5-1973

Impact of the Black-Tailed Jackrabbits (Lepus Californicus) On Vegetation in Curlew Valley, Northern Utah

Mark Westoby
Utah State University

Recommended Citation

Westoby, Mark, "Impact of the Black-Tailed Jackrabbits (Lepus Californicus) On Vegetation in Curlew Valley, Northern Utah" (1973). *All Graduate Theses and Dissertations*. 2151.
https://digitalcommons.usu.edu/etd/2151

IMPACT OF BLACK-TAILED JACKRABBITS (LEPUS CALIFORNICUS) ON VEGETATION IN CURLEW VALLEY, NORTHERN UTAH

by

Mark Westoby

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Science

(Ecology)

ACKNOWLEDGEMENTS

I thank warmly Frederic H. Wagner for his invaluable help throughout this study. I am also very grateful to the other members of my committee, David F. Balph, Kent W. Bridges, David W. Goodall, James A. MacMahon, Ivan G. Palmblad, Neil E. West, for their generous outlays of time.

I thank Charles Stoddart and John Weaver for help in collecting jackrabbits for stomach analysis. Deborah Donahue, Greg Rost, William E. Saul, and Jim Weis analysed stomachs. John C. Malechek gave much time to advising us in that work.

Barbara Rice contributed extensively in field-work, data analysis, and criticism of manuscript and ideas; I am very greatly beholden to her.

This work was supported by NSF grant GB 15886 to the US/IBP Desert Biome.

Mark Westoby

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

ABSTRACT

Impact of Black-tailed Jackrabbits (*Lepus californicus*) on Vegetation in Curlew Valley, Northern Utah

by

Mark Westoby, Doctor of Philosophy

Utah State University, 1973

Major Professor: Dr. Frederic H. Wagner
Department: Wildlife Science

The interrelations of black-tailed jackrabbits and the desert-shrub vegetation on which they were feeding were studied in Curlew Valley, Northern Utah. The vegetation was described as a three-cornered continuum, the corners being types dominated respectively by *Artemisia tridentata*, *Atriplex confertifolia*, and *Sarcobatus vermiculatus*.

Jackrabbit diet was studied by microscopic analysis of plant fragments in stomachs from shot animals. The method was inaccurate, apparently because the ratio of identifiable tissues to all ingested tissues was very low, and varied between plant taxa, and seasonally. This problem seems intractable for desert shrub vegetation.

The diet was similar to that reported by other workers on this species, with perennial grasses and forbs most important in spring and summer, shrubs in autumn and winter. Features new to this vegetation were large percentages of *Halogeton glomeratus*, particularly in autumn and winter, and intense selection for *Kochia americana*. Attempts to explain the foods chosen in terms of their nutrient contents were partically successful.

Diet selection by large generalist herbivores was conceptualized as optimization of nutrient intake, mediated by long-delay learning, and constrained by food availability only at very low levels of availability. Spatial variation in jackrabbit diets confirmed this "cut-off" response to availability.

Percentage utilization was estimated indirectly as jackrabbit density, times yearly food consumption per jackrabbit, times year-round percentage of each taxon in the diet, divided by available biomass of each taxon. Less abundant plants were more intensely used, which is expected if consumption does not vary continuously with availability. Perennial grasses, *Kochia americana* and possibly *Grayia spinosa* seemed to be under damaging pressure at high jackrabbit densities.

Kochia had almost disappeared from outside a sheep- and jackrabbit-proof exclosure since the 1950's. In other exclosures, the presence or absence of jackrabbits seemed to make no difference to the rate of vegetation recovery over 5-7 years after exclusion of sheep.

Jackrabbit use of a crested wheatgrass seeding was concentrated in a 300 m band around its edge.

(178 pages)

INTRODUCTION

The question of the degree to which grazing and browsing herbivores affect the structure and function of vegetation has interested ecologists for many years. The most common sources of information on this question are of an empirical and experimental nature, and (1) either involve purposeful manipulation of animal numbers and their pressure on the vegetation, or (2) they involve observations on vegetative changes which accompany natural variations in herbivore numbers.

The field of range management provides much of the information in the first category, with its experimentation in intensity and timing of livestock grazing (e.g., Hutchings and Stewart, 1953; Blydenstein et al., 1957; Holmgren and Hutchings, 1971), and in the use of exclosures against stock, wild ungulates, and rodents (e.g., Taylor, 1930; Fitch and Bentley, 1949; Norris, 1950). In the second category, natural variations in herbivore numbers provide fortuitous experiments which permit observation on vegetation changes (e.g., Leopold et al., 1947; Buechner and Dawkins, 1961; Glover, 1963; Smith, 1965; Elton, 1966).

Effective as these observations are in demonstrating the effects of grazing pressures on vegetation, they do not often give information on the complex of mechanisms linking the grazer and the vegetation. These mechanisms would seem to include such processes and entities as:

(1) The nature of the vegetation in the first place.

(2) The numbers and kinds of herbivores present on this vegetation.

(3) The quantitative food need of these herbivores.

(4) The qualitative food need in terms of diet selection, and the complex of mechanisms effecting that selection.

(5) The physiological and morphological changes to individual plants of each species under different levels of herbivorous removal.

(6) The population responses of each plant species to the changes in its individuals.

(7) The sum-total vegetation changes which the population changes effect.

This study has sought to make a small start on this complex of processes in the case of black-tailed jackrabbit (Lepus californicus) use of Great Basin desert vegetation in the northern Intermountain area. Specifically, it has explored the question: what changes in the botanical composition of a plant community would result from the presence of a given number of black-tailed jackrabbits for a period? In the language of systems analysis, a time-curve for jackrabbit density is the input variable, and the botanical composition of the plant community is the output variable. Quite likely, changes in the plant community would affect the population dynamics of the jackrabbits. But this feedback has not been studied here.

Given a figure for the density of jackrabbits, we need to answer the following questions:

(1) What amounts of different plant species are available?

(2) What amounts of different plant species are eaten?

(3) What proportion of the available biomass of each plant species is being removed?

(4) What, in detail, is happening to the plant species which are under significant pressure? This question might be subdivided: What other damage is there to the plants beside the removal of material which is eaten (e.g., trampling, rubbing, removal of material which is wasted)? How does the mean utilization of the plant species (from question 3) translate into defoliation patterns of individual plants? What are the responses of individual plants to these patterns of defoliation? To what plant population response do these individual responses add up?

Questions 1-3 constitute a first step. We should try to answer them for all plant species. Question 4 is a second step; it is to be answered for selected plant species.

If these questions could be answered, we would have a prediction of a new plant community, i.e., a new answer to question 1. With a new value for jackrabbit density, we could iterate through the questions again. This would be a simulation.

When we answer the questions the first time, field data on foods selected can be used to answer question 2. On later iterations, though, the plant community will have changed. The foods which are eaten must then be predicted, not measured. (Of course, if the plant community does not change, the whole process is trivial.)

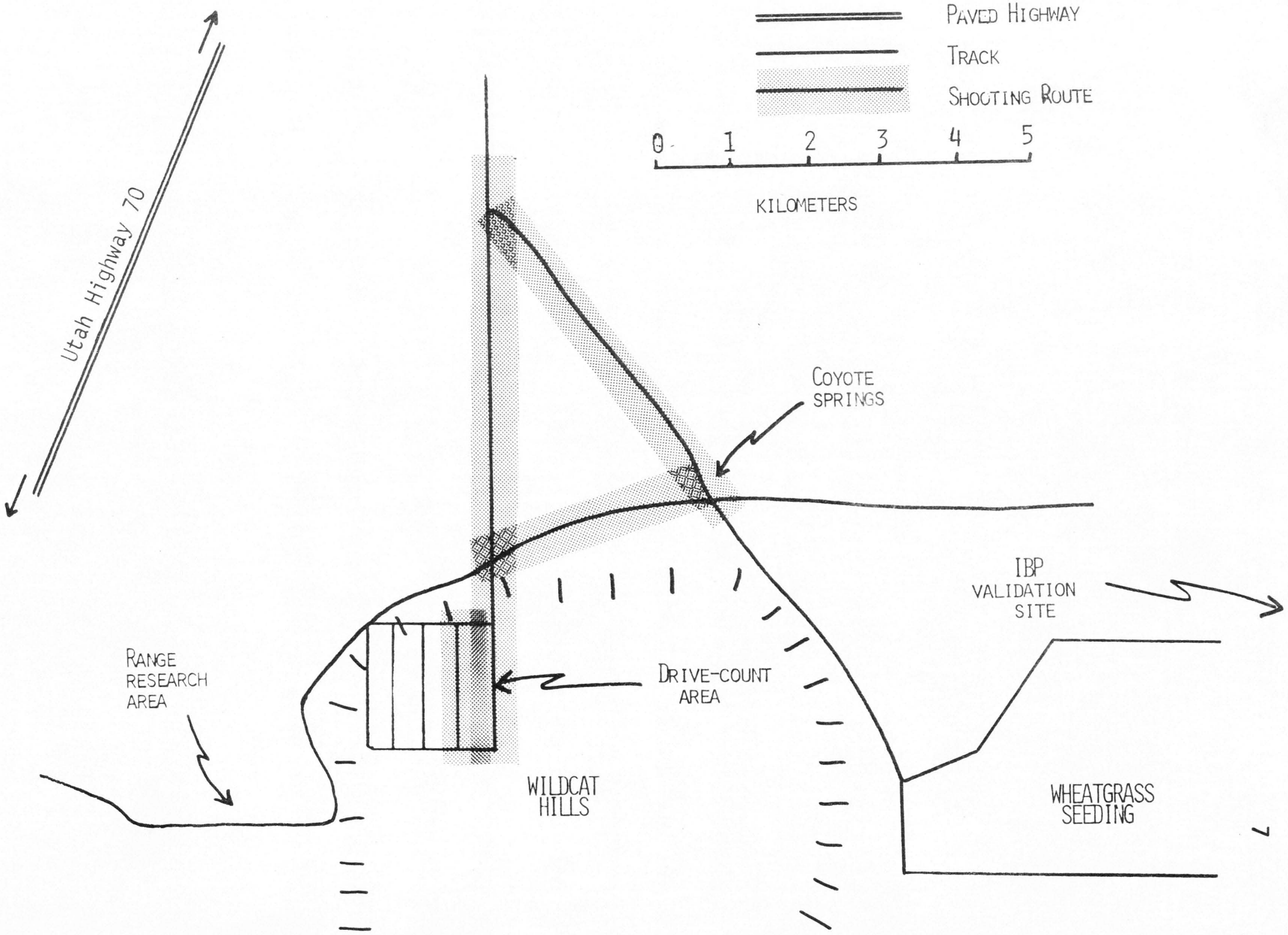
This study has tried to answer the first three questions, and also looked at how the foods chosen might be predicted as the plant community changes. In answering question 3, it has proposed hypotheses about jackrabbit effects on the vegetation. These were then compared with results from some exclosures in Curlew Valley, the Utah-Idaho area in which the study was conducted. Accordingly, the three major parts of this report are (1) an analysis of the vegetation in the study area, (2) an analysis of jackrabbit food selection, and (3) estimates of jackrabbit impact in terms of the vegetative removal from each plant species.

THE STUDY AREA

Curlew Valley extends north across the Utah/Idaho border from the shore of the Great Salt Lake. Elevation increases from about 1300 m at the lake shore to 1600 m at the north end of the valley. Total annual precipitation, while very variable, correlates roughly with elevation, ranging from 15-20 cm in the south to 35-40 cm in the north. Although there are some summer convectional rains, most of this moisture falls between autumn and spring, usually with a peak in April and May. A substantial proportion falls as snow.

There is a series of concentric vegetation zones within the valley, determined partly by the precipitation gradient, and partly by the increasing salinity of the soils left behind by the lake during its retreat. The vegetation of the northern part of the valley is dominated by _Artemisia tridentata_ (Nutt.). (Plant names follow Holmgren and Reveal, 1966.) Saltshrub communities dominate much of the southern end of the valley, with such species as _Atriplex confertifolia_ (Torr. & Frem.) S. Wats., _Atriplex falcata_ (M. E. Jones) Standl., and _Eurotia lanata_ (Pursh.) Moq. Low-lying areas are often dominated by _Sarcobatus vermiculatus_ (Hook.) Torr.

The studies described here were mainly carried out within the area shown in Figure 1, which is in the middle part of the valley. It can be considered a broad transition zone between the sagebrush type to the north and the saltbush types to the south, with associations belonging to both types forming a mosaic in the transitional area. The soils are for


PAVED HIGHWAY
TRACK
SHOOTING ROUTE
0 1 2 3 4 5
KILOMETERS
Utah Highway 70
COYOTE SPRINGS
IBP VALIDATION SITE
RANGE RESEARCH AREA
DRIVE-COUNT AREA
WILDCAT HILLS
WHEATGRASS SEEDING

the most part silty loams. The Wildcat Hills have coarser soils; *Juniperus osteosperma* (Torr.) Little and *Artemisia arbuscula* Nutt. var. *nova* (A. Nels.) Cronq. appear on them. Perennial grasses (mainly *Sitanion hystrix* (Nutt.) J.G. Smith, *Poa Sandbergii* Vasey, and *Oryzopsis hymenoides* (Roem. & Schult.) Ricker are more abundant there, and the forb flora is richer. Similar changes are found on the foothills to each side of the valley.

