzzle width to other body measurements should be the same for rams and ewes. Basilar length of the skull (Cowan 1940) is the measure nearly always used as a surrogate for body size in

Table 25. Mean ($\pm$ SD) of selected skull measurements and ratios for Rocky Mountain and California bighorn rams and ewes. F values are for between-sex tests of significance. Asterisks (*) indicate differences significant at the 5% level of probability.

	<u>O. c. canadensis</u>	<u>O. c. californiana</u>
Premaxillary Width	$\sigma \bar{x} = 34.79 \pm .30, N = 65$ $\phi \bar{x} = 28.86 \pm .35, N = 34$ $\phi:\sigma = 1.00:1.21$ $F = 149.422, d.f. = 1,97^*$	$\sigma \bar{x} = 31.39 \pm .38, N = 21$ $\phi \bar{x} = 26.79 \pm .54, N = 11$ $\phi:\sigma = 1.00:1.17$ $F = 49.018, d.f. = 1,32^*$
Width of Incisor Row Base	$\sigma = 35.54 \pm .85, N = 10$ $\phi = 31.76 \pm .59, N = 10$ $\phi:\sigma = 1.00:1.12$ $F = 13.323, d.f. = 1,18^*$	$\sigma = 35.40 \pm .40, N = 2$ $\phi = 30.68 \pm .41, N = 4$ $\phi:\sigma = 1.00:1.15$ $F = 51.601, d.f. = 1,4^*$
Ratio Pre-maxillary Width to Basilar Length	$\sigma = 0.126 \pm .001, N = 65$ $\phi = 0.118 \pm .001, N = 34$ $F = 24.830, d.f. = 1,97^*$	$\sigma = 0.117 \pm .001, N = 21$ $\phi = 0.110 \pm .002, N = 10$ $F = 12.533, d.f. = 1,29^*$
Ratio Pre-maxillary Width to Width at M ³	$\sigma = 0.617 \pm .005, N = 64$ $\phi = 0.560 \pm .008, N = 30$ $F = 38.216, d.f. = 1,92^*$	$\sigma = 0.541 \pm .008, N = 21$ $\phi = 0.486 \pm .013, N = 11$ $F = 15.128, d.f. = 1,30^*$

allometric studies since it is deemed more nearly free of size-independent variation than any other readily obtainable measure (Gould 1974). Table 25 shows that males of both canadensis and californiana exhibit larger premaxillae in relation to basilar length than do females. The differences are statistically significant (Table 25). As well, Table 25 shows that males of both subspecies have wider muzzles in relation to the breadth between the third molars than do females. Again, the differences are statistically significant (Table 25).

Selander (1972) did not consider the effects of allometric growth. As Lewontin (1978) has stated, patterns of differential growth can produce size relations between body parts which often cannot be wholly understood in terms of adaptation. While the allometrically dependent feature almost certainly cannot be maladaptive (Gould 1974), it may well be adaptively neutral. Joubert (1956) has shown that in domestic sheep, as in most mammals, the cranial region of the skull grows rapidly pre-partum while the facial region is relatively undeveloped at birth and completes the major portion of its growth post-partum. This means that in young animals the facial region grows much faster than does the cranial region. If premaxillary width of canadensis rams and ewes is plotted against basilar length on a log-log scale (Figure 19), an approximately linear relationship is formed (ram $r=.9660$, ewe $r=.9531$). Fitting the allometric

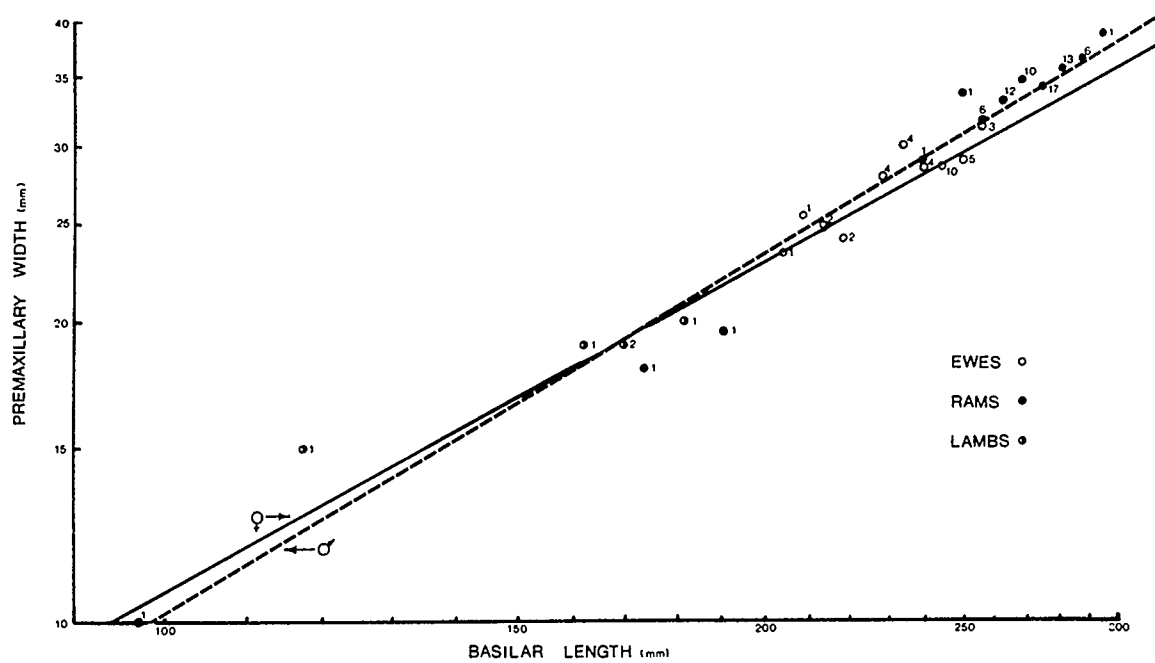


Figure 19. Premaxillary width versus basilar length of Rocky Mountain bighorns plotted on a log-log scale with the regression lines for ewes and rams.

equation (Simpson et al. 1960) using Bartlett's best fit yields the following relations:

$$P_{\sigma} = -1.4311 B_{\sigma}^{1.217 \pm .089}$$

$$P_{\varphi} = -1.1765 B_{\varphi}^{1.121 \pm .135}$$

where P is premaxillary width in mm and B is basilar length in millimetres. As expected, the premaxillary widths of both males and females increase faster than basilar length. Moreover, a t-test (Simpson et al. 1960) shows no significant difference in the exponents ($t = -.0505$, d.f. = 116) indicating no sexual difference in the growth rate of the premaxillae.

These results indicate that rams and ewes exhibit identical growth relations between the premaxillae and basilar length. The observed ram:ewe differences in muzzle width are due to more rapid and sustained male growth of the entire body. Females are therefore paedomorphic in relation to male neotony; a condition Geist (1971 p.332) attributes to sexual selection for increased male body and horn size.

Though dimorphism in mouth part size is attributable wholly to sexual selection, the ecological effect may be significant nevertheless. Hutchinson (1959) concluded that sympatric congeneric species differing morphologically in nothing but size exhibit ratios in linear dimensions averaging 1.2 to 1.4. This "Dyar-Hutchinson Rule" (Horn and May 1977) is a very simple measure of limiting similarity

between competitors. The observed ram:ewe differential in premaxillae width is close enough to the ratio to be of interest.

D. THE THERMAL NICHE

Because of the previously mentioned difficulties encountered in gathering meteorological data, the thermal niche will be treated very briefly.

That the Cascade Valley is subject to a thermal inversion has been pointed out by Geist (1971 p.274). It will be recalled that rams and non-rams exhibit spatial occupations patterns resulting in median elevation occupations nearly 200 ft (60 m) lower in non-rams than in rams. To what extent does this difference correspond with the thermal inversion zone and what are the bioenergetic consequences?

To determine the spatial extent and thermal magnitude of the inversion zone, I analyzed one of the few complete weekly weather records available--that for 22-29 December, 1975. This week was a normal one (no chinooks or heavy snowfall) although it was somewhat warmer than usual. Temperatures were recorded at two-hr intervals. Figure 20 shows the mean difference between the 5600 ft (1707 m) station and the four other stations based on 82 paired data. The mean difference in temperature between stations was different for all combinations of stations as determined by a paired t-test (Sokal and Rohlf 1969 p.330-332) (Table 26).

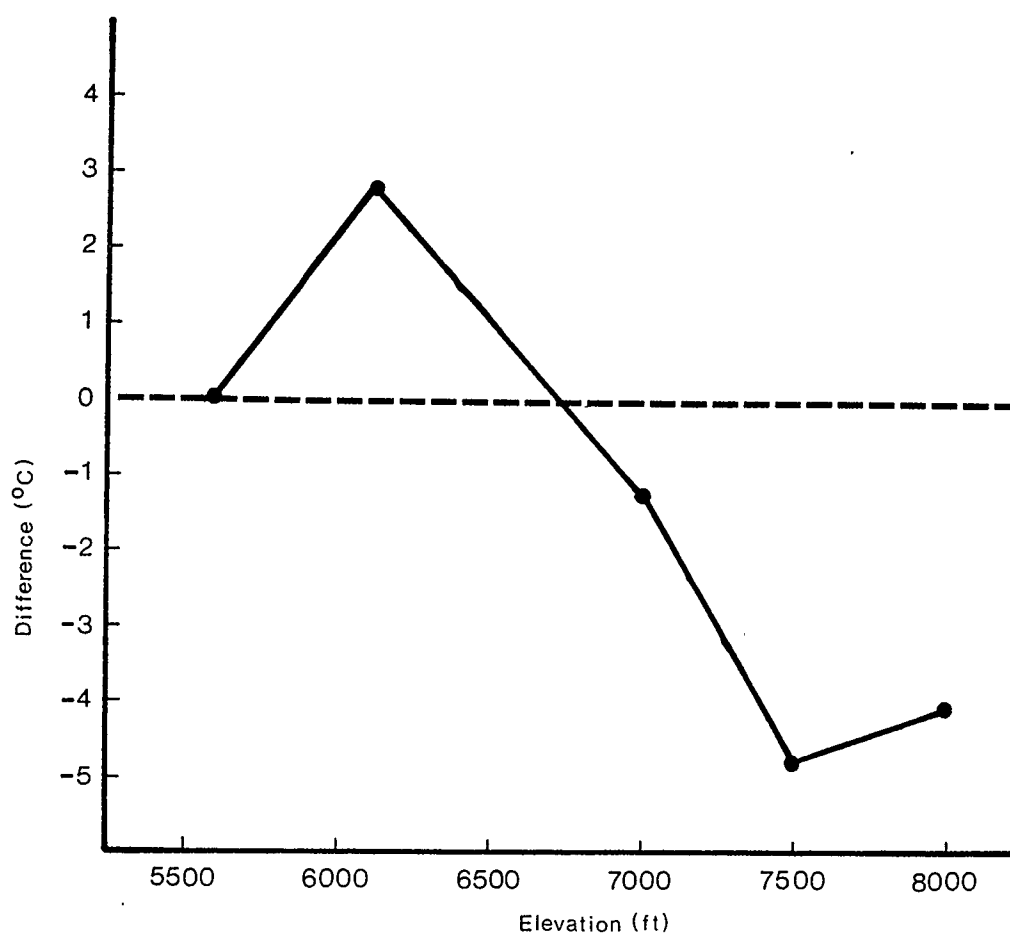


Figure 20. Mean temperature differences ($^{\circ}\text{C}$) between the station located at 5600 ft (1707 m) and stations at other elevations. Data are from the week of 22-29 December 1975.

Table 26. Mean difference (vertical axis minus horizontal axis) between 82 paired temperature observations at five elevations. Data are from the week of 22-29 December 1975. All differences are statistically significant.

	Elevation			
	6250 ft 1707 m	7000 ft 1905 m	7500 ft 2135 m	8000 ft 2285 m
5600 ft 1707 m	-2.8 ± 2.3 t = 11.34 r = .842	1.3 ± 2.4 t = 4.79 r = .831	4.8 ± 2.5 t = 17.26 r = .782	4.0 ± 2.6 t = 14.12 r = .763
	6250 ft 1905 m	4.1 ± 1.2 t = 32.13 r = .911	7.6 ± 1.6 t = 44.36 r = .847	6.9 ± 1.6 t = 40.17 r = .850
Elevation		7000 ft 2135 m	3.5 ± 1.5 t = 21.99 r = .858	2.8 ± 1.7 t = 15.16 r = .815
			7500 ft 2285 m	-0.7 ± 2.0 t = -3.43 r = .759

The temperature inversion zone centres around the 6250 ft (1905 m) level. At 7000 ft (2135 m) and above, temperatures are lower than on the valley floor. This suggests that the favourable thermal zone is a relatively narrow band at the lower extent of the sheep range with increasingly unfavourable temperature regimes at higher elevations.

To determine the effect of the combination of different altitudinal occupation patterns and the altitude effect on temperature, I estimated the mean temperature at 100 ft (30 m) intervals from Figure 20, multiplied by the percentage occupation by rams and non-rams at each elevation and divided the sum of these products by 100 yielding temperatures experienced weighted by occupation. For the week of 22-29 December, 1975, non-rams occupying the range as in Figure 8 would have experienced a mean temperature of -2.0°C ; in contrast, rams would have experienced a mean temperature of -2.5°C . The 0.5° difference cannot be considered as bioenergetically significant in view of the relative lack of importance of temperature to the heat loss of an animal as compared to the effect of wind speed (Shank and Geist, in prep.). Hoefs (1975) investigated occupation of thermal inversion zones by Dall sheep (Ovis dalli dalli) in the Yukon Territories and showed that sheep preferentially occupied colder zones.

V. DISCUSSION

A. SUMMARY AND INTEGRATION OF RESULTS

These investigations have covered a broad range of topics. Differences between rams and non-rams were found to be clear-cut and striking in some instances, in other cases significantly different in a statistical sense but only marginally important in a biological one, and in yet other instances, there were no noticeable differences at all.

The spatial segregation of rams and non-rams previously noted by Geist and Petocz (1977) was confirmed. Rams were shown to exhibit a broader spatial occupation breadth.

There were very noticeable differences in the structural niches of rams and non-rams. Rams utilized meadow terrain, snow-covered areas, and higher elevations to a greater extent than did non-rams. The areas used for feeding by rams and non-rams were characterized by vegetation containing significantly different proportions of common forage taxa.

The diets of rams and non-rams differed significantly while differences in feeding behaviour were less noticeable. Rams ate more Festuca, and less Carex, Poa, and Astragalus than did non-rams but these differences could be attributed to an area effect rather than class-specific diet preferences. Tentatively, at least, the average diet of rams was of higher quality than that of non-rams. Lambs

showed a temporal sequencing of feeding behaviour suggesting a more specialized diet than that utilized by ewes and rams. There was no evidence for this conclusion in the results of the diet analysis suggesting either that the behavioural findings were reflecting non-feeding differences (i.e., nervousness) or that there were actual diet differences in the parts of the plants selected which were not detected by the analyses used. There was no noticeable difference in the mobility of rams and non-rams during feeding which would have been expected if they were utilizing patchily-distributed forage in different manners.

Differences in mouthpart size between ewes and rams were of an order of magnitude found in sympatric congeneric species. These differences were, however, attributable to allometric relations and could not be demonstrated as having ecological significance.

The thermal advantages accruing to non-rams by remaining at lower elevations were shown to be minor and of negligible bioenergetic significance.

A majority of the observed niche differences between rams and non-rams can be related solely to spatial segregation onto areas of the range possessing different properties. Non-rams occupy lower elevations simply because their preferred range is lower in elevation than the rams'. Rams and non-rams forage on different plant communities because their preferred ranges are differentially vegetated.

Similarly, the diets of rams and non-rams reflects the vegetation present on their preferred ranges.

The only observed differences which cannot be related to an area effect are cliff occupation and snow-free area useage. Differential cliff utilization cannot be attributed to susceptibility to snow conditions as suggested by Geist and Petocz (1977) nor can it be explained as resulting from differential forage requirements. It is better explained in terms of susceptibility to predation as determined by body size. Similarly, use of snow-free areas is attributable to differences in body sizes allowing the stronger rams to be less constrained by deep snow than are the smaller and physically weaker non-rams.

The sexual niche differences noted are therefore of two classes; those related to body size differences and those related to differing spatial occupation patterns. Clearly, body size differences result primarily from sexual selection and ontogeny. Sexual differences in cliff occupation and snow-free area use are therefore adaptations to pre-existing sexual differences. In the case of niche differences resulting from range occupation patterns, the nature of the adaptation is not so clear. This problem is discussed in the next section.

B. CAUSATION OF SEXUAL SEGREGATION

The question arises as to whether sexual niche differences are the cause or the result of spatial

separation. If sexual niche separation results in spatial segregation, then niche separation can be viewed as an adaptation in itself. If, however, niche differentiation necessarily results from spatial segregation, sexual niche differences must be viewed as a secondary effect of whatever is causing spatial separation. Williams (1966 p.261) suggests "One should never imply an effect is a function unless he can show it is produced by design and not by happenstance." To evaluate this question it is necessary to develop an adequate explanation for spatial segregation of the sexes. Explanation, in this sense, requires the discovery and explication of the causal links between spatial segregation and those factors imparting maximal individual fitness. These causal links are framed as hypotheses the validity of which may, in some cases, be examined by empirical testing or thought experiments.

Any investigation of sexual group formation requires a prior discussion of why groups should form at all. Alexander (1974) has suggested that group living entails significant disadvantages to the individual and that rather than treat group formation as axiomatic, one must specify the advantages of group maintenance which are necessary and sufficient to offset the inherent disadvantages. In his review, he concludes that there exist only three reasons adequate to account for grouping. These are: (a) decreased likelihood of predation, (b) cooperation in food gathering,

and (c) extreme localization of a resource. He concludes that in primates only factor (a) is an adequate explanation of the phenomenon. Alexander (1974) is certainly too restrictive in this discussion; for example, the importance of grouping in reproductive functions is not discussed.

With respect to ungulates, most authors would, however, agree that grouping as an anti-predator strategy represents the major selective force for the formation and maintenance of groups. Evidence for this conclusion is indirect. Interspecific comparisons of ungulate faunas show that increased tendency to form groups is quite clearly associated with occupation of open terrain (Eisenberg 1966, Estes 1974, Geist 1974). This tendency can be explained as serving the following anti-predator purposes in the absence of hiding places: (a) cover-seeking within the group (Williams 1964, Hamilton 1971, Taylor 1976, Eshel 1978), (b) more effective predator detection (Galton 1883 in Triesmann 1975, Murton 1968, Pulliam 1973), (c) reduced detectability of a compact herd (Vine 1971, 1973; Triesmann 1975) and (d) cooperative defense (review in Wilson 1975). The items on this list are all plausible, non-contradictory, and not necessarily exhaustive. Anti-predation is perhaps not the only reason for grouping in bighorn sheep but there can be little doubt that it is the major force selecting for group formation.

Sexual segregation would appear to have little

importance in any of the above-mentioned anti-predator mechanisms. It would seem probable that sexual segregation is a secondary condition superimposed by selection over the basic tendency to form groups. What constitutes this secondary set of selective forces is a problem which has not yet been resolved by evolutionary theory. Few workers have tackled the subject and the few solutions proffered have been either ad hoc in nature, not broadly relevant, or equally amenable to alternate interpretation. Figure 21 presents a diagram of possible explanations organized into a hierarchical structure. The explanations contained in this diagram cannot be considered as exhaustive nor does acceptance of one necessarily imply rejection of others. Sexual segregation undoubtedly has a complex, multiple causation.