Other noteworthy shrub species in the area are *Grayia spinosa* (Hook.) Moq., mainly found around the skirts of the Wildcat Hills; *Kochia americana* S. Wats., found as an understory in *A. confertifolia* or *Sarcobatus* communities; and two *Chrysothamnus* species. *Chrysothamnus nauseosus* (Pall.) Britton occurs mainly around Coyote Springs. *Chrysothamnus viscidiflorus* (Hook.) Nutt. occurs locally on the valley floor, on coarse soils derived from sandbanks of ancient Lake Bonneville, and more generally on the Wildcat Hills.

The three most abundant annuals are *Halogeton glomeratus* (Bieb.) C.A. Meyer, *Lepidium perfoliatum* L., and *Bromus tectorum* L.

Coyote Springs is a dissected area, which at one time was intermittently flooded by a nearby spring. The water from the spring is now collected in cattle troughs, but the soil in the area is still saline. The vegetation contains a number of characteristically salt-tolerant species, such as *Distichlis spicata* (L.) Greene, and *Sporobolus airoides* (Torr.) Torr.

To the east of the Wildcat Hills is an area which was chained in 1963 to remove *Artemisia tridentata*, and seeded to *Agropyron desertorum* (Fisch.) Shult. Such seedings are common in the *Artemisia* zone. A "validation site" of the US/IBP Desert Biome lies across the boundary of this seeding further to the east. This is a site where selected ecosystem variables are regularly monitored, providing a check on the simulation models built by the Biome program.

A series of unpaved roads, henceforth called the shooting route, was driven while collecting jackrabbits for stomach analysis. This route is shown in Figure 1.

On the north slope of the Wildcat Hills is a square mile which is used for drive-counts of jackrabbits in demographic studies (Gross et al., in press). This provided a valuable reference point, as a definite location at which the absolute abundance of jackrabbits was comparatively accurately known.

To the west of the Wildcat Hills is an area which has been used for many studies of range ecology over the past 25 years. In particular, it contains a number of exclosures, established in 1957, 1966, and 1968.

The black-tailed jackrabbit, *Lepus californicus*, is the only *Lepus* species on the study area, although there are two *Sylvilagus* species. Parts of the area are subject to winter sheep grazing and year-round cattle grazing.

PART I. VEGETATION ANALYSIS

Introduction

This section deals with studies of the composition of the vegetation on the study area. The object was to describe the vegetation universe from which jackrabbits were selecting their food, and which that feeding activity was affecting. Results are expressed as two main kinds of data. First, mean available biomass of each taxon over the shooting route is estimated. These figures, combined with data on removals of material by jackrabbits from each taxon, allow utilization estimates to be derived; and these in turn permit comparison of the relative impact of jackrabbits on different plant taxa. Second, some of the spatial variation in availability of different foods was estimated. Combined with data on the stomach contents of animals shot at known locations, this allows conclusions to be drawn about the response of diet to availability.

Methods and Materials

Vegetation Composition

During the spring of 1972, 36 step-point transects (NAS/NRC 1962) were placed arbitrarily along the shooting route, in order to measure the perennial vegetation (Figure 7). They were located in such a way that each subjectively recognizable vegetation type had some transects placed in it. To make a step-point transect the observer walks across the vegetation in even paces, with the eyes fixed upon the distant horizon. A mark is made on the toe of one boot. When that boot is planted at each pace, a vertical line is imagined through the point on the toe. Vegetation which is intercepted by this line is recorded. A point was said to be covered by a plant species if it fell within a continuous curve drawn around the outline of the plant canopy. Each transect thus gives presence/absence data at a number of points (here usually 150-300). The points were two paces apart, so the transects were 300-600 paces long. The data are converted into percentage cover values. The method generally tends to overestimate cover values, because the intercepting line is not in practice infinitely thin.

These data were examined by principal components analysis. The mathematical basis of this method is discussed by Pielou (1969) among others. The sequence of operations is as follows: first an n-space is set up, where n is the number of attributes which have been used to describe the transects--in this case the number of plant taxa, plus the two categories "open space" and "dead plants." Each transect then becomes a data-point in this n-space. The procedure then constructs a new axis, which explains as much as possible of the variation in this cloud of points; i.e., it finds a line about which variance is minimal. Then a second axis is found, which explains as much as possible of the variance remaining after that explained by the first axis is removed. This procedure can be continued for as many principal components as seems fruitful. A weighting of each attribute along each principal component is also obtained. The data were not standardized, so the analysis is dominated by variation in attributes with the largest numerical values.

Principal components analysis has been criticized lately (e.g., Gauch and Whittaker, 1972; Beals, 1973). When the abundance of some of the species studied has a maximum within the range sampled, the response across the range must clearly be nonlinear. But the variance-minimizing principal components analysis assumes linear response. The result is distortion of one-dimensional continua, twisting them into other dimensions.

To check whether or not principal components analysis was generating spurious results, I also analysed the data by Bray-Curtis ordination (Bray and Curtis, 1957). This method gave the least twisting of continua when compared with several other ordination procedures (Gauch and Whittaker, 1972) and was also recommended by Beals (1973).

The data from the step-point transects were used as the starting point in mapping the abundance of chosen species. For each species, the percentage cover measured in a given transect was written in at the appropriate location for that transect on a preliminary map of the area. The transect results were then grouped into two to four "cover-classes." Generally, each cover-class corresponded to a recognizable vegetation type. For example, *Artemisia tridentata* abundance was described in three cover-classes of 0-5, 5-10, and 10-15 percent. The first had the aspect of an *Atriplex confertifolia* type with scattered clumps or bands of *Artemisia*; the second had continuous *Artemisia* cover with greater or lesser admixtures of *Sarcobatus*; the third was *Artemisia* without important amounts of other large shrubs.

In this way preliminary maps were drawn, assigning a cover-class to each section of the shooting route. The shooting route was then examined carefully on the groud. Cover-classes were assigned visually to parts of the route where no step-point transects had been made, and the boundaries between cover-classes were placed more exactly.

Biomass Estimates

Available biomass was estimated from percentage cover. I have assumed that there is a relationship between the two of the form

$$\text{Biomass} = k(\text{Cover}) \qquad [1]$$

since in semi-desert shrub vegetation the density of plant foliage does not seem to vary with plant abundance. In order to estimate available biomass from cover we need a "biomass/cover ratio" (k in equation 1). This can be estimated from any location where measures of both biomass and cover are available.

Some available biomass data existed from the US/IBP Desert Biome validation site. Accordingly I took four step-point transects on this site. This allowed the biomass/cover ratio to be estimated for *Artemisia tridentata*, *Atriplex confertifolia*, and *Sitanion hystrix*. The biomass/cover ratio for *Artemisia* was also applied to *Sarcobatus* and to *Grayia*, which are of similar growth form.

Kochia americana and *Chrysothamnus viscidiflorus*, although not very abundant, were found to be important in the jackrabbit diets. Accordingly special methods were used to estimate biomass/cover ratios for them. Cover had also to be estimated for *Kochia*, which was not detected by the step-point transects due to its low abundance, and because most transects were examined rather early in the spring before it had made much growth from the root crown.

Transects were placed at various locations along the shooting route. Circular quadrats, with 1 m radii, were placed ten paces apart along each transect. Long and short crown diameters and height were measured for each individual *Kochia* and *Chrysothamnus* plant. The available biomass was harvested from each plant in arbitrarily chosen quadrats, oven-dried and weighed. Utilization was estimated by eye for *Chrysothamnus*. *Kochia* data were collected between the 6th and 10th of May, 1972, and *Chrysothamnus* data between the 8th and 10th of October, 1972.

Volume (V) of *Kochia* was computed as the volume of a hemi-ellipsoid (Figure 2a):

$$V = \frac{\pi}{3} \cdot (\text{height})^2 \left(\frac{3}{2} (\text{long diameter x short diameter})^{1/2} - \text{height}\right) \qquad [2]$$

Volume of *Chrysothamnus* was computed as the volume of an inverted cone (Figure 2b):

$$V = \frac{\pi}{12} \cdot (\text{long diameter x short diameter x height}) \qquad [3]$$

Regressions of available biomass on volume were calculated for each species. The regression equations were then applied to the measurements on individual plants to obtain estimates of biomass per unit area. Cover was estimated for both species as:

$$\text{Cover} = \frac{\pi}{4} (\text{long diameter x short diameter}) \qquad [4]$$

(a)

(b)

Figure 2. Photographs of (a) Kochia americana, at top, and (b) Chrysothamnus viscidiflorus, at bottom, to show their outlines.

These data allowed biomass/cover ratios to be obtained for *Kochia* and for *C. viscidiflorus*, and *Kochia* to be mapped into cover-classes.

Estimates of mean biomass over the shooting route as a whole were obtained as follows. The median percentage cover of each cover-class was multiplied by the biomass/cover ratio. This gave an estimate of biomass for each cover-class. These biomass estimates were then weighted according to the proportion of the shooting route occupied by that cover-class, and averaged.

Results and Discussion

Vegetation Composition

Results from 36 transects along the shooting route and four on the Desert Biome validation site (Table 1) show that *Sarcobatus vermiculatus* and *Artemisia tridentata*, followed by *Atriplex confertifolia*, dominate the vegetation of the study area. Live vegetation covered 23.1 percent of the ground, and standing dead vegetation a further 9.1 percent, leaving 67.8 percent uncovered.

When the data were subjected to principal components analysis, the first principal component mainly described variation in the amount of open space; the second variation from *Artemisia*-dominated to *Atriplex*-dominated communities (Table 2 and Figure 3).

Table 1 . Percentage cover by bare ground, standing dead, and perennial plant species on the transects

	Percentage Cover at Transect Number									
Covering object	1	2	3	4	5	6	7	8	9	10
1. *Open Space*	62.9	65.9	68.5	66.8	60.5	63.2	91.7	55.1	84.9	84.7
2. *Standing Dead*	16.1	15.9	10.3	10.2	7.9	3.8	0.8	1.1	3.8	3.6
3. *Artemisia tridentata*	6.3	7.9	9.4	5.1	2.6	0.5	0.4		0.9	1.8
4. *Atriplex confertifolia*										
5. *Sarcobatus vermiculatus*	14.6	10.3	11.8	17.5	15.3	18.1	1.8	10.3	10.4	8.4
6. *Chrysothamnus viscidiflorus*					7.4	9.3				
7. *Chrysothamnus nauseosus*							2.2	8.6		1.1
8. *Sitanion hystrix*										
9. *Oryzopsis hymenoides*										
10. *Opuntia polyacantha* [a]				0.5	0.5					
11. *Sporobolus airoides*					5.3	4.9	0.7	11.9		0.4
12. *Distichlis spicata*					0.5		2.5	10.8		
13. *Suaeda fruticosa* [a]								2.2		
14. *Leptodactylon pungens* [a]										
15. *Tetradymia spinosa* [a]										
16. *Phlox hoodii* [a]										
17. *Artemisia arbuscula*										
18. *Elymus cinereus* [a]										
19. *Grayia spinosa*										

---

[a] Opuntia polyacantha Haw.; Suaeda fruticosa (L.) Forsk.; Leptodactylon pungens (Torr.) Nutt.; Tetradymia spinosa Hook. & Arn.; Phlox hoodii Rich.; Elymus cinereus Scribn. & Merr.

Table 1 . (Continued.)

Covering	Percentage Cover at Transect Number										
object.	11	12	13	14	15	16	17	18	19	20	21
1.	66.3	86.3	58.2	51.7	60.0	68.8	76.5	62.9	54.0	70.8	70.0
2.	23.6	7.5	17.6	10.2	11.4		4.4	9.5	15.1	2.9	5.2
3.		3.1	1.3	3.4		5.0	2.2			2.4	3.3
4.	10.1	3.1	15.7	23.1	23.8	3.5	13.2	26.7	30.2		
5.			5.9	10.9	6.7	10.6	2.2		0.8	24.4	21.9
6.											
7.						7.1	1.5				
8.	6.3		7.2	5.4	4.8	1.4	2.9	1.7			
9.						2.1					
10.			0.7								
11.											
12.						5.7	1.5				
13.											
14.											
15.											
16.											
17.											
18.											
19.											

Table 1 . (Continued.)

Covering	Percentage Cover at Transect Number											
object.	22	23	24	25	26	27	28	29	30	31	32	33
1.	75.8	76.1	75.0	76.2	92.5	70.6	63.6	39.2	44.3	64.9	66.4	65.3
2.	2.4	4.3	6.3	2.3	0.7	13.4	11.4	20.0	17.1	14.9	16.4	11.1
3.	2.1	3.6	8.6	10.0		10.3	13.0	32.3	32.1	19.3	8.2	16.7
4.									0.7			
5.	19.7	13.8	9.4	9.2	2.2	4.1	9.2	0.8			3.6	4.2
6.						2.6	2.7	2.3	6.4	0.9	5.5	2.8
7.					3.0							
8.		0.7	0.8	0.7				13.1	7.8	3.5	1.8	
9.				2.3				2.3	1.4	0.9		
10.								1.5			0.9	
11.												
12.		2.2										
13.												
14.			0.8									
15.					1.5							
16.								0.8				
17.								0.8				
18.												
19.												

Table 1 . (Continued.)