At the most inclusive hierarchical level of explanation, sexual spatial segregation can be considered as resulting from either a spatial difference in the distribution of resources which corresponds to different resource requirements of the sexes mechanically leading to separation of the sexes or from a necessity for the sexes to remain separate regardless of the properties of the areas occupied resulting in an arbitrary partitioning of space, created psychologically and maintained by cultural tradition. This primary separation is depicted in Figure 21 as the difference between "deterministic partitioning" and

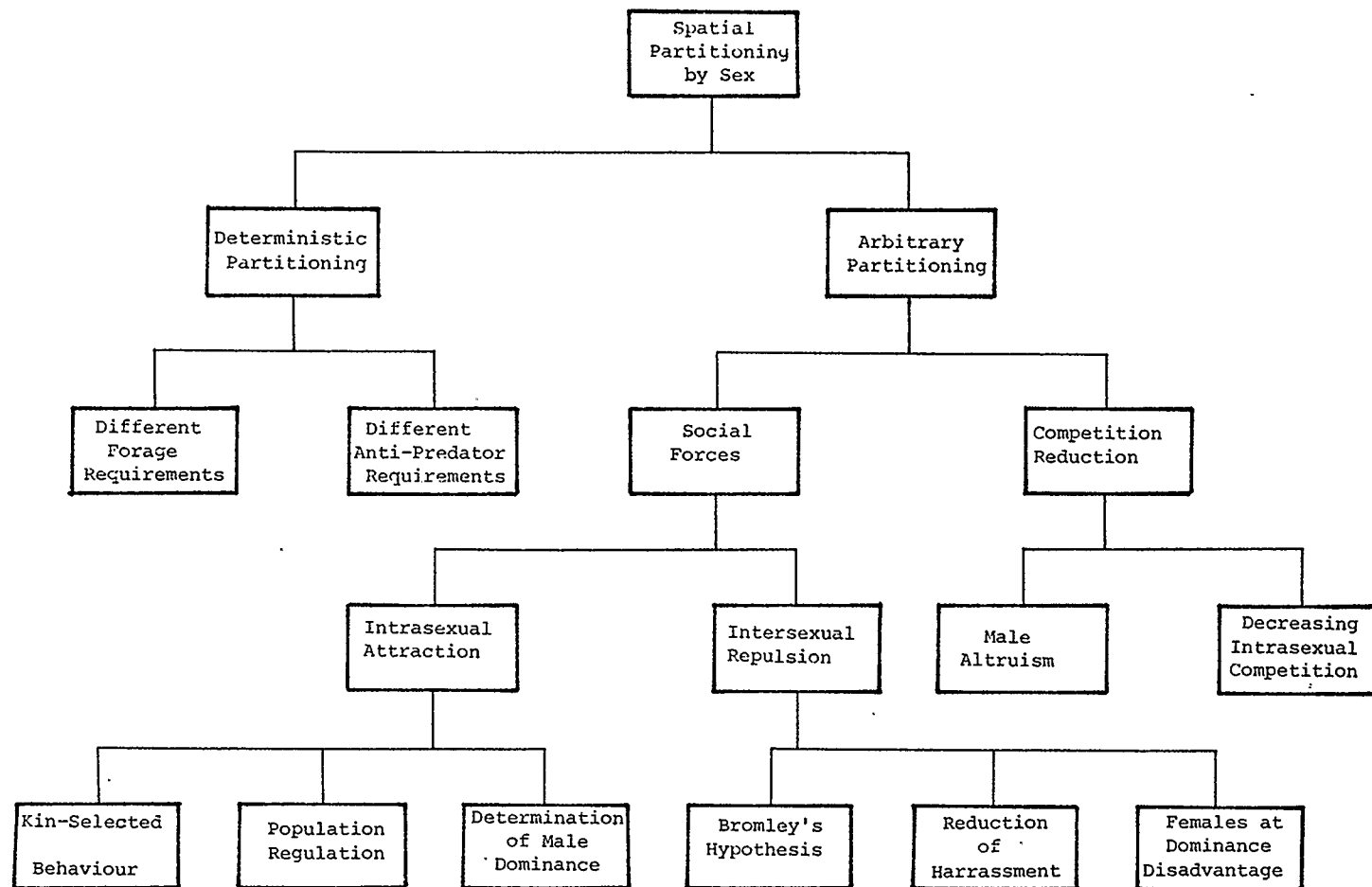


Figure 21. Hierarchical structure of possible explanations for spatial segregation of the sexes.

"traditional partitioning".

1. Deterministic Partitioning

It is to be expected that various components of the bighorn population will have different requirements and abilities to exploit the environment. For example, lambs, being small in body size, can be expected to require a higher quality diet than do the large rams and ewes (Bell 1971). Most ewes will bear a fetus and can be expected to maximize their nutrient intake in an attempt to produce as large and healthy a lamb as is possible. By contrast, rams have no pressing biological imperatives until summer when they must maximize their nutrient intake so as to enter the rut in prime condition. In the terminology for feeding strategies introduced by Schoener (1971), ewes will tend to be "energy maximizers" during winter while rams will tend to utilize the "time minimizer" strategy. Many other examples of class differences in winter requirements and abilities could be given. If the resources differentially required by the sexes were not uniformly distributed on the range, spatial segregation would result as rams and non-rams move to their separate preferred areas. This process is termed "deterministic partitioning" to suggest its straightforward, mechanical nature.

Unfortunately, this sort of hypothesis is inherently unfalsifiable since the set of resource requirements possibly causing separation is unbounded. Another problem

lies in the complexity of causation as is illustrated by the work of Shannon et al. (1975) wherein the predictability of the spatial distributions of non-ram bighorn sheep in British Columbia was determined through multiple regression against, and correlation with, 11 environmental variables. The study demonstrated strong interdependencies in the response to environmental factors which can best be explained as resulting from optimization over several conflicting demands. Similarly, Anderson et al. (1972) were able to explain only 13% of total mule deer (Odocoileus hemionus) spatial patterning by the presence of their favoured forage species. These studies suggest that environmental influence on spatial distribution is so complex that it is difficult or impossible to explain spatial distribution on the Palliser as any simple function of easily measured environmental influences.

A plausible hypothesis for spatial segregation based on deterministic partitioning might be that non-rams require more Carex and less Festuca than do rams hence they remain on ASU S where Carex is common and Festuca relatively rare. This hypothesis would appear to be false. All measures of forage quality showed Festuca to be superior in quality to Carex. It is possible that some unmeasured quality of these forage plants renders Carex more palatable to non-rams than is Festuca however this seems unlikely in view of the very high Festuca intakes of the non-rams on ASU M and ASU N

where Festuca is common. The inescapable conclusion is that non-rams are remaining on a range which is, in terms of available forage, inferior to that of rams.

Another hypothesis of this nature concerns the use of cliffs as escape terrain. Lambs appear to be susceptible to winter predation by coyotes (Canis latrans) on the Palliser Range while healthy rams would seem to be very nearly immune to such mortality (Shank 1977). Murie (1944) suggested that the presence of suitable escape terrain governs the size of Dall sheep range. It appeared that non-rams remained closer to cliffs than did rams on all portions of the range but the nature of my observations did not allow determination of linear distances. The favoured non-ram area, ASU S, contains a low-elevation rock rib running down its spine to the Stoney Creek valley (Figure 2) and therefore presents considerable escape terrain in close proximity to favoured feeding areas. ASU S, however, is apparently overgrazed and supports a plant community largely comprised of lower quality forage species. Rams, being less susceptible to predation could then be expected to move to areas offering less favourable escape terrain but better grazing. Spatial segregation would result.

This explanation is difficult to accept. First, it was not obvious that the escape terrain on ASU S was better than that of other portions of the range. If it were better, it would have to be so much so as to offset the disadvantages

of poorer grazing. This would imply that predator pressure on non-rams is extremely intense. In fact, there is little evidence that, at the present day, coyotes take more than a few sheep each winter. The phenomenon could of course have arisen as a result of intense predation in the past.

Secondly, Shannon et al. (1975) showed that proximity to escape terrain had no noticeable simple correlation with spatial distribution but a more complex multiple causation as indicated through partial correlation suggesting that anti-predation does not disproportionately influence distribution.

It is impossible to completely eliminate the possibility that rams and non-rams separate on the Palliser Range partly or wholly as a result of different resource requirements. However, the fact that non-rams are restricted to a small, low quality portion of the range with no obvious advantages accruing suggests that the range is not being partitioned deterministically.

2. Traditional Partitioning

Geist (1971) has emphasized that bighorn sheep are creatures of tradition which maintain from generation to generation the same patterns of distribution. Geist considers that bighorn sheep follow the pattern shown by domestic hill sheep wherein the home ranges are passed down as a tradition from mother to daughter (Hunter and Milner 1963). Geist (1971) states that young rams of 3-5 years of

age develop a life-long pattern of seasonal home range occupation based on the wanderings of the older rams whose company they keep during those formative years. If then, it were advantageous for any reason for rams and non-rams to remain separated from each other, a division of the range which is arbitrary in terms of environmental attributes could be strictly maintained by tradition for generations. The following discussion explores possible causes for such sexual separation in space.

i. Intrasexual Attraction--It is quite clear that intrasexual attractions can be a proximal reason for the formation of unisexual groups. For example, monkeys of the genus Callicebus typically form mated pairs in the wild while Saimiri monkeys form large unisexual aggregations. Under artificial conditions, Mason (1975) showed that Saimiri monkeys were far more attracted to members of their own sex than were Callicebus monkeys.

While intrasexual attraction may represent a perfectly understandable proximal mechanism causing sexual segregation in sheep, the ultimate selective advantages are unclear. One hypothesis is that the sexes might be more closely related to conspecifics than to members of the opposite sex. In this case, kin selected group behaviours would be most efficacious in closed unisexual groups.

There are several lines of evidence indicating that the individuals of non-ram groups are more closely related than

are the individuals of ram groups. In the most trivial case, lambs and yearlings share approximately 50% of their mother's genes. Although maternal investment (Trivers 1972) is considerably reduced following weaning, the lambs remain with the mother throughout the winter (Geist 1971 p.103-107). That ewes are solicitous of their lambs welfare in winter is evidenced by personal observations of obvious anxiety behaviour on the part of ewes whose lambs were being chased by coyotes.

As was mentioned above, ewes tend to remain with the female group into which they were born while rams at about three years of age begin to associate with adult ram groups which are continually splitting and coalescing as they move from one seasonal range to another. This is illustrated by the tagging experiments reported by Geist (1971 pp.91,108). The net result is that ewe groups will tend to have higher coefficients of relationship than will ram groups.

A third factor capable of contributing somewhat to higher inclusive fitnesses in non-ram groups has been discussed by Whitney (1976). In mammals, females have two X-chromosomes to the male's one. Assuming there is no genetic information on the Y-chromosome, daughters of a single mating receive 50% of the maternal sex-linked genes and 100% of the paternal ones while sons receive one of the mother's two X-chromosomes and no sex-linked material from the father. With respect to the sex-linked genes only,

sibling daughters therefore have a coefficient of relationship of 0.75 as compared to 0.50 for sibling brothers. The situation is identical to haplodiploidy in insects (Hamilton 1964, Trivers and Hare 1976) except that the asymmetrical relatedness occurs not in the entire genome but only in the sex-linked genes which account for only about 5% of the entire genetic composition of most mammals (Ohno 1969).

This asymmetry will of course only occur when the father of all offspring is identical as happens in multiparous clutches or repeated matings by a monogamous pair. Bighorn sheep are uniparous which limits the applicability of this mechanism. However, sheep are also highly polygynous with a very small number of rams doing most of the breeding during any single season. Therefore, female offspring from different mothers and the same father will be slightly more related than male offspring since the daughters will share the common father's X-chromosome while the sons will receive only one from the separate mothers. With respect to the sex-linked genetic material then, male offspring of a single breeding season will be essentially unrelated, while females sharing the same father will have a coefficient of relationship of 0.50. Hence, members of ewe groups will tend to be marginally more closely related to each other than will members of ram groups.

Unfortunately for this idea, the only suggested cases

of non-maternal altruism or cooperative behaviour observed in bighorn sheep has been performed by rams. These include apparently cooperative snow trenching (Geist and Petocz 1977) and cooperative defense against predators (Shank 1977).

Rams might be expected to exhibit intrasexual attraction based not on kin selection but on the high level of social interaction required for maintenance of the social mechanics of ram society during the mating season. Successful mating by a ram is dependent on its horn size and it is only through frequent sparring that an individual learns to relate his own horn size to that of other rams (Geist 1971 p.351). Gregariousness is a prerequisite for such a system to function. Rams are attracted to each other for the ultimate purpose of determining which of them will be doing the breeding in the next mating season. This mechanism does not fall into any of the categories listed by Alexander (1974) in his discussion of the causes of group formation and it might be argued whether this factor is a cause or a result of group formation.

Wynne-Edwards (1962) put forward a somewhat similar hypothesis of sexual grouping. He suggested that sexual aggregations allow assessment of population levels and adaptive response to overpopulation by determining how many individuals will breed. This type of explanation has been largely out of favour since Williams (1966) argued that the

group selection model that it presupposes is untenable.

ii. Intersexual Repulsion--Intersexual repulsion occurs when individuals of one sex either drive away individuals of the other or dissociate themselves from the vicinity of the other sex. It does not necessarily exclude the possibility of intrasexual attraction and would be most effective in causing spatial segregation if the two social forces were acting in a complementary fashion.

Bromley (1977) (in Geist and Petocz 1977) and Geist and Bromley (1978) have suggested a sexual segregating mechanism based on the principle of repulsion. The hypothesis states that males, exhausted from rutting activity, should either discard their obviously male morphological attributes such as horns or they should dissociate themselves from the unexhausted ewes. By doing either, predators will not associate the novelty of their male appearance in the non-ram group with their relative ease of capture and thereafter hunt them preferentially.

For a number of reasons, it appears that Bromley's hypothesis cannot explain sexual segregation in bighorn sheep. First, if the male's appearance in the ewe group is to be perceived as novel by the predator, then rams must occur in the group in small numbers or there is no disadvantage over the situation of the all-male group. This is homologous to the situation of a Batesian mimic (Wickler 1968). Nearly as many rams winter on the Palliser Range as

do non-rams (Figure 3). Therefore, either many rams will join the non-ram groups at no gain in fitness or some will dissociate from the non-ram group for reasons not specified by the hypothesis. Secondly, observations on the Palliser Range bighorns (Shank 1977) and on other ungulates (Murie 1944, Mech 1970, Schaller 1972) indicate that lambs and senile individuals are usually the most susceptible classes to predation. In bighorn sheep, this might not be the case immediately following the rut when large rams are completely debilitated by mating activity and therefore perhaps more prone to predation than lambs. Lambs are, of course, small in body size and fully as identifiable to a predator as are rams. Contrary then to Bromley's hypothesis, a ram might be expected to derive significant benefits throughout the late winter by remaining with the non-ram group since lambs are expected to be the primary target of any predators encountering the group. Lastly, sexual segregation is greatest in summer when rams are not exhausted from the rut and are clearly the least susceptible population component. Bromley's hypothesis is not adequate to explain sexual segregation on the Palliser Range although it may explain antler shedding in deer (Geist and Bromley 1978).

Another explanation based on social repulsion rests in the dominance relations of feeding sheep during winter. Petocz (1973) has shown that dominant rams on the Palliser Range exhibit a higher level of purely aggressive social

patterns to subordinate individuals when the winter is a strenuous one. If a subdominant individual is continually being displaced from favoured feeding or bedding sites or is excluded to the periphery of the group where he is more susceptible to predation, that individual should weigh whether he stands to gain more by remaining with the group or by leaving it (Pulliam 1973).

Ewes and juveniles are subdominant to all adult rams (Geist 1971). Automatically they are at a dominance and competitive disadvantage when in the company of rams. It is therefore advantageous for non-rams to dissociate themselves as a group from the rams. By doing so, all but the lowest ranking individuals gain relative dominance advantage and hence greater access to resources and less susceptibility to peripheral predation. Evidence against such an explanation is that very rarely do rams overtly displace ewes from either bedding or feeding sites suggesting that non-rams have little to lose by remaining with the rams.

Intersexual repulsion is susceptible to testing. If social repulsion does occur, we would expect that when any spatial unit of the Palliser Range has on it greater than the expected number of rams, there should also be less than the expected number of non-rams and the converse. This is a highly asymmetrical test in that a negative result does not necessarily mean that the hypothesis should be discarded. A positive result however, would be solid evidence for the

existence of intersexual repulsions.

The expected number of individuals was defined as the mean number of rams and non-rams observed per census trip during each month. For each census, the number of rams and non-rams was compared to the expected number and, if greater, a plus (+) was recorded. If less, a minus (-) was recorded. For each census on each unit, a plus-minus dyad can be defined indicating more rams than non-rams (+,-), more non-rams than rams (-,+) or more or less than expected of both ((+,+),(-,-)). If the repulsion hypothesis is correct, the numbers of rams and non-rams on any unit should be dependent while the number of heterogeneous dyads should exceed the number of homogeneous ones.

Table 27 shows the number of plus-minus dyads of each combination recorded over the entire winter. A 2 x 2 test of independence using the G-statistic (Sokal and Rohlf 1969 p.591-592) shows significant dependence of ram and non-ram numbers ($G=64.44$, d.f.=1). However, contrary to the requirements of the repulsion hypothesis, the homogeneous dyads outnumber the heterogeneous ones. This indicates that where there are more than the expected number of rams, there are also more than the expected number of non-rams. Therefore, if intersexual repulsion does occur, it is more subtle than can be detected by this test.

iii. Competition Reduction--Geist and Petocz (1977) suggest that the spatial segregation observed on the

Table 27. Repulsion-attraction dyads between rams and non-rams for the entire winter of 1975-1976. Pluses and minuses indicate respectively greater and lesser than the expected number of individuals observed on a unit during a particular census.

		Non-Rams	
		+	-
Rams	+	98	90
	-	76	322

Palliser Range can be explained by rams segregating themselves onto a separate portion of the range so as to reduce competition for food with their potential mates and present offspring. Competition reduction of this sort is as close to food-sharing or cooperative offspring rearing as a polygamous herbivore is ever likely to attain. The strongest element in favour of this hypothesis is that it explains why smaller rams do not dissociate themselves from the non-rams as completely as do the larger, breeding rams (Section IV.A.). Small rams have not, as yet, had the opportunity to breed and hence have no offspring to be altruistic towards. Also, rams less than 5 years of age will very likely fix a life-long breeding range occupied by females other than individuals of their maternal group. Therefore, by remaining and competing with the maternal group, they are unlikely to jeopardize the fitness of the prospective mothers of their offspring.

This hypothesis cannot, however, be sustained. If the range were uniform in its resource composition and if the rams and non-rams partitioned the range equally, neither class would gain since an identical number of animal-days grazing would accrue to any particular spatial unit under both regimes. Clearly, the partitioning must be unequal for the principle to be effective. If rams are considered as acting altruistically, it follows that non-rams must receive the "better" range; or at least more of it. It is very

difficult to test this for the same reasons that it is difficult to test deterministic partitioning. However, it would seem contrary to the actual case since the favoured forage genus, Festuca, is rare on ASU S and the spatial breadth of rams is larger than that of non-rams. If the rams are effecting a partitioning of the range, it is a very selfish one.

Another explanation of spatial segregation based on competition reduction is based upon a hypothesis to be outlined below. This hypothesis suggests that if ewes are better ecological competitors than are rams, and if intersexual competition is greater than intrasexual competition, the ram component of the population should be maintained only at the numerical level adequate for servicing of the ewes. It therefore becomes adaptive for rams to segregate themselves from the ewes thereby partitioning the total intrapopulation competition in a manner which minimizes intrasexual competition. This does not necessarily reduce the total amount of competition experienced by an individual but does alter the classes of the competitors. Derivation of this result first requires some explanation of standard competition theory which I have taken largely from the excellent discussion in Pianka (1975).