Covering object.	34	35	36	81	82	83	84	Mean of shooting route.	Percentage of live vegetation.
1.	73.8	62.5	64.0	48.1	43.2	52.4	54.5	67.8	
2.	6.9	10.0	8.1	17.1	20.0	12.5	13.2	9.1	
3.	10.8	8.8	11.6	19.2	19.0	12.5	13.2	6.8	26.9
4.				10.8	11.4	11.9	12.6	4.2	16.6
5.	3.8	16.3	3.5					8.4	33.2
6.	4.6	3.8	12.8	3.1	2.9	10.1	6.0	1.7	6.7
7.								0.7	2.8
8.	0.8		1.2	13.9	17.5	6.0	13.2	1.7	6.7
9.								0.3	1.2
10.			1.2					0.1	0.4
11.								0.6	2.4
12.								0.6	2.4
13.								0.1	0.4
14.								0.0	0.0
15.								0.0	0.0
16.								0.0	0.0
17.								0.0	0.0
18.								0.0	0.0
19.								0.1	0.4

Table 2. Loadings of site attributes along the first four principal components of variation in 40 step-point transects, and percentages of total variation explained by each component

Attribute	Loading Along Principal Component			
	1	2	3	4
Open Space	100.0	4.7	-62.1	22.0
Standing Dead	-42.0	0.3	-23.1	100.0
Artemisia tridentata	-47.0	-69.7	-41.8	-12.7
Atriplex confertifolia	-32.2	100.0	-6.3	-6.0
Sarcobatus vermiculatus	25.7	-19.8	100.0	41.0
Chrysothamnus viscidiflorus	-10.6	-14.5	0.4	-27.0
Chrysothamnus nauseosus	3.3	0.9	4.3	-39.3
Sitanion hystrix	-31.9	5.0	-18.7	-5.7
Oryzopsis hymenoides	-2.2	-3.9	-2.2	-6.1
Opuntia polyacantha	-1.8	-2.2	-1.0	0.4
Sporobolus airoides	0.8	-2.3	16.8	-36.8
Distichlis spicata	2.2	0.4	8.7	-41.4
Suaeda fruticosa	0.0	-1.0	1.7	-6.6
Leptodactylon pungens	0.1	-1.1	-1.1	0.1
Tetradymia spinosa	0.6	0.1	-2.1	-1.9
Phlox hoodii	-1.4	-1.5	-1.1	-1.1
Artemisia arbuscula	-1.4	-1.5	-1.2	-1.1
Elymus cinereus	-1.5	0.1	-1.4	-1.5
Grayia spinosa	0.0	-1.7	0.1	-1.5
Percentage of variation explained	55	20	13	4
			Total = 93%	

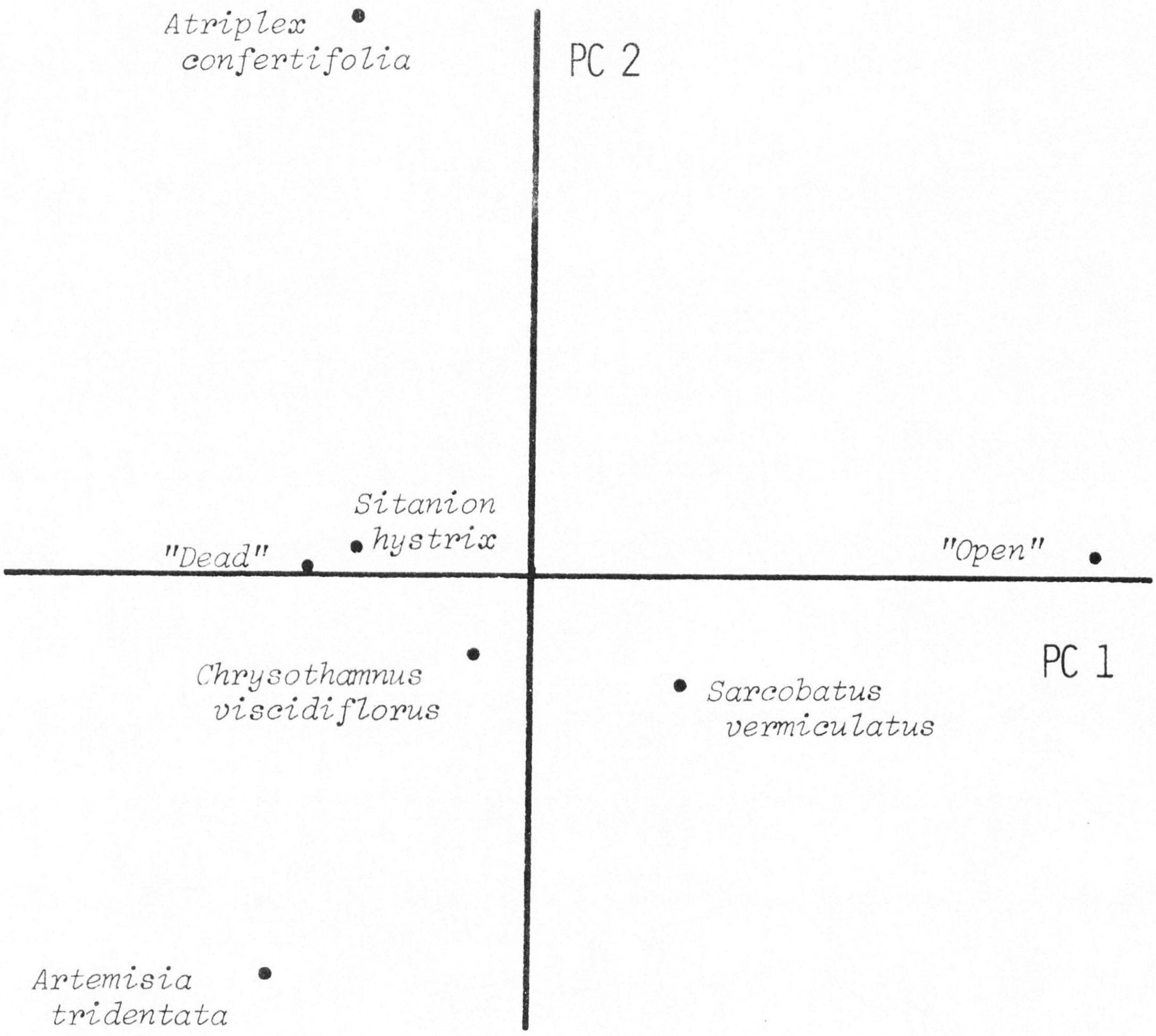


Figure 3. Loadings of percentage cover of plant species and other properties along the first two principal components of variation in vegetation composition of 40 step-point transects.

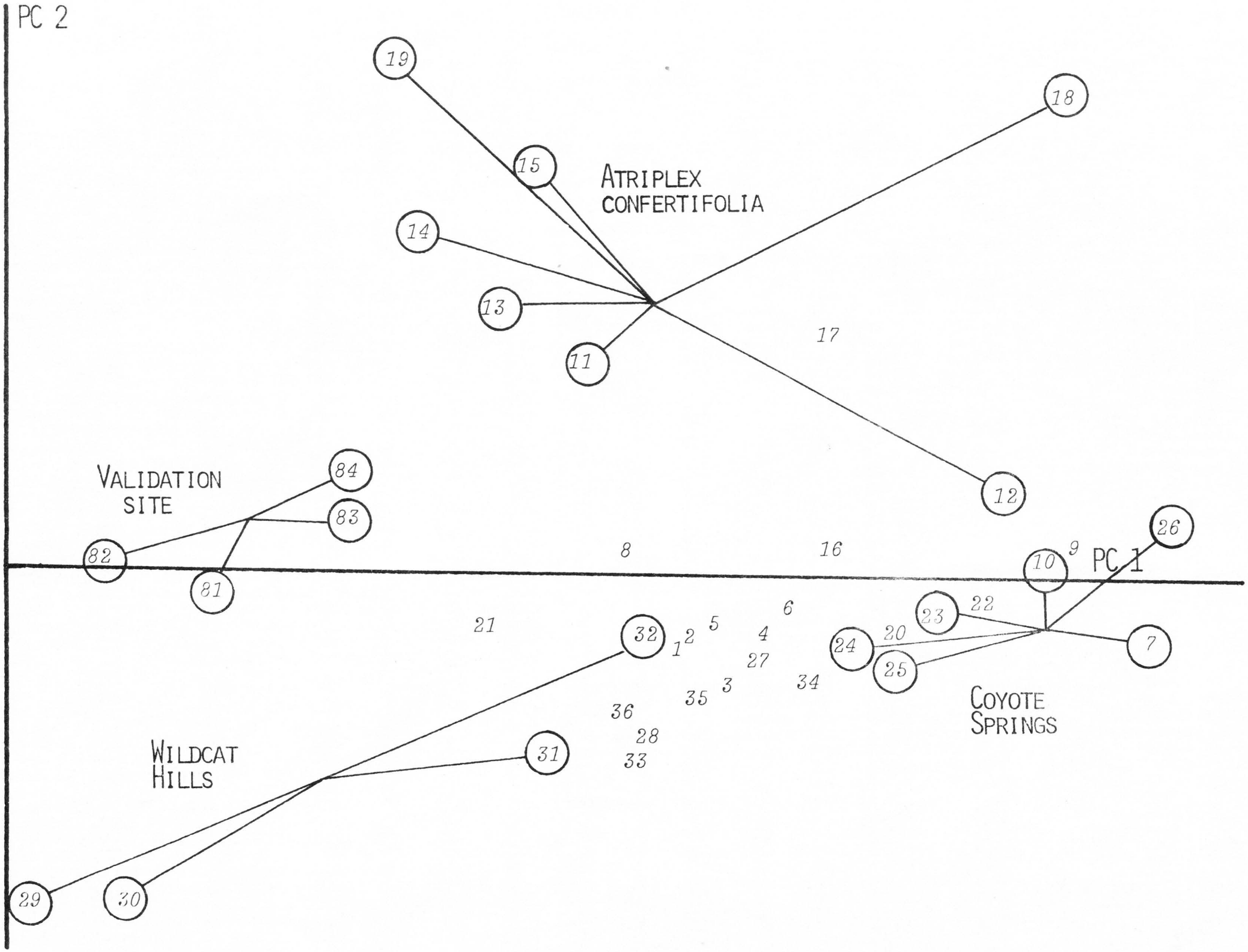
When the 40 transects are ordinated along the first two principal components, they show little clustering (Figure 4). Four subjective groupings of transects are indicated in Figure 4 by circles and connecting lines. These are transects dominated by *Atriplex confertifolia*, from the saline area of Coyote Springs, from the coarser soils of the Wildcat Hills, and from the Desert Biome validation site.

The third principal component seems to express variation from *Artemisia*-dominated to *Sarcobatus*-dominated communities (Figure 5). No main trend is obvious along the fourth component.

Results of Bray-Curtis ordination in the first two dimensions (Figure 6) are similar to the results of principal components analysis (Figure 4). I thus conclude that the principal components procedure has given an undistorted ordination of sites.

On the basis of this analysis, I would characterize the vegetation of the shooting route as a three-cornered continuum. The three corners are communities dominated by *Atriplex confertifolia*, *Artemisia*, and *Sarcobatus*, respectively. Of the less common shrubs, *Chrysothamnus viscidiflorus* and *Grayia spinosa* tend to occur in Artemisia types, while *Kochia americana* tends to occur in *Atriplex* or *Sarcobatus* types. *Sitanion hystrix*, the important perennial grass, tends to be restricted to *Atriplex*-dominated areas.

It would have been possible to apply to these data one of the methods (reviewed by Goodall, 1970) for dividing the area into communities. But these communities did not seem likely to be very clear-cut. The biomass of species would have varied a good deal within them. Rather the important species were mapped into 2-4 cover-classes, as explained above.


PC 2
19
18
15
ATRIPLEX
CONFERTIFOLIA
14
13
11
17
VALIDATION
SITE
84
83
12
26
82
8
16
10
9
PC 1
81
6
23
22
21
32
5
1
2
4
20
24
7
27
25
3
34
35
COYOTE
SPRINGS
36
28
33
31
WILDCAT
HILLS
29
30

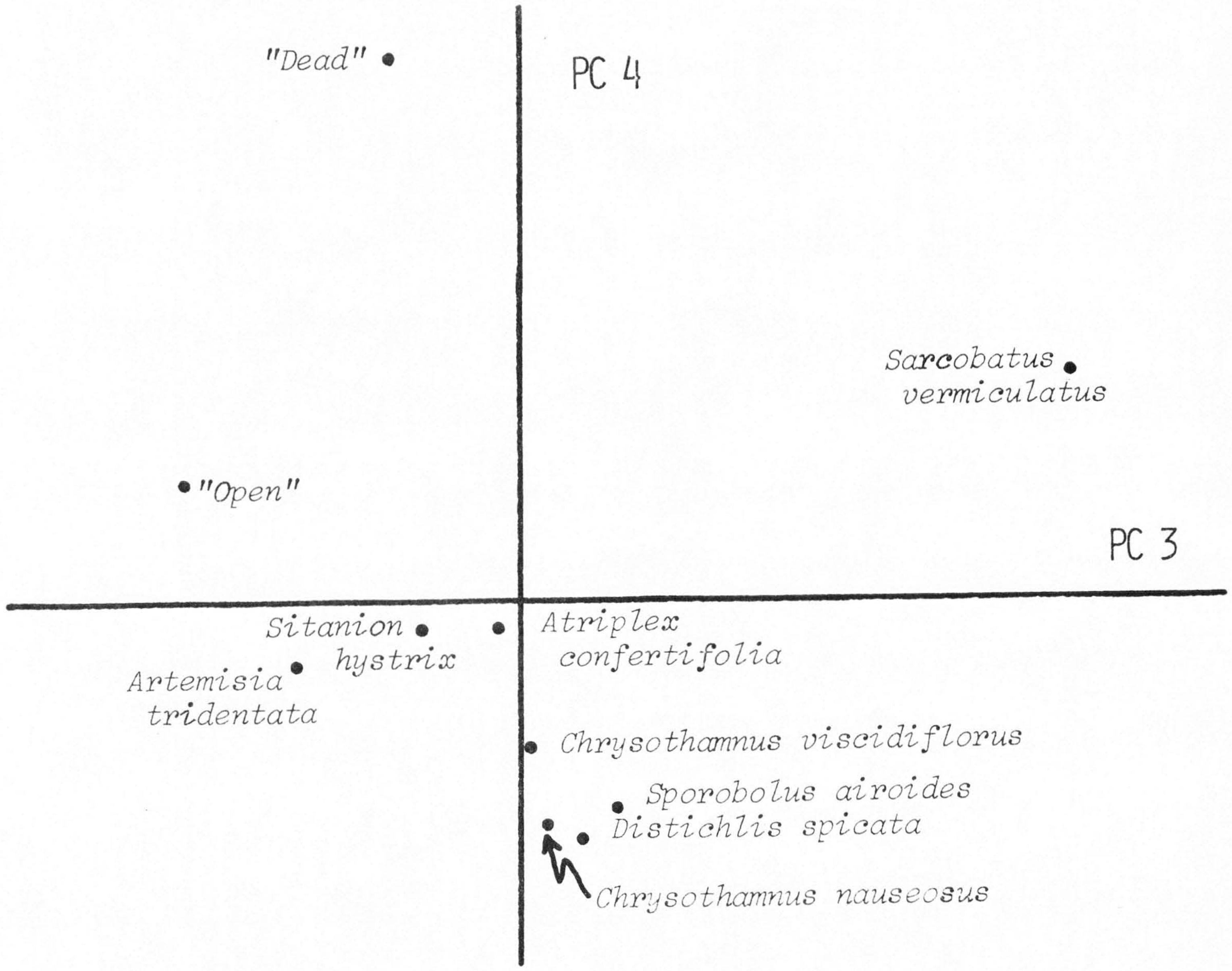


Figure 5. Loadings of percentage cover of plant species and other properties along the third and fourth principal components of variation in vegetation composition of 40 step-point transects.