Given orthogonal axes representing numbers of two competing species (N_1 and N_2), an equilibrium isocline can

be drawn representing the numbers of Species 1 and 2 at which no change will occur in the numbers of either one of the species. In Figure 22, the line represents the condition where there is no increase or decrease in the numbers of Species 1; i.e., $dN_1/dt=0$. At Point A, Species 1 has reached its carrying capacity in the absence of Species 2, while at Point B, Species 2 has increased to the point that Species 1 can no longer exist. At any point to the right of the isocline, population levels of N_1 are too high for equilibrium and N_1 will decrease in the direction of the arrows. The converse holds when N_1 is to the left of the isocline as indicated by the right-pointing arrows. If the isocline representing $dN_2/dt=0$ is added, arrows signifying the approach to Species 2's equilibrium will run vertically. When both species are represented together, the approach to equilibrium is represented as the summation vector of the two arrow sets.

When the population equilibrium isoclines are represented for both species simultaneously, one of four conditions may hold (Figure 23). In Figure 23A, the Species 1 isocline lies above that for Species 2 and equilibrium will result where $N_2=0$ as indicated by the arrows. In Figure 23B, the converse situation holds and Species 2 outcompetes Species 1. In Figure 23C, each species limits the other more than itself. Three possible equilibrium points exist but there is no stable equilibrium point for

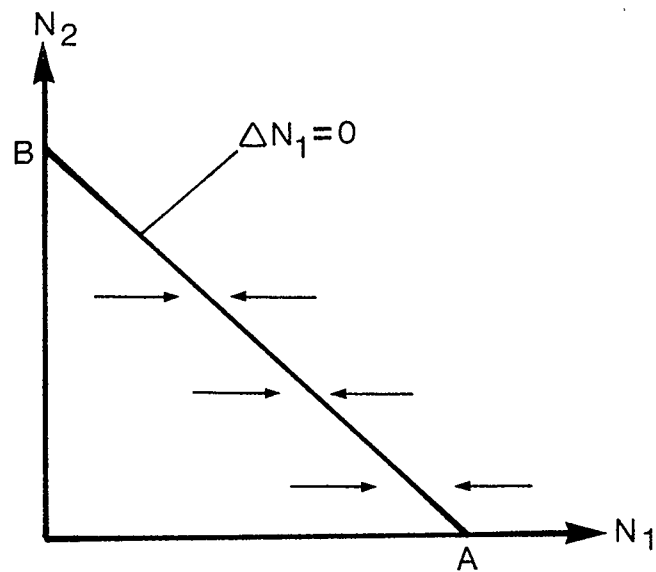


Figure 22. Conditions for population equilibrium of Species 1 in competition with Species 2.

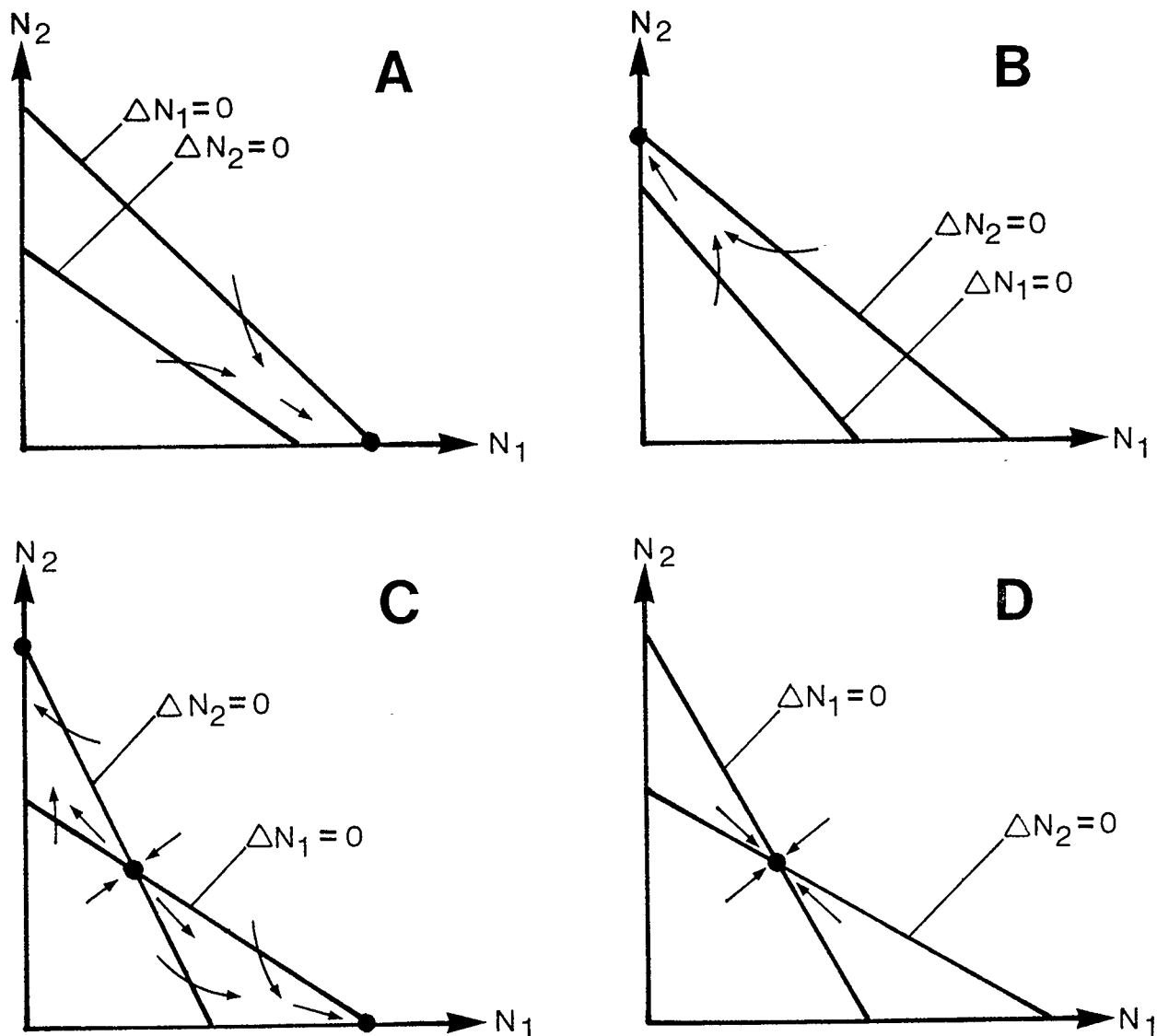


Figure 23. Population responses of two species in competition under four different competitive conditions. A represents the case of Species 1 being the better competitor. B represents the case in which Species 2 is the superior competitor. In the case of C, both species limit the other more than they limit themselves. Case D is the equilibrium condition in which both species limit themselves more than the other species.

coexistence. Either species could exterminate the other. Figure 23D represents the condition where each species inhibits its own population growth more than that of the other. A stable equilibrium point exists where the two species can coexist. The major point of this discussion is that necessary and sufficient conditions for stable coexistence of two competing species are that intraspecific competition exceeds interspecific competition.

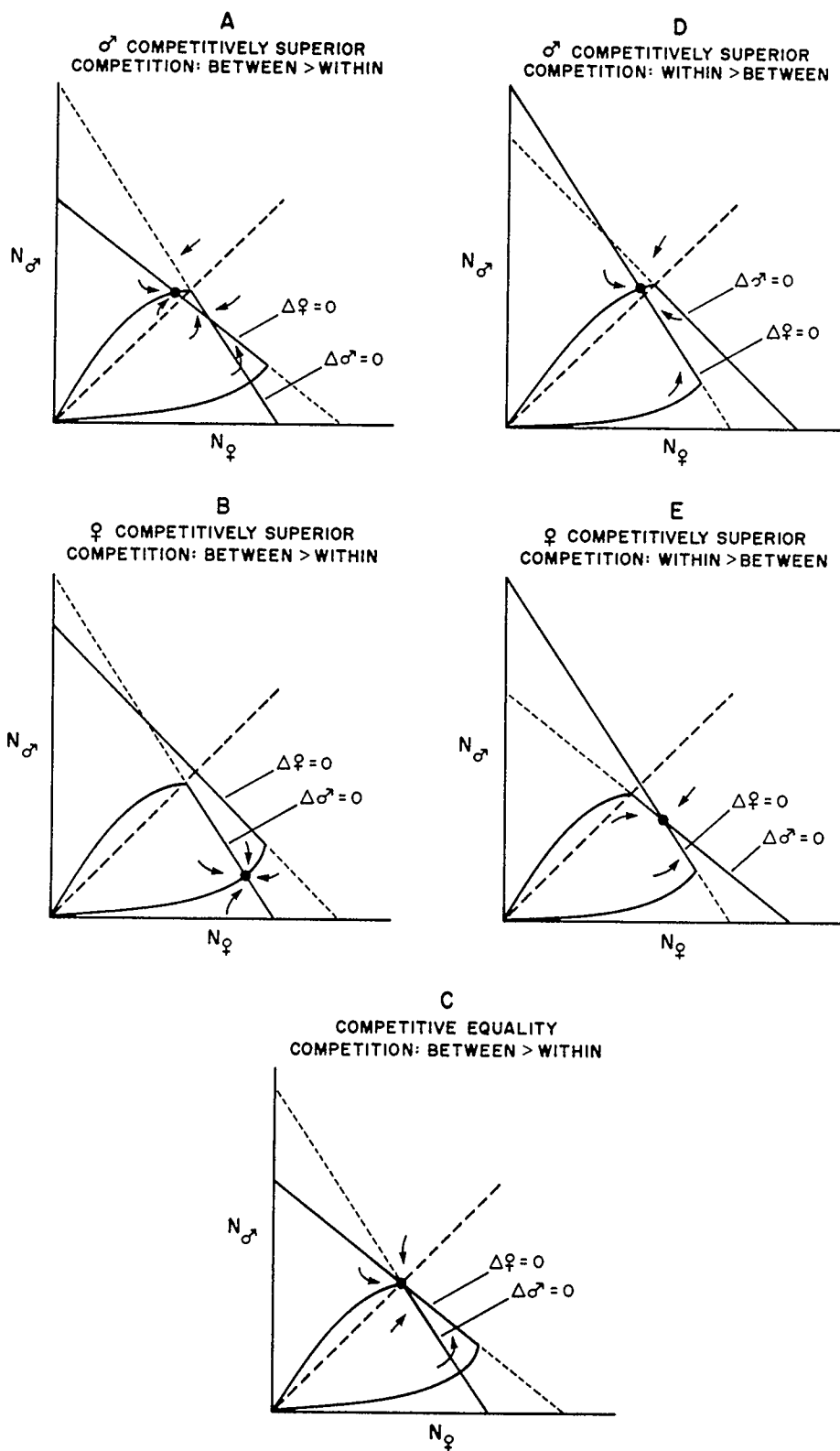
Utilizing a variation of the theoretical approach outlined above, Smouse (1971) examined the competitive relationships between competing sexes. He discovered that, as expected, competing sexes do not show the same responses as do competing species. In the case of monogamy, he found that intrasexual competition need not exceed intersexual competition for stable coexistence of the two sexes. Rather, the competitively superior sex occurs in the population in a greater proportion than the sex with the lesser competitive abilities. Continued coexistence of the sexes is a result of their reproductive interdependence wherein both male and female gametes are required for formation of a zygote and the offspring produced by the females tend to a 1:1 sex ratio (Fisher 1958, first published 1930). Smouse (1971) further suggested that this situation would apply, at least qualitatively, to polygamous species.

Quantitatively, however, the condition of polygyny does

result in significant differences in the numerical response of the sexes dependent on the relative amounts of intersexual and intrasexual competition. Figure 24 presents a series of diagrams describing several intersexual competitive situations. The curved components of the isoclines illustrate the reproductive interdependence of the sexes. An increase in the numbers of one sex requires the presence of the other. The lines are curved due to the approach to carrying capacity. The following analysis is dependent upon the basic sexual asymmetry in the curved portions of these isoclines. For either sex to increase in number, there cannot be significantly more males than females in the population. Hence the curved portion of the male isocline remains close to an equal sex ratio. However, when the population is below carrying capacity, both sexes of a polygynous population increase in number fastest when the number of females is great regardless of the number of males so long as there are enough males to service all of the females. Hence, the curved portion of the female isocline exhibits a very low slope.

Figure 24A indicates the case of male competitive superiority where intersexual competition exceeds intrasexual competition. As indicated by Smouse's model, males occur in a greater proportion in the population. Figure 24B presents the case of female competitive superiority again where intersexual competition exceeds

Figure 24. Conditions of ecological competition between sexes of a polygynous species. The curved portions of the isoclines represent reproductive interdependence of the sexes with the curvedness resulting from the influence of intersexual competition. A represents the case of male competitive superiority wherein intersexual competition exceeds intrasexual competition. B is the case of female competitive superiority again where intersexual competition exceeds intrasexual competition. Case C represents competitive equality between the sexes. Cases D and E show male and female superiority respectively wherein intrasexual competition exceeds intersexual competition.



intrasexual competition. Contrary to Smouse's model, males are maintained in the population not in a proportion relative to their competitive ability but only at the numerical level adequate for inseminating females. The sex ratio then reflects the degree of polygyny exhibited by the species.. Figure 24C shows the the case of competitive equality between the sexes where intersexual exceeds intrasexual competition. It indicates that, as in Smouse's model, the sex ratio will tend to equality. Figures 24D and E represent the cases of male and female competitive superiority respectively when intrasexual competition exceeds intrasexual competition. Comparison of Cases D and A shows that in the case of male superiority, the relative amounts of intra- and intersexual competition makes little difference in the sex ratio. Comparison of Cases E and B, however, shows that in the case of female superiority the relative importance of intra- and intersexual competition can influence the sex ratio profoundly. This is illustrated in Figure 25 which depicts the change in sex ratio under the influence of male and female competitive superiority and differing degrees of intra- and intersexual competition. As an initially superior competitive ability of males decreases to that of the females', the sex ratio approaches equality slowly and continuously (Figure 25A and B). However, in the case of female competitive superiority, the change in the sex ratio as competitive equality is approached, is

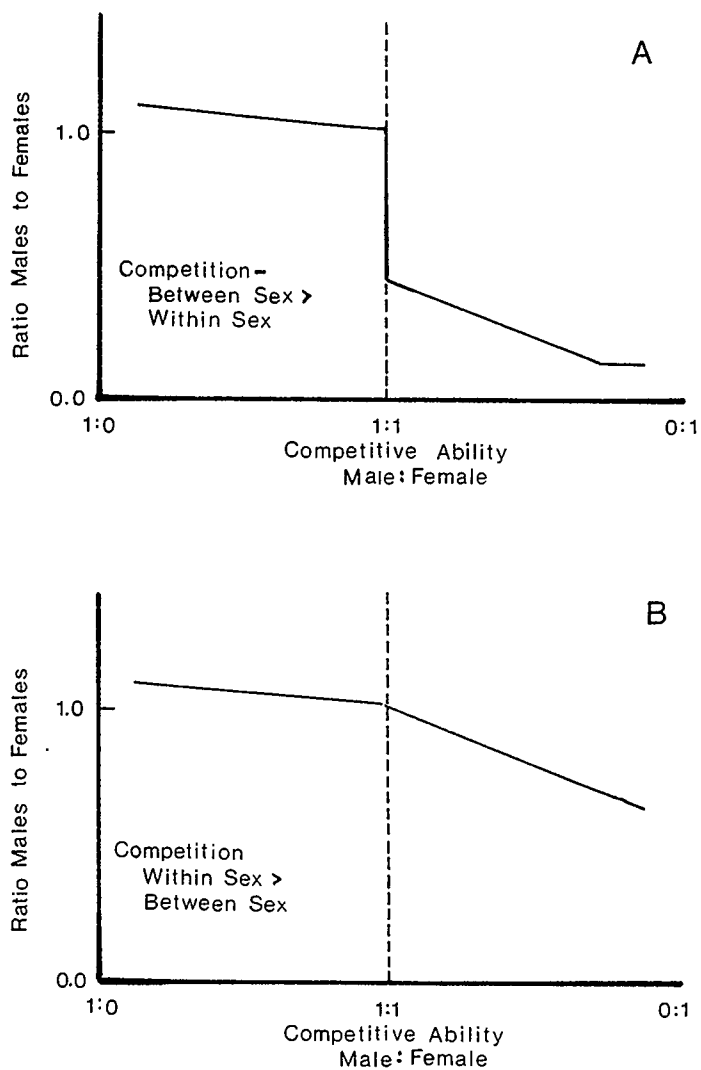


Figure 25. Approach to equal sex ratio under different conditions of male-female competitive superiority. In Case A, intersexual competition exceeds intrasexual competition. In B, the opposite case is represented.

dependent upon the relative importance of intra- and intersexual competition. As female ability decreases towards that of the male, the sex ratio does not change significantly from a decidedly female bias; that is, the sex ratio is insensitive to the relative competitive abilities of the sexes. As competitive equality is reached however, there is a sudden change in the sex ratio to equality. Unlike the case of male competitive superiority, this approach to an equal sex ratio is not continuous but a step function (Figure 25A).

These relationships between competitive abilities and partitioning of total population competition, suggest that it is to the advantage of individual males to partition the total intraspecific competition so as to minimize the intersexual component by maximizing the intrasexual component. If this were not possible and females were even slightly competitively superior, the males would tend to be maintained at a very low numerical level.

This phenomenon will be manifested only under certain conditions. First, intraspecific competition must actually be limiting the population. The characterization of the population quality as "poor" (Shackleton 1973) or "fair" (Stelfox 1976) and the generally stable number of individuals on the winter range over the past decade (Geist and Petocz 1977) both indicate that the Palliser bighorn population is proximally resource limited. Secondly, the

process should only be operative if the female range is not superior in quality to the male range. If the female range were the better one, it would be to the advantage of individual males to "cheat" and forage on the female range causing the entire system to break down. It has been repeatedly stated that in terms of forage quality the non-ram range is inferior to that of the rams. Lastly, non-rams must be such superior ecological competitors that density-dependent mortality is significantly greater among rams than among non-rams. There is no evidence for this supposition in bighorn sheep.

This rather lengthy discussion has not solved the problem of sexual segregation on the winter ranges of bighorn sheep but has suggested that some explanations outlined in Figure 21 are more plausible than are others. It seems unlikely that the sexes have partitioned the Palliser Range in such a manner as to best satisfy sex-specific requirements. It seems much more likely that one or several factors which are unrelated to site characteristics have dictated that the sexes should remain apart. This separation is most likely maintained by conventional occupation of different ranges the determination of which may originally have been arbitrary but has now become fixed by tradition. Hence, the observed differences between the sexes in diet are primarily results rather than causes of spatial separation.

C. SEXUAL NICHE SEPARATION AS AN ADAPTATION

The study was entered into with the full expectation that sexual niche differences would be noted in bighorn sheep that could be considered as adaptations for the reduction of intraspecific competition. This expectation was prompted by a number of factors. First, there were the initial findings of Geist and Petocz (1977) that rams and non-rams vary in use of cliffs and their suggestion that this had an ecological causation. Secondly, there was Ernst Mayr's assurance (1966 p.247-248) that the "...more closely a species is studied, the more likely it is that some evidence will be found for ecological polymorphism or gradual ecological variation.". Thirdly, there were the findings reviewed in Selander (1972) and Keast (1977) suggesting how widespread sexual niche differences are; particularly in birds. And lastly, there was the attractiveness of the idea that the sexes should reduce the competition between them by specializing in separate niches. Sexual niche differences were noted in this study but, as I argued above, they are better attributed to the results of sexual spatial segregation and adaptations to pre-existing body size differences than to primary adaptations for the purpose of competition reduction. In the following discussion, I suggest that sexual niche segregation as an adaptation for competition reduction has perhaps been

accepted too enthusiastically by some workers and that there are excellent reasons why bighorn sheep in particular should not be expected to exhibit this phenomenon regardless of its ultimate causation.

1. The Evolution of Sexual Niche Separation

Contemporary ecological theory has as one of its cornerstones, the premise that the width of a species' ecological niche will tend to be as broad as is allowed by the productivity of the environment and the presence of competing species.