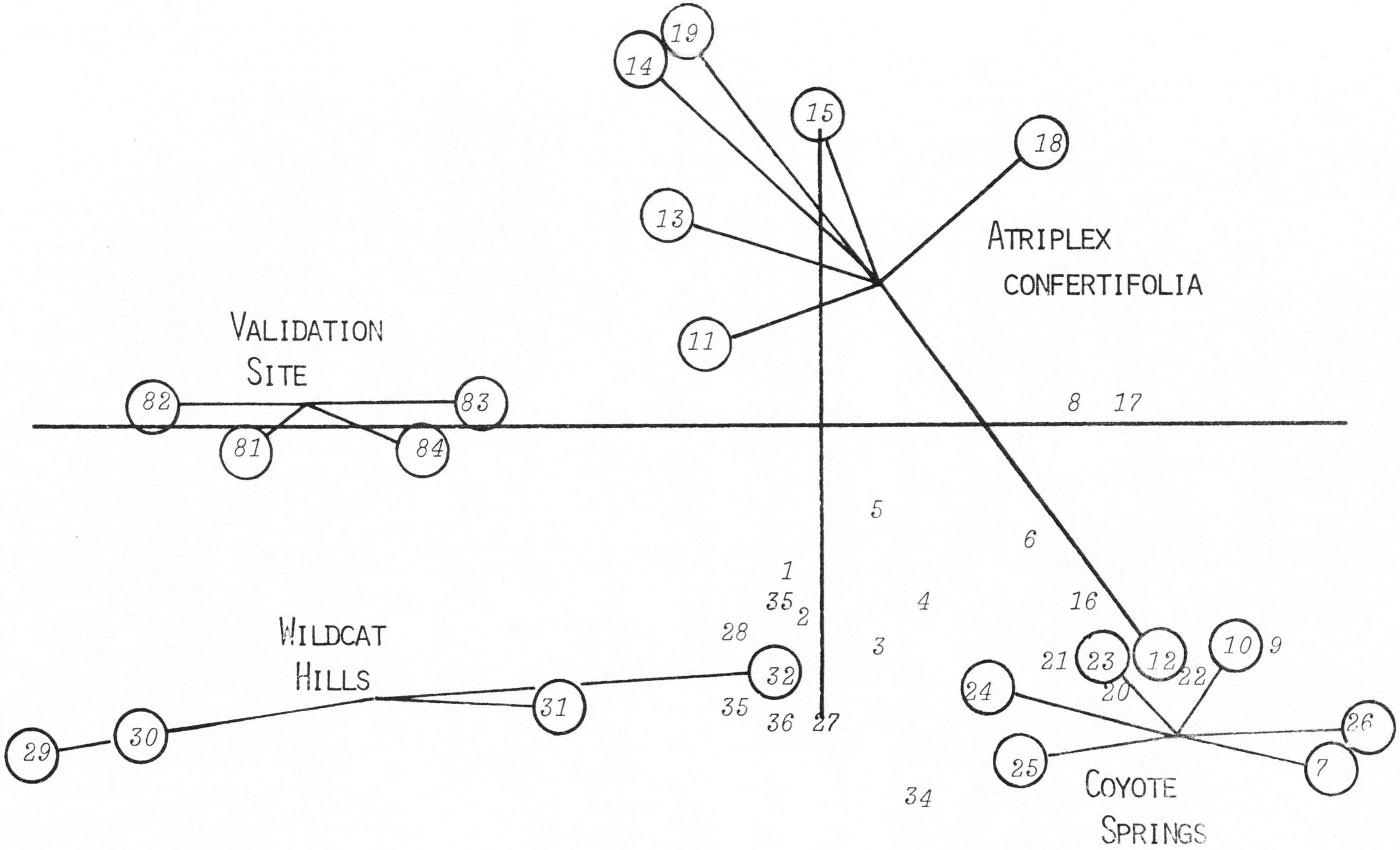


Figure 6. Ordination of 40 step-point transects along the first two axes of a Bray-Curtis ordination procedure. Grouping of some of the transects into subjectively-defined locations or types is denoted by the circles and connecting lines.

These maps are shown in Figures 7-13. (*Kochia* is mapped on the basis of the data given below.)

Biomass Estimates

The regressions of dry weight of available biomass (W) in grams on volume (V) in liters, for *Kochia* and *Chrysothamnus viscidiflorus*, were as follows:

For *Kochia*

$$W = .083 + 15.44V \qquad (r^2 = .71,\ df = 57) \qquad [5]$$

For *Chrysothamnus*

$$W = 2.29 + 0.68V \qquad (r^2 = .76,\ df = 37) \qquad [6]$$

Including percentage utilization in this last regression increased r^2 by only .006.

Estimates of available biomass and cover for *Kochia* transects range from 0 kg/ha at transect 8, on the Wildcat Hills, to 23.6 kg/ha, with 0.46 percent cover, at transect 5 in the understory of a *Sarcobatus* community (Table 3). Similar estimates for *Chrysothamnus* transects range from 9.9 to 44.0 kg/ha (Table 4). Exact locations of the sampling transects are superposed on the distribution maps (Figures 11 and 12 for *Chrysothamnus* and *Kochia*, respectively). The 95 percent confidence limits on the figures have been estimated from the variance among quadrats; no allowance has been made for variance around the regression line. They were estimated using the t-statistic.

Table 3. Estimates of cover and available biomass of *Kochia americana* examined 6-10 May 1972

Transect	Number of Quadrats	Percentage Cover (95% confidence)	Dry Weight of Available Biomass (kg/ha, with 95% confidence)
1	40	.22 ± .10	12.3 ± 7.0
2	39	.28 ± .11	16.6 ± 7.0
3	40	.01 ± .01	0.4 ± 0.4
4	40	.01 ± .01	0.3 ± 0.3
5	10	.46 ± .18	23.6 ± 13.7
6	24	.05 ± .05	2.7 ± 2.4
7	12	.13 ± .13	6.8 ± 6.9
8	40	.00 + .00	0.0 + 0.0

Table 4. Estimates of cover and available biomass of *Chrysothamnus viscidiflorus* examined 8-10 October 1972

Transects	Number of Quadrats	Percentage Cover (95% confidence)	Dry Weight of Available Biomass (kg/ha, with 95% confidence)
12	12	1.2 ± 1.5	15.0 ± 17.8
13	12	0.8 ± 0.9	9.9 ± 10.6
14	9	3.3 ± 3.5	44.0 ± 46.3

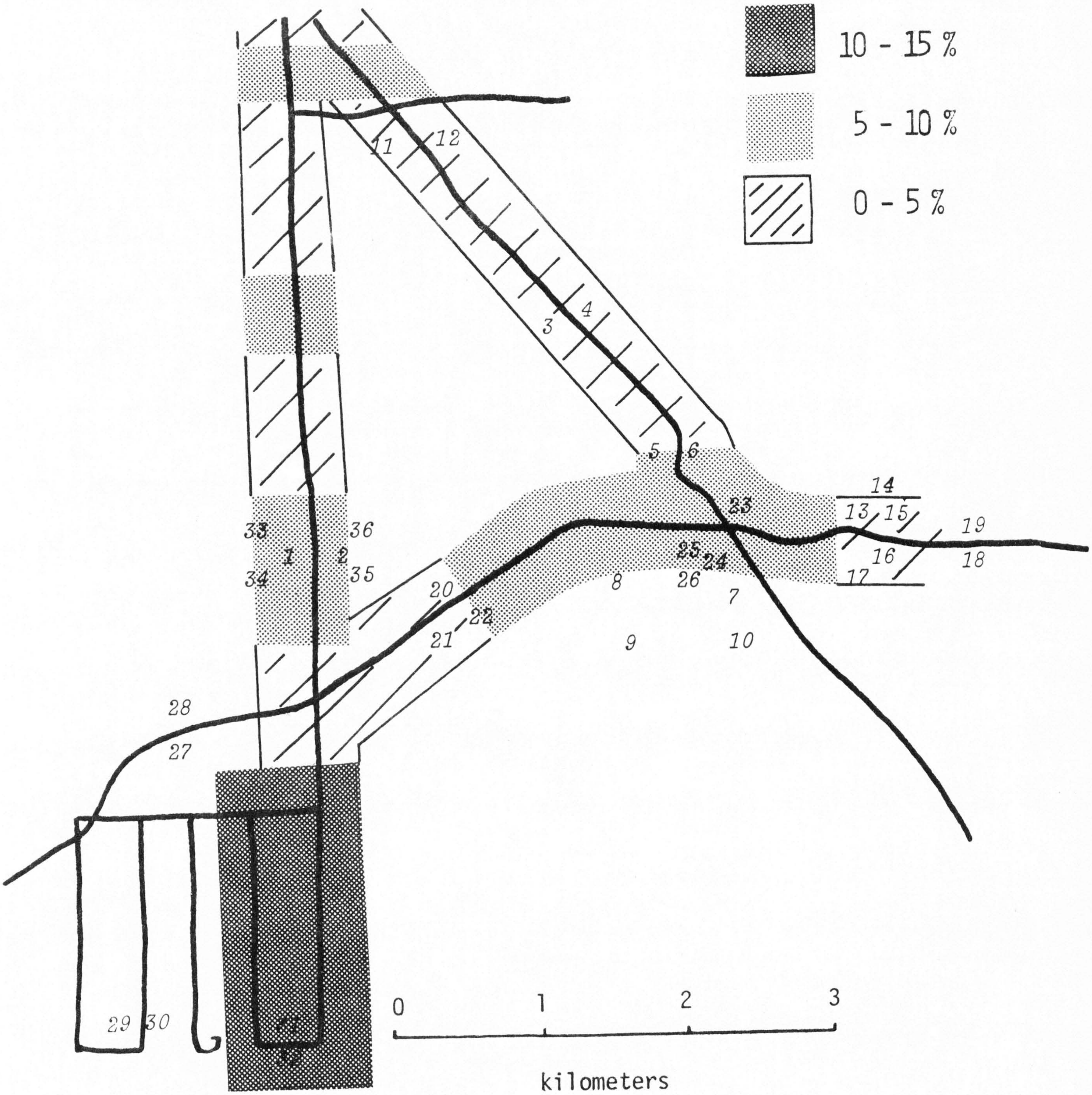


Figure 7. Distribution of cover-classes of Artemisia tridentata along the shooting route. Numbers indicate the locations of step-point transects.