A broad ecological niche can be the result of a monomorphic population composed of similar ecological generalists or it can result from a population maintaining several polymorphic specialist types. These morphs may be determined phenotypically, genotypically, or through some interaction of the two. Since sexual differences are in question here, I will limit the discussion to genetically determined differences. One form that ecological polymorphism can assume is sexual differences which adapt males and females to specialize in separate ecological niches. In recent years, this explanation has been commonly invoked to explain sexual differences in morphology and behaviour. Herein, I develop the thesis that the constraints on the evolution of such a system are more severe than is commonly realized.

i. Randomly Segregating Ecological Polymorphism--

Levene (1953), Maynard Smith (1962, 1970), Levins and MacArthur (1966) and Prout (1968) have produced theoretical arguments which show that stable multiple niche polymorphisms are possible without heterozygote advantage. Van Valen (1965) proposed a model based on this theory set and sought empirical validation by showing that populations inhabiting broad niches exhibit greater variance in the size of their trophic structures (i.e., bird bills). Diamond (1970) presented empirical evidence for behavioural differences in niches of different widths. The validity of this "niche variation" hypothesis has attracted considerable controversy (Grant et al. 1976).

The nature of genetically determined variation of this sort is that ecologically significant differences segregate out randomly with respect to sex and the parental niche. Since the morphs have different fitnesses in different niches, it is to the advantage of the parents to produce a mix of offspring types which produces the highest total fitness. If selection is density-dependent, natural selection will tend to adjust the numbers in the morph classes so as to equalize their fitnesses. This is the basis of Fisher's (1958, first published in 1930) theory of the sex ratio. Roughgarden (1972) has modelled the process whereby the distribution of the offspring becomes optimized based on the fitness of the various morphs in the various niches. If selection is density-dependent, at stable

equilibrium, which is reached very slowly in sexual species, the maximum number of individuals is maintained in the population. If selection is fluctuating and/or frequency dependent, population size need not be maximized (Slatkin 1978). That polymorphism tends to actually increase population size in nature is indicated by the extensive literature showing that polymorphic Drosophila populations maintain higher biomasses than do monomorphic ones (review in Souza et al. 1970).

ii. Sexual Niche Polymorphism--The above discussion considers the conditions under which randomly segregating ecological polymorphisms and interspecific character differences can evolve. What conditions favour segregation of ecologically polymorphic characters along sexual lines? Of particular interest is the question whether sexual niche differences can ever evolve purely as a means of reducing ecological competition between the sexes. In other words, given an adjacent "empty" niche, can one of the originally ecologically identical sexes evolve to fill it? Given that sufficient conditions exist for an ecological polymorphism as they are defined by Maynard Smith (1970), sexual niche differences might be attained if the genes governing the polymorphism were sex-linked. The necessary conditions for maintenance of a sex-linked polymorphism have been investigated by Bennett (1957, 1958), Haldane and Jayakar (1963), and Crow and Kimura (1970). Their results indicate

that stable polymorphism without heterozygote advantage can be maintained if it confers a relative selective advantage on one sex and if the allele at selective disadvantage in the homogametic sex is not dominant. The genetic mechanism therefore exists for the persistence of a stable, sex-linked genetic polymorphism.

From the viewpoint of the optimally reproducing parent, though, it seems unlikely that such a system could be maintained as an evolutionarily stable strategy (Maynard Smith 1976), or ESS, though it might be a genetically stable one. As Roughgarden (1972) has shown, if the niche polymorphism were to segregate randomly with respect to sex, the variance of the parents' offspring will gradually adjust toward a stable, optimal distribution wherein each parent maximizes his own fitness relative to other population members. If the morphs were to segregate sexually however, no such adjustment would be possible as this would entail changing the neonatal sex ratio. Fisher (1958, first published 1930) presented an argument to show that the sex ratio at birth should tend always to remain at equality. Leigh (1970) extended this argument to show that the principle is valid despite differential density-dependent mortality of the (adult) sexes. Hence, a parent cannot manipulate the proportion of sexual ecological morphs to an optimal distribution. Since the sexual niches cannot be expected to yield equal fitnesses due to the necessary

conditions of sex-linked polymorphism, it follows that the parents must place half of their offspring into a relatively inferior niche. This then is not an evolutionarily stable strategy since the individual parent can increase its own fitness by producing monomorphic offspring of both sexes which are adapted to the superior niche. By doing so, the parent decreases the niche breadth of the population and, hence population fitness, but momentarily at least, maximizes its own. Therefore, we would expect separate sexual niches evolved as sex-linked polymorphisms to eventually converge (see Ghiselin 1974 p.133). It should be noted that the mechanism as herein described implicitly requires that the nature of the polymorphism and its maintenance be controlled by separate loci. The use of such modifier loci in predicting long-term evolutionary trends is widespread in theoretical arguments (see Slatkin 1978).

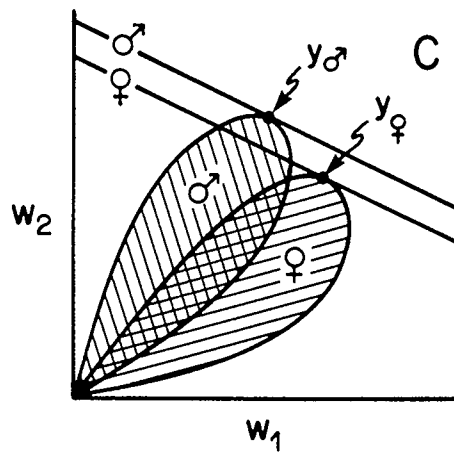
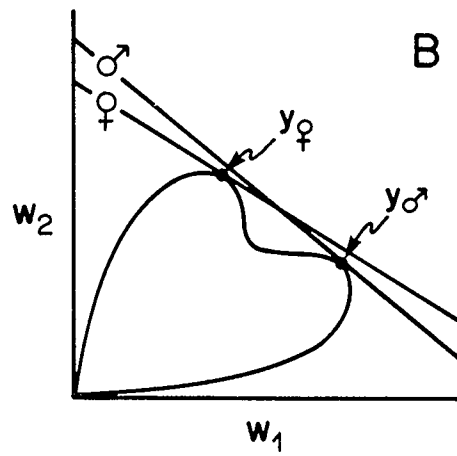
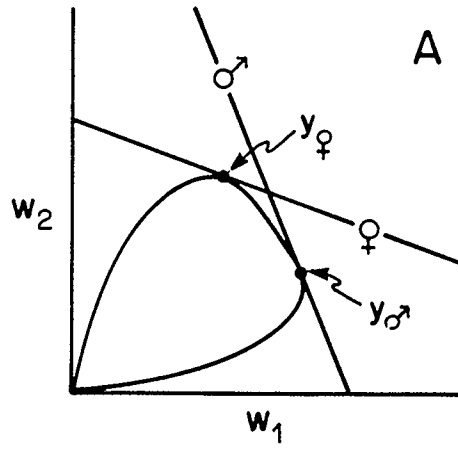
The question then becomes one of under what conditions will sexual niches not tend to converge and be stably maintained?

iii. Maintenance of Sexual Niche Separation-- There are at least two sets of conditions in which sexual separation of ecological niches can be maintained as a stable system. One instance is where pre-existing adaptively unrelated sexual differences act as a switch mechanism creating very different sexual niches which cannot converge because of the barrier erected by the

non-ecological selection. This can best be seen through the use of fitness set theory (Levins 1968, for a simple explanation see Wilson and Bossert 1971). Briefly, this theory utilizes two components; the "fitness set" and the "adaptive function". The fitness set is simply the cloud of points representing the fitnesses of each population member to two distinct aspects of its environment (W_1 and W_2 in Figure 26A). In some cases, high fitness with respect to one factor (high W_1) will be associated with high fitness with respect to the other (high W_2) yielding a fitness set convex in shape (Figure 26A). In other cases, a high W_1 will be associated with a low W_2 (or vice versa) resulting in a fitness set concave in shape (Figure 26B). The adaptive function is a family of parallel lines representing the relative fitness W_1 and W_2 needed to produce a constant overall fitness (K) in a particular environment. If the environment were to contain more of Resource 1 than of Resource 2, W_1 need not be as great as W_2 to produce a given K hence the adaptive function would exhibit a steep slope. The optimal strategy (y) is indicated by the intersection of the adaptive function with the fitness set at the point on the fitness set furthest from origin.

If, for a grazing animal, the fitness for use of Plant 1 is represented as W_1 and the fitness for use of Plant 2 as W_2 , the fitness of the population with respect to the use of these plants can be displayed as a fitness set. If males

Figure 26. Fitness sets for optimal strategies of the sexes under different conditions. In Case A, males and females are genetically similar but occupy different fine-grained habitats. Case B illustrates a convex fitness set. Case C illustrates the situation in which males and females differ genetically but occupy the same fine-grained habitat.



and females do not differ consistently in their ability to use these two plants and if there is little genetic influence on ability to use them, the fitness set will be convex (Figure 26A). Suppose further that females are more susceptible to predation than are males and hence remain closer to cliff terrain where Plant 2 is more common than Plant 1 while on the open slopes, where the rams remain, Plant 1 is more common than is Plant 2. The adaptive functions of the two sexes will therefore differ with that of the females being shallower in slope than that of the males (Figure 26A). The phenotypes corresponding to the sexually optimal strategy will also differ ($y_{\text{♀}}$ and $y_{\text{♂}}$) (Figure 26A). In the case shown in Figure 26A the male's phenotype yields the higher fitness but females would be unable to converge on it due to selection by predators to remain near the cliffs. If the genotypically determined ability to exploit Plant 1 and 2 differs markedly, the fitness set broadens and finally becomes convex (Figure 26B). In this case, even a minor difference in the slope of the adaptive functions can produce major sexual niche differences.