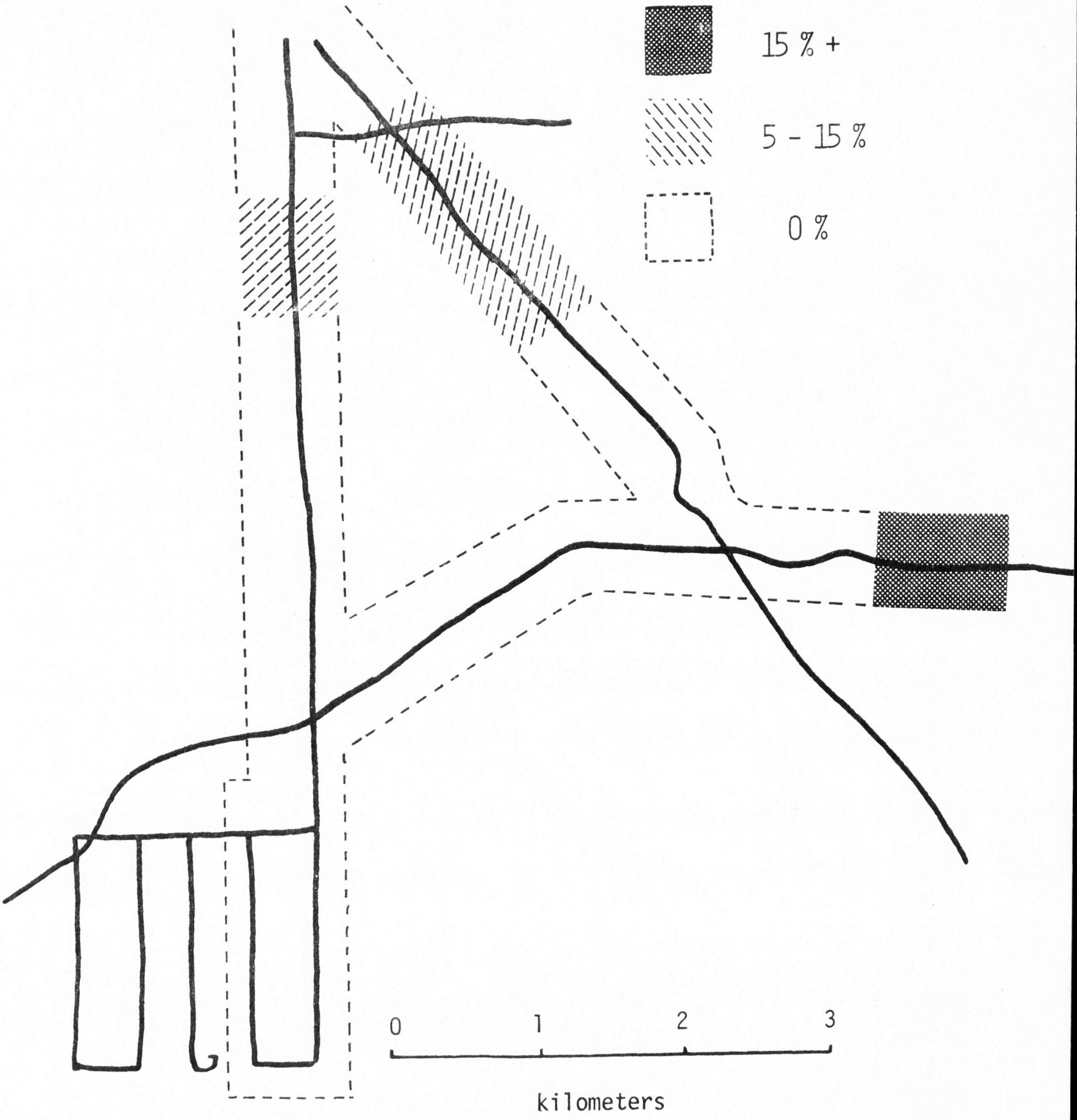


Figure 8. Distribution of cover-classes of *Atriplex confertifolia* along the shooting route.

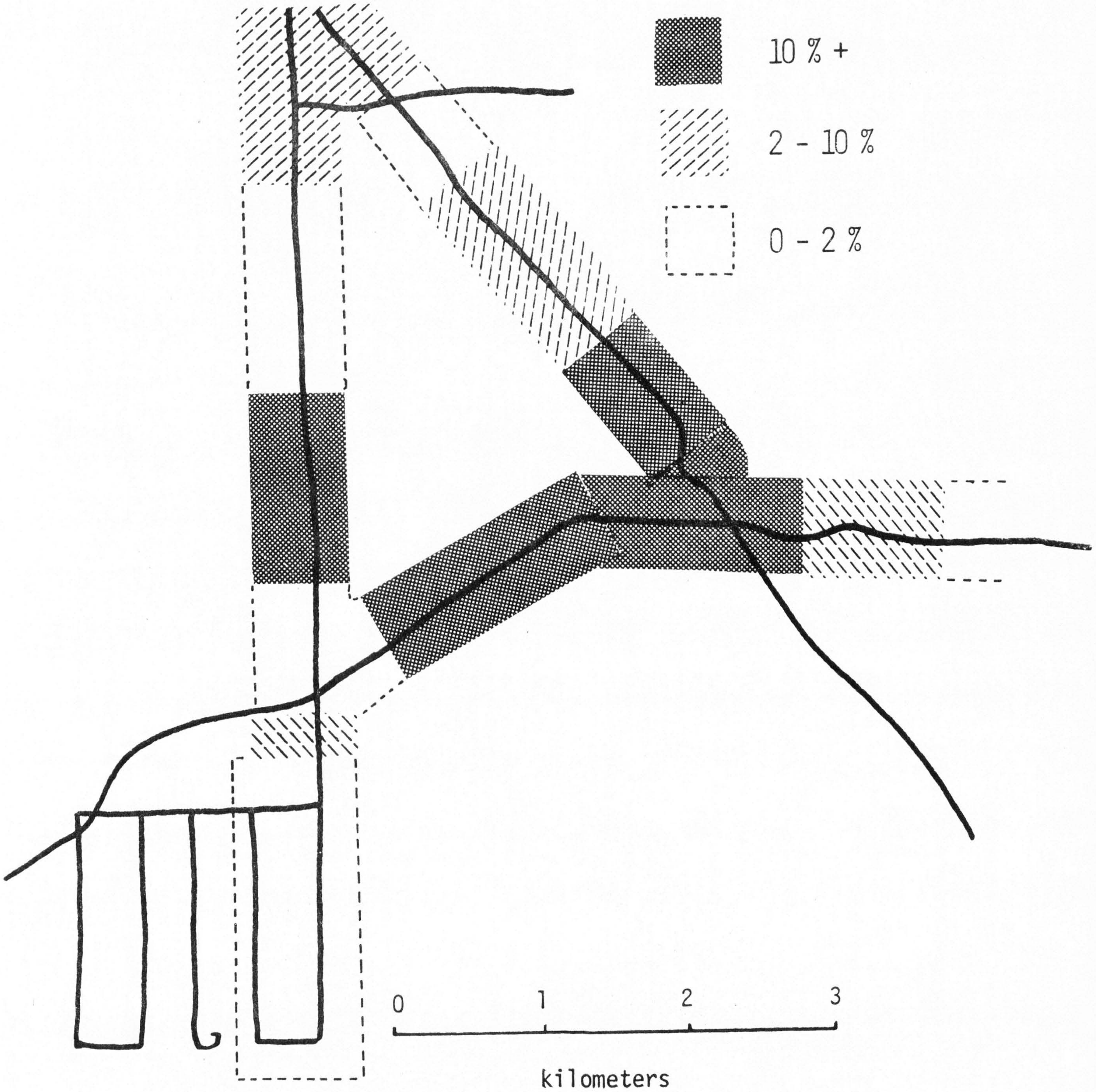


Figure 9 . Distribution of cover-classes of *Sarcobatus vermiculatus* along the shooting-route.

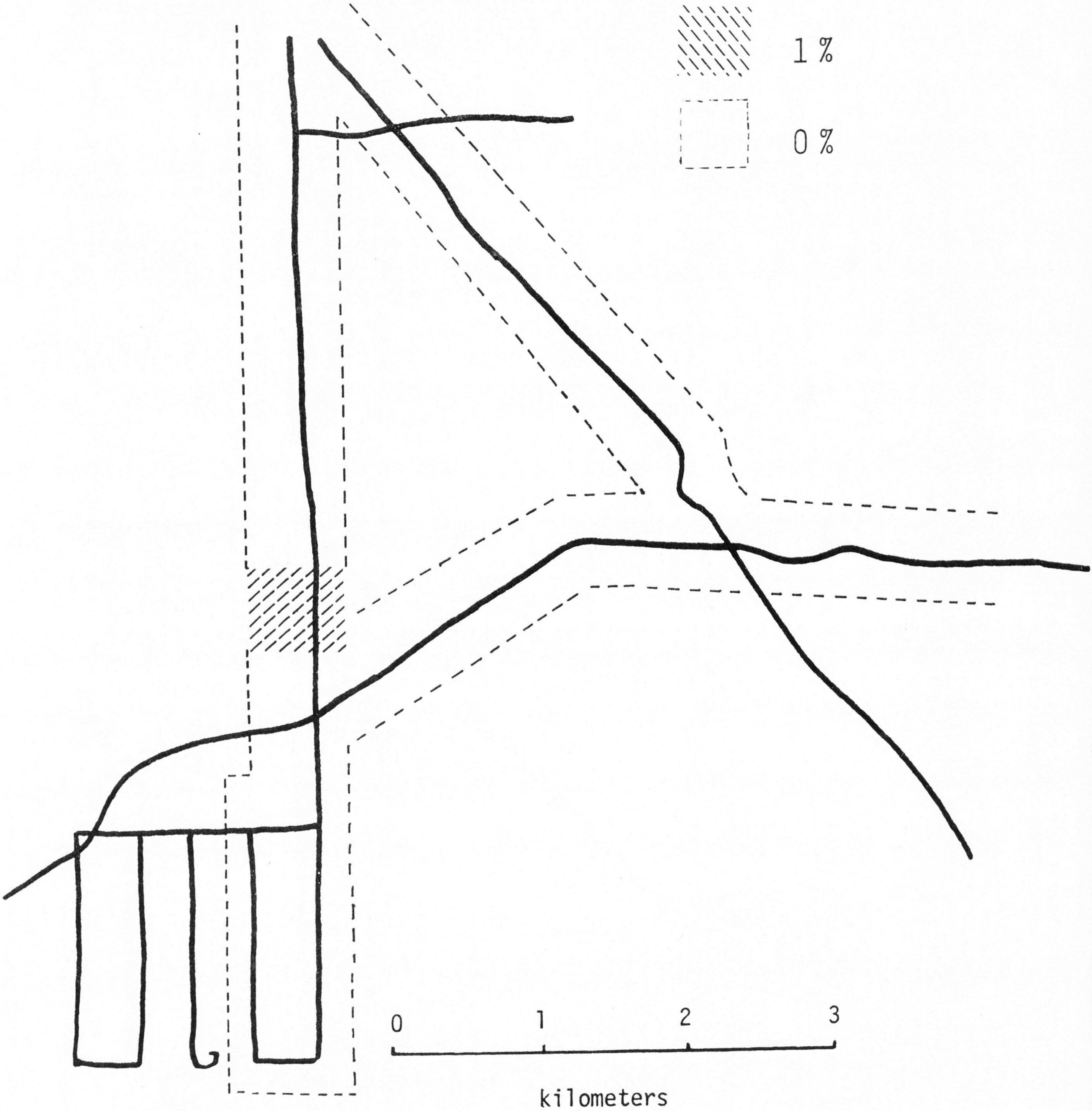


Figure 10. Distribution of cover-classes of *Grayia spinosa* along the shooting route.

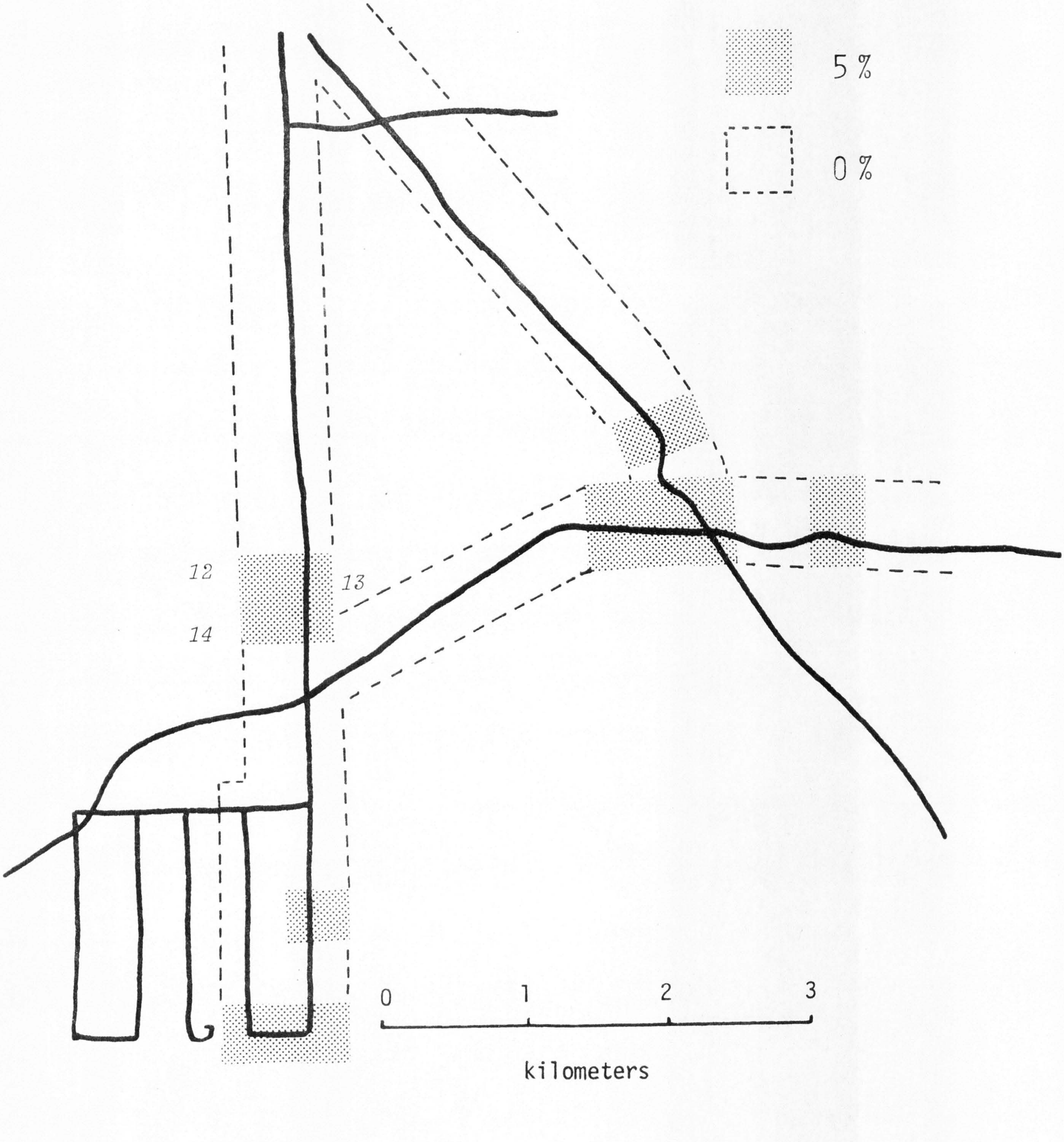


Figure 11. Distribution of cover-classes of Chrysothamnus spp. along the shooting-route. Numbers indicate locations of transects for Chrysothamnus biomass sampling.

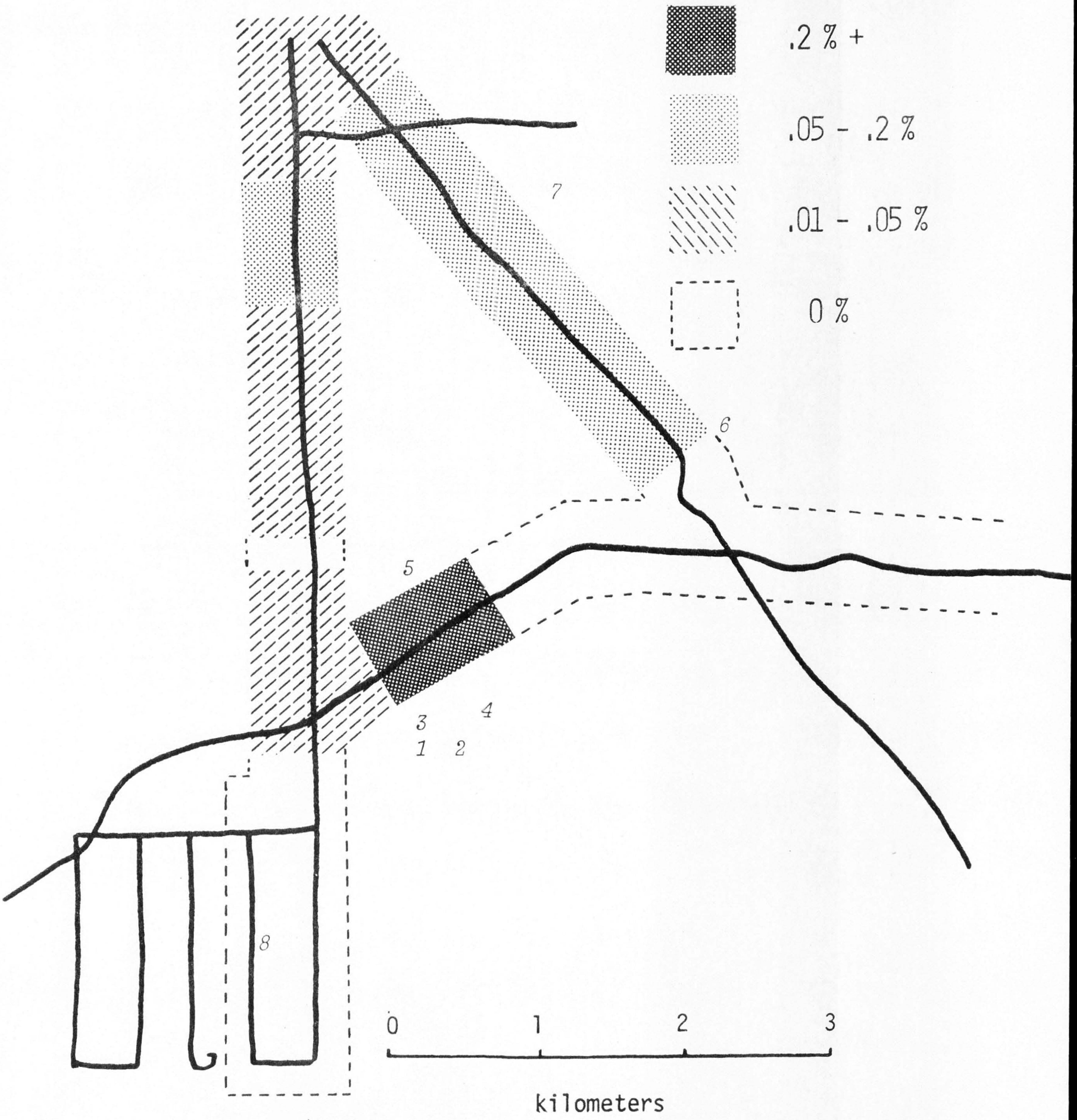


Figure 12. Distribution of cover-classes of Kochia americana along the shooting route. Numbers indicate locations of transects for Kochia biomass sampling.

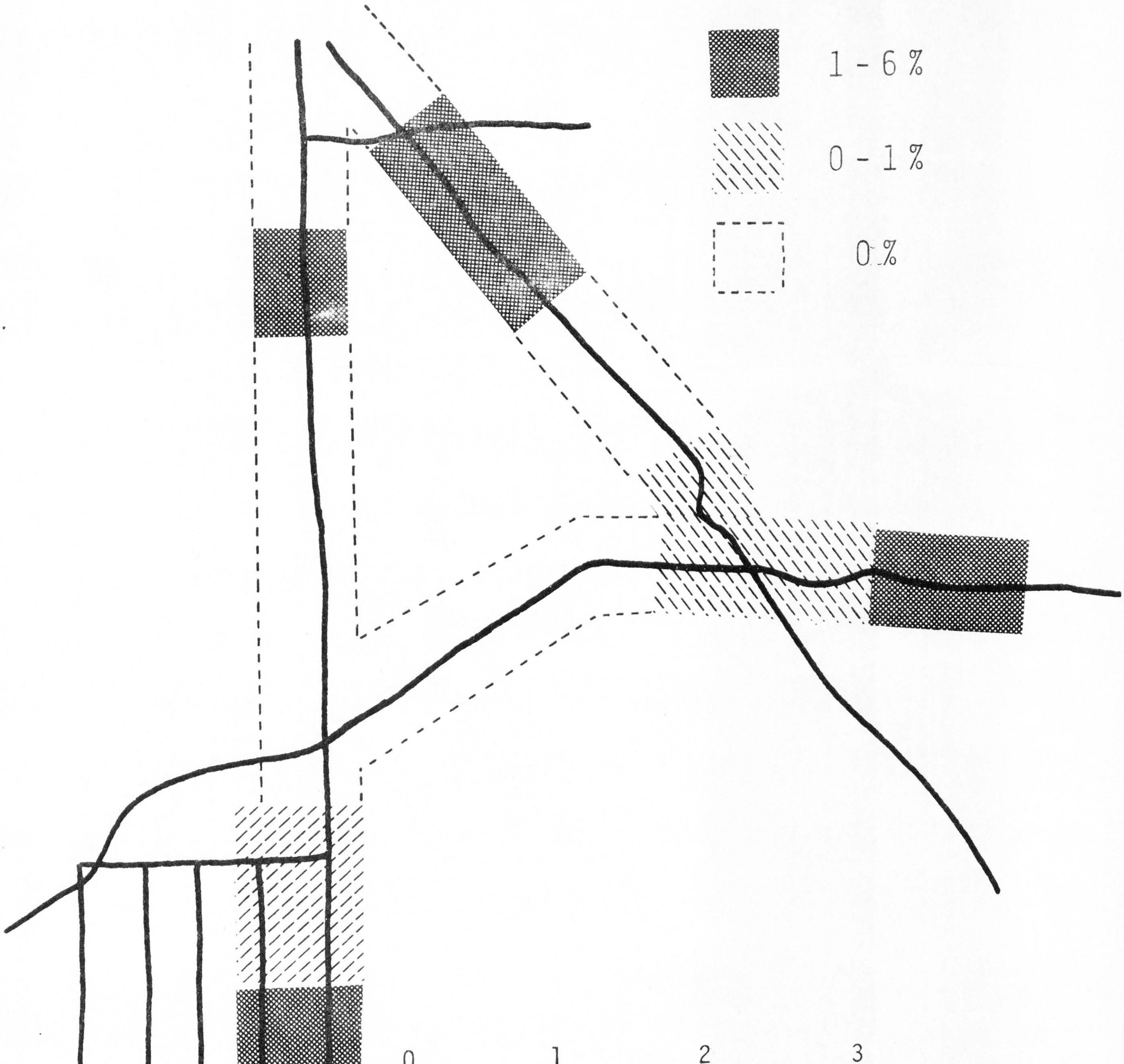


Figure 13. Distribution of cover-classes of Sitanion hystrix along the shooting route.

Available biomass values of Artemisia, Sitanion, and Atriplex confertifolia on the Desert Biome validation site were 450, 50, and 220 kg/ha, respectively (Table 5). Corresponding cover figures, means of step-point transects 81-84 on the validation site (Table 1), were 16.9, 13.6, and 11.5 percent, respectively. Biomass/cover ratios were thus 26.6, 3.7, and 19.1 kg/ha/percent, respectively (Table 5).

Mean biomass/cover ratios for Kochia and Chrysothamnus are 49.0 and 12.7 (Table 5), calculated from the data of Tables 3 and 4.

Mean biomass over the shooting route as a whole is estimated by summing the biomass/cover ratio, times the median cover, times the proportion of the route occupied by that cover-class, across all cover-classes (Table 6). A figure for biomass of the annual Halogeton glomeratus is also given. It is the value estimated for the validation site.

The dominant shrubs Artemisia, Atriplex, and Sarcobatus account for more than 80 percent of the available perennial biomass as calculated. Chrysothamnus, while abundant where it occurs, is very locally distributed, and has low average biomass. The dominant annuals, such as Halogeton, have available biomasses in the same order as the dominant shrubs. Kochia, Sitanion, and Grayia have low mean biomasses.

These "available biomasses" are used below for two distinct purposes. First, they are used as measures of year-round supply ("availability"); that is, of the standing crop of edible material. Second, they are used as the divisor in estimating percentage utilization, usually defined as 100 x consumption/current growth.

Table 5. Biomass/cover ratios for various species, and data from which they were derived

Species	Percentage Cover[a]	Available Biomass (kg/ha)[b]	Biomass/cover Ratio (kg/ha/%)
Artemisia tridentata	16.9	450	26.6
Atriplex confertifolia	11.5	220	19.1
Sitanion hystrix	13.6	50	3.7
Kochia americana[c]	-	-	49.0
Chrysothamnus viscidiflorus[c]	-	-	12.7

[a] Estimated by step-point transects 81-84 on the validation site

[b] Unpublished Desert Biome data for the validation site, August 1972. "Available biomass" is taken to be "young stems and leaves" for the shrubs,all aboveground biomass for Sitanion

[c] Biomass/cover ratio calculated from data of Tables 3 and 4, respectively

Table 6. Estimated mean available biomass of various plant species over the shooting route

Taxon	Biomass/ Cover Ratio (kg/ha/%)	Median Cover Cover-Class				Proportion of Route Cover-Class				Estimated Mean Biomass (kg/ha)	Percentage of Total Estimated Biomass
		1	2	3	4	1	2	3	4		
Artemisia tridentata	26.6	2.5	7.5	12.5	-	.50	.28	.22	-	162.3	19.5
Atriplex confertifolia	19.1	0.0	10.0	20.0	-	.84	.13	.03	-	36.3	4.4
Sarcobatus vermiculatus	26.6[a]	1.0	6.0	12.0	-	.44	.24	.32	-	152.1	18.3
Grayia spinosa	26.6[a]	0.0	1.0	-	-	.98	.02	-	-	0.5	0.1
Chrysothamnus spp.	12.7[b]	0.0	5.0	-	-	.84	.16	-	-	10.2	1.2
Kochia americana	49.0	0.0	0.03	0.12	0.25	.45	.29	.22	.05	2.3	0.3
Sitanion hystrix	3.7	0.0	0.5	3.5	-	.53	.22	.25	-	3.7	0.4
Halogeton glomeratus[c]										465.0	55.9

[a] Value for *Artemisia tridentata* used.

[b] Value for *Chrysothamnus viscidiflorus* used. These species are lumped at this point because they were not distinguished in the stomachs.

[c] Unpublished Desert Biome Data for the validation site, August 1972.

Generally, the available biomass estimated has been close to the year's highest value. For example, most biomass/cover ratios were derived from August data. Peak available biomass is being taken as an index of year-round availability; the assumption is that the seasonal changes in availability are similar for each species.

Current growth cannot be measured directly without sampling in an exclosure. In principle current growth can be estimated by (peak available biomass) + (consumption before the peak is reached). Thus, percentage utilization estimated as a ratio of consumption to available biomass will tend to overestimate true percentage utilization, especially when consumption is large compared to available biomass. I have not attempted to correct, adding consumption to peak available biomass to estimate current growth, because (1) this would involve the complication of estimating what proportion of year-round consumption occurred before available biomass was estimated, and (2) available biomass was estimated by projecting a biomass/cover ratio from another location onto cover values for the shooting route. But grazing often thins, rather than hedges, plants; that is it changes biomass without changing cover. Moreover, there is no reason to suppose that consumption on the validation site was the same as on the shooting route.

PART II. FOOD SELECTION

Introduction

The first overall objective of this study was to estimate the mean utilization of each plant taxon (question 3 -- see the Introduction). Part III of this report uses the diet data which will be presented to do this. But the longer-term objective of the study was to be able to project estimates of mean utilization into the future. This involves predicting what diets will be chosen from a plant community which has, *ex hypothesi*, changed.