This argument can be inverted with the same results. Assume that the adaptive functions of the sexes are the same; i.e., males and females utilize the same environment. Assume, however, that there is some ecologically unrelated sexual adaptation, for example different body size, which

secondarily influences the fitness of the sexes when utilizing Plants 1 and 2. The fitness set for the population will then become divided sexually (Figure 26C). A single adaptive function will therefore produce different optimal strategies for the two sexes ($y_{\text{♀}}$ and $y_{\text{♂}}$) (Figure 26C). As shown by Levins (1968), this difference becomes yet more pronounced if the environment is coarse-grained. In the case shown as Figure 26C, males have the higher fitness but the females cannot utilize the same strategy by increasing their body size because body size is an adaptive response to a separate set of selective pressures. The major point is that sexual niche differentiation requires the pre-existence of sexual differences either in requirements or abilities which are maintained by unrelated selective forces. These conclusions are logically similar to Vance's (1978) findings that switching predators (May 1977) can maintain coexistence of two prey species which are exploiting identical resources only if the prey species differ in ways unrelated to resource competition.

Another instance in which sexual niches will not converge is the case in which males and females cooperate in the care of their mutual offspring. Sexual niche segregation allows specialization on different portions of the species niche and hence more efficient provision for the needs of the young. In this case, individuals of one sex should be "willing" to exploit a relatively inferior niche if it were to increase the fitness of the offspring.

This is commonly interpreted as sexual niche separation as a means of reducing competition between the parents. As Ghiselin (1974 p.133) has pointed out, this interpretation is incorrect. Competition requires that two or more individuals each have their own "wants" which are fulfillable by a single resource (Milne 1961). In the case of parental cooperation, there is a mutually held "want" (raising offspring) and often the capability of using more than one resource to fulfill it. The parents are not in competition with each other but are acting as a unit in competition with other parental units. Similarly, the sporting goods department of a large department store is not competing for customers with the hardware section but is acting cooperatively with it in competition with other department stores.

In summary, sexual niche differentiation would appear never to evolve as a means of reducing competition between the sexes since the sexual niches would tend to converge toward the better one. Only two situations were found capable of accounting for the maintenance of separate sexual niches as an evolutionarily stable strategy. These were (a) the prior existence of sexual differences in requirements or abilities as adaptations to unrelated selective pressures, and (b) division of labour between mates cooperating in the care of their offspring.

2. Resource Type

The existence of ecological polymorphism necessitates that the environment be partitionable. The degree to which resources can be partitioned is dependent upon a combination of the productivity and graininess of the environment. Levins and MacArthur (1966) defined a fine-grained resource as one which is encountered in the proportion that it occurs in the environment while a coarse-grained resource is one which is unevenly distributed allowing it, through consumer choice, to be encountered either more or less than in the proportion that it exists. All things being equal, coarse-grained resources are therefore more easily partitionable since once the "space" of a coarse-grained resource is entered, it may be exploited preferentially without the need to enter another resource space.

Highly productive environments, such as those encountered by populations invading an island with an impoverished fauna, allow the occupation of very broad niches. Individuals will tend to specialize in various portions of the wide niche thereby lessening competition among them. This is the condition of "ecological release" defined by MacArthur and Wilson (1967).

Highly productive environments can be partitioned regardless of resource grain. Since resources are present in surfeit, morphs may specialize on different components of a fine-grained resource or may specialize on certain patch types. However, ecological polymorphism is possible in low

productivity environments only when the resource is coarse-grained and available in large, but rare, units. If the resource unit is common but contributes little to the individual's total requirements, no particular item can be passed up in the hope of finding a better one with the result that all individuals will act as generalists. If, however, each rare occurrence with a resource unit satisfies a large proportion of an individual's requirements, it can afford to be discriminating. Schoener (1965) showed that those closely related bird species which utilize large prey of low total biomass differ more in bill size than closely related species subsisting on common, low quality food. Earhart and Johnson (1970) demonstrated this in the intraspecific case of owls in which species specializing on large and rare vertebrate prey exhibit more sexual dimorphism than do species preying on small but ubiquitous arthropods. The existence of ecological polymorphism therefore requires that resources be located at either end of the spectrum; either they must be extremely common or rare but high in quality.

Based on these criteria, it seems most unlikely that bighorn sheep should exhibit sexual niche partitioning during winter. First, the productivity of the range is low since the quality of the forage decreases with weathering. Wallmo et al. (1977) showed that winter deer range was not adequate in quality to maintain any deer at all on a

sustained basis. Although alpine vegetation is of higher quality than lowland forage (Johnston et al. 1968, Hebert 1973) the harsher conditions at high elevation will tend to offset this advantage. Secondly, the forage resources on the Palliser Range are evenly distributed and more fairly characterized as fine- than coarse-grained with respect to grazing sheep. Keast (1977) concluded that this factor alone was adequate to dismiss out of hand the possibility of sexual niche segregation in ungulates.

3. Interspecific Competition

MacArthur (1968) pointed out the dangers of a species becoming highly specialized in separate niches. He showed graphically that if two phenotypes exploit a given resource space as generalists with considerable niche overlap, it is very difficult for another phenotype to invade. However, if the phenotypes become differentially specialized, a generalist phenotype can, under some conditions, invade and replace one or both of the specialist types. Hence, broad niche width through ecological specialization of the sexes may allow high population levels but it also leaves the population susceptible to replacement. Species which coexist with ecologically similar competitors can therefore be expected to show little sexual niche differentiation. This is particularly true when more than two species compete and thus allow "diffuse competition" (Pianka 1974) to come into effect.

The effect of interspecific competition on sexual niche differences is clearly illustrated by Husar's (1976) work on the food habits of Myotis bats. When these species exist sympatrically, there are significant differences in the diets of the species but no sexual differences. When allopatric populations were compared, there were no interspecific differences noted but sexual diet differences were obvious in both species.

Bighorn sheep share the Palliser Range with elk (Cervus canadensis) and mountain goats (Oreamnos americanus). Until late winter, elk graze during the mornings on the lower and middle portions of the meadow zone. Particularly in late fall and early winter, though, they are frequently seen as high as the rock-meadow interface. Mountain goats, by contrast, remain in the cliff zone throughout most of the winter with their lowest distribution overlapping the sheep's highest use of the cliff terrain.

Van Dyne et al. (1979) have calculated a similarity index (Kulczynski's) for the diets of elk, mountain goats, and mountain sheep based on reports in the literature. Utilizing the percentages of grass, forbs, and shrubs, they found that the three species were about 90% similar in their diets (Van Dyne et al. 1979, Table 4.9). To obtain a rough idea of the diet similarities of elk, goats, and sheep on the Palliser Range, I collected a small number of faecal samples from elk and goats in March 1978. These samples

were analyzed by the same method as were the sheep samples. Fifteen elk samples were compounded and 20 fields were read while 20 fields were read from each of five goat samples. This meagre sample size is adequate only to suggest very general diet trends.

The data, together with the corresponding March values for sheep, are presented as Table 28. This table shows that all three ungulates are concentrating heavily on Festuca. Elk also consume large quantities of Bromus while goats utilize Picea extensively. Kulczynski's index (Oosting 1956) is an appropriate measure of similarity in this case. Because of the unequal sample sizes, more taxa appear in the sheep sample. Therefore, only the shared taxa may be used in the comparison. This index indicates that the diets of goats is 64% similar to both elk and sheep while the elk diet is 72% similar to that of sheep.

These findings are rather crude but adequate to suggest that interspecific competition might well become significant if Festuca were a limiting resource. This is perhaps adequate to create selection pressures against sexual niche specialization in bighorn sheep.

D. IMPLICATIONS FOR WILDLIFE MANAGEMENT

As discussed in the Introduction, documentation of specific sexual niche differences would allow wildlife managers a greater level of precision in determining carrying capacity and planning management programmes. In

Table 28. Diets of elk, mountain goats, and bighorns. Elk data are based on one reading of 15 samples. Mountain goat data are based on five samples each with one reading. Bighorn data are the total March set consisting of 51 samples.

Taxon	Elk	Goats	Sheep
<u>Bromus</u> sp.	25.2	2.0	4.7
<u>Carex</u> sp.	3.6	9.8	8.9
<u>Danthonia</u> sp.	--	0.6	--
<u>Festuca</u> sp.	56.6	47.3	70.5
<u>Koeleria</u> sp.	3.6	4.3	8.5
<u>Poa</u> sp.	--	0.6	1.1
<u>Equisetum</u> sp.	3.6	--	--
<u>Picea</u> sp.	3.6	35.5	0.5
<u>Shepherdia</u> sp.	3.6	--	--
Total	99.8	100.1	94.2

fact, little sexual niche separation was noted in this study of wintering bighorn sheep suggesting that wildlife managers would be justified in treating the niche requirements of bighorn sheep as singular. What was shown in this study however, was that spatial segregation of the sexes can entail significant sexual niche differences as a secondary effect. In those species exhibiting sexual segregation, wildlife managers would be well advised to take this factor into account.

A study in which treatment of such spatial differences might well have resulted in different results is exemplified by Stelfox's (1975, 1976) investigation of bighorns on the Palliser Range and elsewhere in the Canadian Rocky Mountain Parks. On the Palliser Range, Stelfox limited his habitat study to the area characterized as Unit 3 in this study. Unit 3 is almost solely occupied by rams during the winter while non-rams remain largely on Unit 12 (Figure 7). By extending his findings of the conditions of Unit 3 to the entire range and the entire population, Stelfox was, in effect, characterizing the population's habitat from data pertinent primarily to rams. My findings indicate that Unit 12 is characterized as maintaining less favourable forage resources than other portions of the range. Had Stelfox investigated conditions on the non-ram range as well, he would perhaps have revised his characterization of the Palliser population quality from "fair" to the "poor"

condition suggested by Shackleton (1973) based on a completely different analysis.

This criticism should not be construed as a denigration of Stelfox's valuable work. Rather, it is an example of the manner in which repeated studies of the same subject can generate findings that are increasingly detailed. Without the data base provided by the work of Stelfox, Geist, Petocz, Shackleton, and the Banff Warden Service, this study would have been impossible. Hopefully, Parks Canada will continue to approve non-manipulative studies of the Palliser bighorns so that this capital of existing information can continue to produce returns in the form of a better understanding of bighorn sheep biology.

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