Accordingly I have sought, beside presenting empirical results on diets, to explain the results, looking particularly for types of explanation which potentially have predictive power. The concepts now used in range management to analyse food selection are not intended to be predictive. The main concept is "palatability", which is often operationally defined as the ratio of consumption to availability. The literature contains many empirical studies of diets. For example, the Journal of Wildlife Management from 1957-1966 published ten reports on the food habits of white-tailed deer alone, not counting observations on individual foods, or methodological or nutritional studies. Measures of palatability were calculated in many of these cases, and had great interpretive value. But to predict that a food will be eaten because it is palatable, amounts to saying that it will be eaten because it was eaten. This is scientifically unsatisfying. It would be more desirable to have a theory which predicts diets as a function of animal properties and plant properties taken separately, rather than as a function of what happens when they are brought together.

The evolutionary object of feeding is to obtain nutriment. The nutritional values of foods to a particular animal are thus the obvious candidates as predictors of its diet. In this section, after presenting stomach data, I look at the possibilities of predicting diets from the nutritional properties of foods in two ways. First, the main features of the jackrabbit diet are discussed in terms of their nutritional reasonableness. Second, the mechanisms involved in food selection are reviewed, and the properties of some models which reflect the mechanisms discussed.

Methods and Materials

Jackrabbit Collections

Jackrabbits were collected by shooting from a truck at night with the help of a spotlight. The main collection period was from September 1971 to January 1973. Typically 8-15 animals were shot per month, but this fell as low as 3 on one occasion and rose as high as 25 on another.

Between September 1971 and April 1972, animals were taken either from the western edge of the wheatgrass seeding or along the shooting route (Figure 1). From April to September 1972, they were taken along the shooting route, and the location of each kill was recorded using the distance on the speedometer. These locations are probably accurate to within about 200 m. After September 1972, animals were taken elsewhere in Curlew Valley, wherever they could be found.

Since the kill-sites over the April-September 1972 period could be placed on a map of the area, it was possible to associate each stomach with a cover-class (Figures 7-13) of each major plant taxon. Thus the response to availability could be studied, assuming that the animals had been feeding around where they were shot. Probably they had been: jackrabbits feed nocturnally, and so were shot during the feeding period; and in Curlew Valley they have home ranges in the order of 15 ha, which do not shift from day to day (Nelson 1970). The length of a step-point transect, the radius of the jackrabbit's home range, and the likely limit of error in placing the kill-site on a map, are all in the same order, at 2-300 m. While some stomachs may have been said to be associated with higher or lower cover-classes than those in which they had actually been feeding, there is no reason to suppose that this happened other than randomly.

Usually the animals were returned to Logan within a few hours of shooting and stored in a cool room at 0°C for a few days, until autopsy. At autopsy the stomach contents were removed and stored in formalin. Sometimes the animals were autopsied in the field.

Stomach Analyses

Preparation and examination of materials

Microscopic analysis of stomach contents was carried out by two groups of people. Stomachs collected during 1971 were analysed by Dr. W. E. Saul, of Idaho State University. His procedures were described in Saul (1972). Stomachs collected during 1972 were analysed at Utah State University.

The method used in this study was similar to that described by Sparks and Malechek (1968) and Flinders and Hansen (1972). It consisted of the following steps:

(1) The stomach contents were dried and ground in a Wiley mill.

(2) Two slides were made from each stomach from the milled material. A small amount (less than 0.5 gm of the dry, milled material) was placed in a test tube, and an excess of digestion solution (composed of 10 percent nitric and 10 percent chromic acid) added. This mixture was boiled briefly. After cooling, the digested mixture was placed in a Waring blender, with 30-40 ml of water, and agitated

for perhaps 10 secs. The sample was transferred to a 200-mesh screen and washed thoroughly with running water to remove small particles and silt.

Material remaining was transferred to a 50 ml beaker, which was filled half full of water. One or two drops of Safaranin-O stain, stock solution, were added. This mixture was left overnight, then the staining solution was strained off. A small amount of the residue was transferred to a clean microscope slide, and two drops of white Karo syrup were added. The material was mixed with the syrup with a teasing needle, and dispersed over the slide surface. The cover slip was applied and left for about an hour to allow the mounting medium to fill the space beneath it.

After a few days, when the syrup had dried, a thin bead of Dupont "Duco Cement" was applied around the edge of the cover slip, to seal the slide permanently.

(3) 100 fields, at 100-power magnification, were examined on the slides for each stomach. When one or more particles of a given plant species could be positively identified in a field, it was recorded as present, otherwise absent. This examination gave a percentage frequency of occurrence of the species in the 100 microscope fields. These frequencies were converted into densities, using the table given by Hansen and Flinders (1969). The densities were then transformed into relative densities, which were equivalent to "percentage composition", as used in reporting the data from here on.

One significant deviation of Dr. Saul's procedure from the one just described was that he also made up slides of unground material. These were examined first to identify the major species present. Then the slides of ground material were examined to determine the quantitative composition of the stomach.

Accuracy of the microscopic analysis procedure

Dr. Saul carried out three experiments whose results I have analysed. The first was to analyse some 60 stomachs from 1971 by a "quick-scan" method, as well as by the slower method described above. In the quick-scan analysis the slide as a whole is examined briefly, without looking at particular fields. A subjective estimate of the composition is recorded. These data were analysed by regressing percentage estimated by the quick-scan method (as Y), on percentage estimated by the slower analysis (as X), for each species.

Dr. Saul also made up mixtures of known composition and analysed them. In a second experiment, three mixtures were made up. Each contained the same set of species, but had different quantitative composition. He analysed each of these mixtures nine times. In a third experiment an assortment of mixtures of varied composition was made up. The mixtures were analysed various numbers of times.

Both of these experiments were analysed by regressing percentage estimated (as Y) on percentage actual composition (as X) for each species.

Before the analysis of stomachs shot during 1972 was undertaken at Utah State University, there was a training period of approximately 4 months. Three technicians were given practice in identifying and assessing materials. During this period 35 mixtures of known composition were analysed by each technician. The mixtures were made up by weighing out known amounts of dried, ground plant material. This had been hand-collected in the field by clipping plants in ways similar to those in which jackrabbits were thought to feed on each plant species. The mixtures were made into slides according to the procedures described above. A few of the mixtures were analysed by only one or two of the technicians.

The main objective of analysing these known mixtures was to learn to use the method as quickly and as well as possible, rather than to conduct experiments on it. The composition of the mixtures was therefore chosen arbitrarily, not according to any particular design. In particular, pairs of taxa which were hard to tell apart were presented increasingly as the learning period went on. When it became apparent that certain pairs of taxa could not be reliably distinguished, these were lumped in reporting the data. The two most important cases of this lumping were that the two *Chrysothamnus* species were grouped, and so were all grasses other than *Bromus tectorum*.

The following measures of the success of the procedure were calculated. First the quality of the overall estimate of the compositon of each stomach was considered. A Coefficient of Community (CC) (Sørensen 1948 variant) between the estimated species composition of the mixture and the actual one was found. It was defined as

$$CC = \frac{200\ S_c}{S_a + S_e} \qquad [7]$$

where S_a and S_e are the numbers of species present in the actual and estimated composition, respectively, and S_c is the number of species present in both actual and estimated composition.

A Euclidean Distance (ED) between actual and estimated composition in a species-space was found. It was defined as

$$ED = (\overset{i}{\Sigma}(P_{ia} - P_{ie})^2)^{1/2} \qquad [8]$$

where P_{ia} and P_{ie} are the percentage composition of species i in the actual and estimated mixture, respectively.

Second, estimates were sought of the quality with which the contributions of particular taxa to the composition of mixtures were estimated. A Recognition Success (RS), a measure related to the Coefficient of Community, was found. It was defined as

$$RS = \frac{200\ N_c}{N_a + N_e} \qquad [9]$$

where N_c is the number of mixtures in which the taxon was both actually present and identified, and N_a and N_e are the numbers of mixtures in which the taxon was actually present and in which it was identified, respectively.

Finally, the value of

$$\text{Arcsin}\ ((P_{ie}/100)^{\frac{1}{2}}) - \text{Arcsin}\ ((P_{ia}/100)^{\frac{1}{2}}) \qquad [10]$$

was found for all mixtures in which either P_{ie} or P_{ia} were non-zero. Mean and 95 percent confidence limits of this population of values were found.

Correction equations were calculated. These were regressions of percentage actual on percentage estimated composition. Cases where both actual and estimated composition were zero were included.

If the quick-scan and slower methods were giving the same results, the regression coefficient b should be 1.0. Of the six taxa with sample sizes greater than 9, four show significantly different results by the two methods (Table 7). The quick-scan method is apparently not reliable as a predictor of the results obtained by the slower method.

Tables 8 and 9 show the results of regressing actual on estimated composition of mixtures in Dr. Saul's other two experiments. In both cases the grass Hordeum was overestimated compared to the dicotyledons Chrysothamnus and Kochia. Medicago and Artemisia have slopes greater than 1.0 and

Table 7. Properties of regression lines obtained by regressing percentage composition of stomach contents as estimated by "quick-scan" method (as Y) on that estimated by slower method (as X). The intercept was not significantly different from 0.0 for any taxon

Taxon	Sample Size	Slope	Probability that slope is from a population with mean of 1.0
Artemisia tridentata	10	1.32	>.2
Atriplex confertifolia	13	.97	>.5
Chrysothamnus viscidiflorus	25	.89	<.002
Descurainia spp. [a]	6	2.34	<.002
Grass	50	.97	<.002
Grayia spinosa	6	1.25	<.002
Halogeton glomeratus	41	1.08	<.002
Kochia americana	22	.84	<.002
Mentzelia albicaulis [b]	5	.49	>.5
Sphaeralcea sp. [c]	9	.10	<.002

[a] Mainly Descurainia Richardsonii (Sweet) O. E. Schulz and D. pinnata (Walt.) Britton

[b] Mentzelia albicaulis (Dougl.) T. & G.

[c] Probably mainly Sphaeralcea grossulariaefolia (Hook. & Arn.) Rydb.

Table 8. Results from regressing estimated percentage contribution of three species (as Y) on actual percentage contribution (as X). There were three mixtures with the same species complement but different compositions; each was analysed nine times

Taxon	Slope	Intercept
Hordeum jubatum[b]	.833[a]	19.001[a]
Salsola kali[b]	1.041	-5.597
Chrysothamnus viscidiflorus	.645[a]	4.526

[a] Significantly different from 1.0 or 0.0 at P = .05.

[b] Hordeum jubatum L.; Salsola kali L.

Table 9. Results from regressing estimated percentage contribution of various species (as Y) on actual contribution (as X) in an assortment of mixtures of known composition

Taxon	Slope	Intercept	df
Kochia americana	.986	-0.224	45
Medicago sativa[b]	1.304[a]	-14.533[a]	50
Artemisia tridentata	1.044	-2.908[a]	35
Hordeum jubatum	.934	7.616[a]	13
Salsola kali	-4.889	352.267[a]	6

[a] Significantly different from 1.0 or 0.0 at P = .05.

[b] Medicago sativa L.

intercepts below 0.0. They were apparently underestimated at low values and overestimated at high values.

Results from analysing mixtures at Logan show a slight but erratic increase in accuracy during the learning period (Figure 14). These were tests in which the analysts did not know the composition of the mixtures in advance. In Figure 14 the solid line plots the progress of the Coefficient of Community (CC) during the learning period. A CC of 100 would be perfect recognition of the species composition of a mixture. This was never achieved by all analysts for any one mixture. Apparently even recognition of the species list in a mixture is poor. Both increased experience, and lumping difficult discriminations, probably contributed to the slight increase in CC.

Euclidean Distance (ED) measures how well the percentage of each species was estimated, as well as the accuracy of the species list. A small ED describes a good estimate, so the ED axis is inverted in Figure 14 . Suppose all species in a three-species mixture were identified correctly, but their percentages were estimated wrongly by 15, 10 and 5 percent. This would give an ED of 18.7. A mean estimate better than this was achieved only once.

Table 10 shows biases in the estimates of particular taxa. If the estimates are unbiased, the mean of expression 10

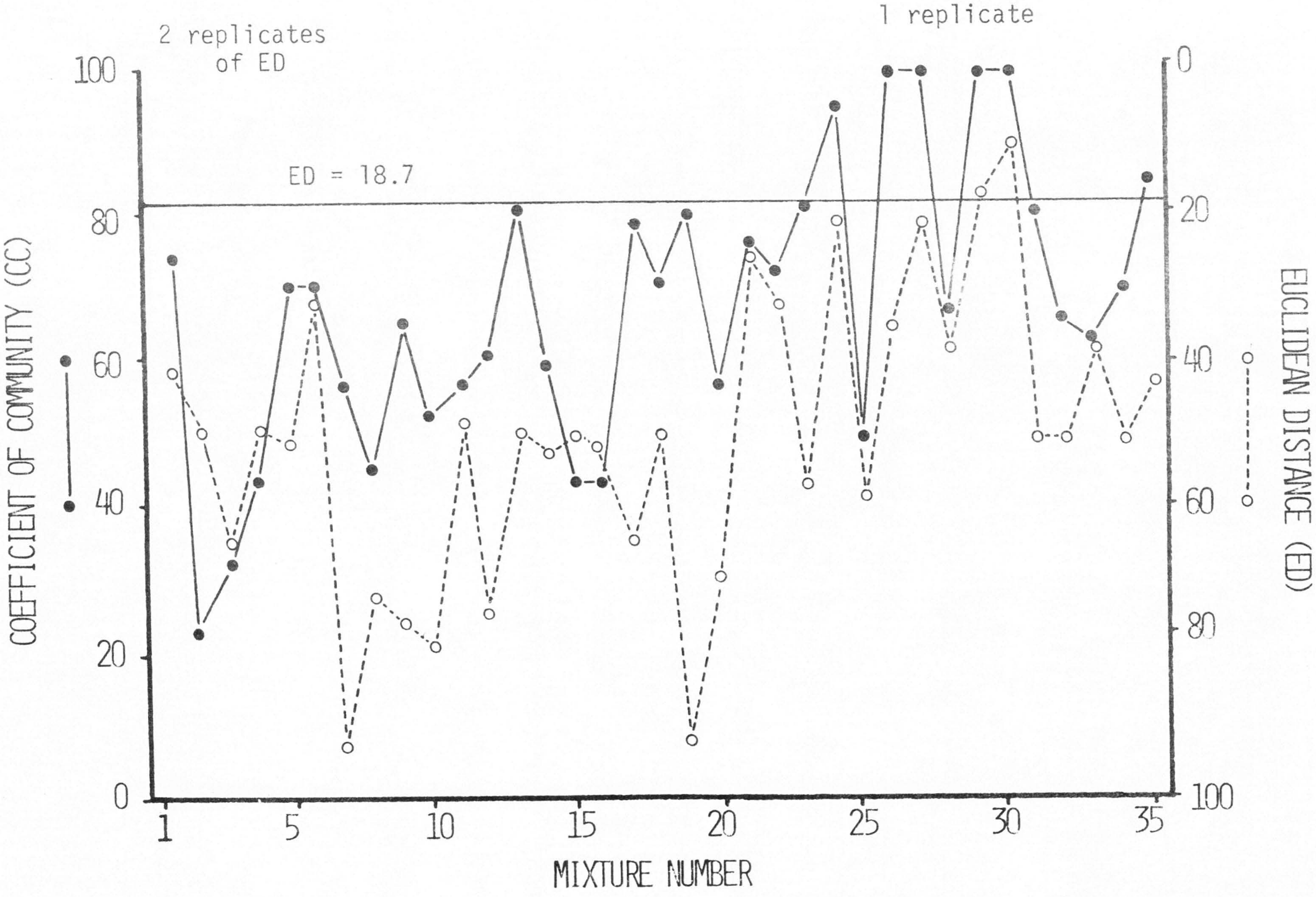

2 replicates of ED
1 replicate
ED = 18.7
100
80
60
40
20
0
0
20
40
60
80
100
1
5
10
15
20
25
30
35
COEFFICIENT OF COMMUNITY (CC)
EUCLIDEAN DISTANCE (ED)
MIXTURE NUMBER

Table 10. Analysis of biases in estimating particular taxa. Given are the properties of populations of values of (Arcsin $((P_{ie}/100)^{1/2})$ - Arcsin $((P_{ia}/100)^{1/2})$), where P_{ia} and P_{ie} are the percentages actually present, and estimated, of a taxon in a mixture. Cases where $P_{ia} = P_{ie} = 0.0$ are omitted. Recognition Success is defined in the text

Taxon	Number	Mean	95% Confidence Limits (Tchebycheff)	Recognition Success
Kochia americana	28	.086	± .279	80
Halogeton glomeratus	35	-.080	± .280	67
Grasses other than Bromus	60	.148[b]	± .198	82
Bromus tectorum	23	-.049	± .317	52
Artemisia tridentata	42	.053	± .194	81
Sarcobatus vermiculatus	45	-.257[b]	± .303	59
Chrysothamnus spp.	58	-.059	± .207	72
Grayia spinosa	20	.213[a]	± .367	64
Atriplex confertifolia	40	-.078	± .268	73
Descurainia spp.	15	.207	± .504	0
Opuntia polyacantha	9	-.077	± .464	57
Sphaeralcea spp.	11	.317[c]	± .259	76

[a] Significantly different from 0 by Tchebycheff Inequality (Freund, 1962) at P = .1

[b] Significantly different from 0 by Tchebycheff Inequality at P = .1 and by t-test at P = .05

[c] Significantly different from 0 by Tchebycheff Inequality at P = .05

should not be significantly different from 0.0. (It could not be assumed that (P_{ie} - P_{ia}) was distributed normally, both because percentages are ratios, and because P_{ie} and P_{ia} are truncated at 0 and at 100. This problem has been minimized by using an angular transform and by calculating confidence limits on the basis of Tchebycheff's Inequality (Freund 1962) rather than with the t-statistic.)

By the most conservative statistic (Tchebycheff at $P = .05$) only Sphaeralcea is overestimated. At $P = .1$, or using the t-statistic, grass and Grayia spinosa are overestimated and Sarcobatus vermiculatus is underestimated. The overestimation of Grayia results from a period when one analyst confused it with Sarcobatus.

The coefficients of the correction equations (Table 11) all have positive intercepts and slopes less than 1.0.

To interpret these results we should consider the ways in which errors might arise in the microscopic analysis procedure. These are:

(1) Species may grind to particles of different sizes.

(2) Species may lose different proportions of material. as the slides are made (in the digestion process, for example).

(3) Species may contain different proportions of tissues which are in principle identifiable. (Generally, only epidermis of non-woody tissue, particularly leaf epidermis, is identifiable.)

Table 11. Parameters of correction equations, which are regressions of the form (Actual percentage) = a + b (Estimated percentage). Data are from analyses by three individuals of 35 mixtures of known composition. Cases where both actual and estimated percentage was zero are included; df = 88 for all taxa.

Taxon	Intercept (a)	Slope (b)	r^2
Sphaeralcea spp.	.0112	.1572	.88
Opuntia polyacantha	.8333	.7334	.48
Descurainia spp.	.8348	-0.0804	.00
Atriplex falcata	.9358	.3751	.18
Atriplex confertifolia	6.2556	.6012	.32
Grayia spinosa	.6870	.1842	.35
Chrysothamnus spp.	7.7923	.6284	.46
Sarcobatus vermiculatus	12.2255	.5886	.18
Artemisia tridentata	3.3321	.7048	.61
Bromus tectorum	2.1435	.3572	.14
Grasses other than Bromus	4.3976	.5205	.38
Halogeton glomeratus	4.0185	.7699	.44
Kochia americana	2.0835	.5558	.59

(4) Even "identifiable" material may vary between species in how easily it is recognized.

(5) Material may be identified wrongly.

(6) It may take several occurrences of a species in a slide for the analyst to acquire a "search image" for it.

(7) If material is encountered which is identifiable but unknown, this may be classed as unidentifiable. The unknown's contribution to the mixture will then be divided among the other components.

(8) If a species is subject to underestimation, the species which often occur with it will tend to be overestimated; and *vice versa*.

There are three sources of error in estimating the species list. First, the wrong name may be given to all particles of some identifiable material. Second, the analyst may attempt (and fail) to name material which was not reliably identifiable. Third, material may be missed entirely, as an extreme form of quantitative underestimate. The Coefficient of Community (CC) and the Recognition Success (RS) compound these three errors.

The first kind of mistake seemed to be eliminated by the end of the training period. The remaining errors in identifying the species list (which were large -- see Figure 14 and Table 10) were presumably caused by the second and third kind of mistake. The second could be reduced by being more cautious about identifying material. However this would decrease the frequencies of "identifiable" material, and so increase the third kind of error.

The contribution of species to mixtures was also estimated badly (see Table 10, the r^2 values in Table 11, and Figure 14--but ED includes the effect of getting the species list wrong). Sparks and Malechek (1968) tested the accuracy of the procedure using grassland species, and found it satisfactory. Biases in our estimates (Table 10) seem to result mainly from how easily species are identified. Grasses and <u>Sphaeralcea</u>, which were overestimated, have characteristic oblong epidermal cells and stellate hairs, respectively. <u>Sarcobatus</u>, which was underestimated, had only leafless twigs at the time most of the reference material was collected. In general, desert species vary much more than grassland species in the proportion of material which is leaf epidermis.

The correction equations indicate that there was a tendency to underestimate or miss entirely species which were present in small amounts, and to overestimate those present in large amounts. Perhaps the former effect is because it is hard to form a "search image" for uncommon material, and the latter is the result of underestimating less common species.

The following conclusions seem to follow from these tests:

(1) The microscopic stomach analysis procedure gives

data of poor quality when applied to animals which sometimes browse desert shrub vegetation.

(2) This is mainly because the proportion of reliably identifiable tissues in the ingesta varies greatly between species.

(3) There is a tendency to underestimate or miss material present in small amounts, and correspondingly to overestimate the more common species.

Only problems involved in estimating the composition of a mixture of plant fragments, such as the contents of a stomach, have been discussed here. Other problems arise in extrapolating from a sample of stomach contents to the diet of a population. The main assumptions involved are that plant species are not differentially digested, and that the animals have been taken at random from the population.

Results

Stomach content data are presented in full in Appendix A. There means for each sampling date are given, and taxa are separated as far as possible. Here the data are lumped into four seasons (Table 12): winter (December-February), spring (March-May), summer (June-August), and autumn (September-November). Forbs other than Halogeton are lumped, and so are all unknowns. Table 12 separates data from the edge of the wheatgrass seeding, and from away from it.

The year-round averages for the shooting route in Table 12 are not simple means of the four seasonal values. They have been obtained for the period 10 October 1971 to 27 September 1972, when all stomachs were shot on the shooting route. This period was cut into segments of time at the dates midway between sampling dates. The mean percentage on a given sampling date was then multiplied by the number of days in the corresponding time segment. These values were then summed over the year and divided by 365 to estimate the mean percentage of the year-round diet on the shooting route. The only notable difference between averages obtained this way and those that would have been obtained by averaging seasonal values is the absence of Atriplex falcata; this species occurred only in the sample of 2 November 1972, which did not come from the shooting route.

The jackrabbits will apparently accept almost any plant species on the study area. All the important perennial species occur in the diet at some time. The only plants which are noticeably rejected are

Table 12. Mean percentages of plant taxa in stomach contents by season

Taxon	Percentage of Total Stomach Contents						
	Away from wheatgrass seeding				Year-round average on shooting route	Near wheatgrass seeding	
	Spring	Summer	Autumn	Winter		Summer	Autumn
Artemisia tridentata	11.1	0.0	2.6	18.1	7.8	0.1	0.4
Sarcobatus vermiculatus	9.0	9.1	3.7	3.5	6.7	0.0	0.0
Chrysothamnus spp.	0.1	3.6	6.1	3.3	2.1	0.3	24.1
Grayia spinosa	0.0	0.0	3.4	0.0	0.6	0.0	0.0
C4 *Atriplex confertifolia*	1.2	0.0	4.6	0.5	1.6	5.1	2.4
C4 *Atriplex falcata*	0.0	0.0	6.3	0.0	0.0	0.0	0.0
C4 *Kochia americana*	22.6	8.5	15.3	7.7	10.8	0.1	7.7
Bromus tectorum	0.1	0.8	0.2	0.0	0.2	0.0	0.0
? *Grasses besides Bromus*	27.4	38.5	9.3	3.8	21.0	85.3	55.0
C4 *Halogeton glomeratus*	16.0	20.9	42.4	58.0	38.8	6.4	10.0
Forbs besides Halogeton	6.5	16.1	3.8	5.1	7.7	0.5	0.4
Unknowns	5.8	2.0	2.3	0.0	2.1	1.8	0.1
Number of stomachs	29	26	68	13	98	23	58

the crucifers Descurainia and Lepidium. These are quite abundant--they each reach perhaps 10-50 percent of the biomass of Halogeton, depending on the year's weather--but are uncommon in the diet. They have (to humans) the characteristic mustardy taste of crucifers. The winter annual grass, Bromus tectorum, also seldom appears in the diet. This may be because the analysts usually lumped it with the other grasses, however.

Although nearly all species on the study area are acceptable, there is strong preference between them. "Electivities" (Ivlev, 1961) have been calculated for those taxa for which I have availability estimates (Table 13). This measure can vary from - 1 (rejected) to + 1 (highly preferred). On a year-round basis, grass and Kochia are highly preferred. Chrysothamnus, Grayia, and Halogeton are moderately preferred, while the dominant large shrubs, Artemisia, Sarcobatus, and Atriplex confertifolia, have low electivities.

As a result of these preferences, three taxa (grass, Halogeton, and Kochia) account for 65-70 percent of the diet in each of the four seasons. These three occupy the three leading places in the diet in all four seasons, with only two exceptions: Artemisia displaces grass in winter, and forbs displace Kochia in summer (Figure 15). The diet has the highest equitability in spring and the lowest in winter, with summer and autumn intermediate.

The following are notable features of the diet:

(1) Artemisia is used mainly in winter and spring.

(2) Sarcobatus is most important in spring and summer.

Table 13. Relative preferences of jackrabbits for plant taxa on the shooting route, on a year-round basis. E = (C - A) /(C + A), where E = Electivity, C = Relative Consumption, and A = Relative Availability

Taxon	Relative Consumption (Table 12)	Relative Availability (Table 6)	Electivity
Artemisia tridentata	7.8	19.5	- .43
Sarcobatus vermiculatus	6.7	18.3	- .46
Chrysothamnus spp.	2.1	1.2	+ .27
Grayia spinosa	0.6	0.1	+ .71
Atriplex confertifolia	1.6	4.4	- .47
Kochia americana	10.8	0.3	+ .95
Grass	21.0[a]	0.4[b]	+ .96
Halogeton glomeratus	38.8	55.9	- .18

[a] All perennial grasses.

[b] Sitanion hystrix only.

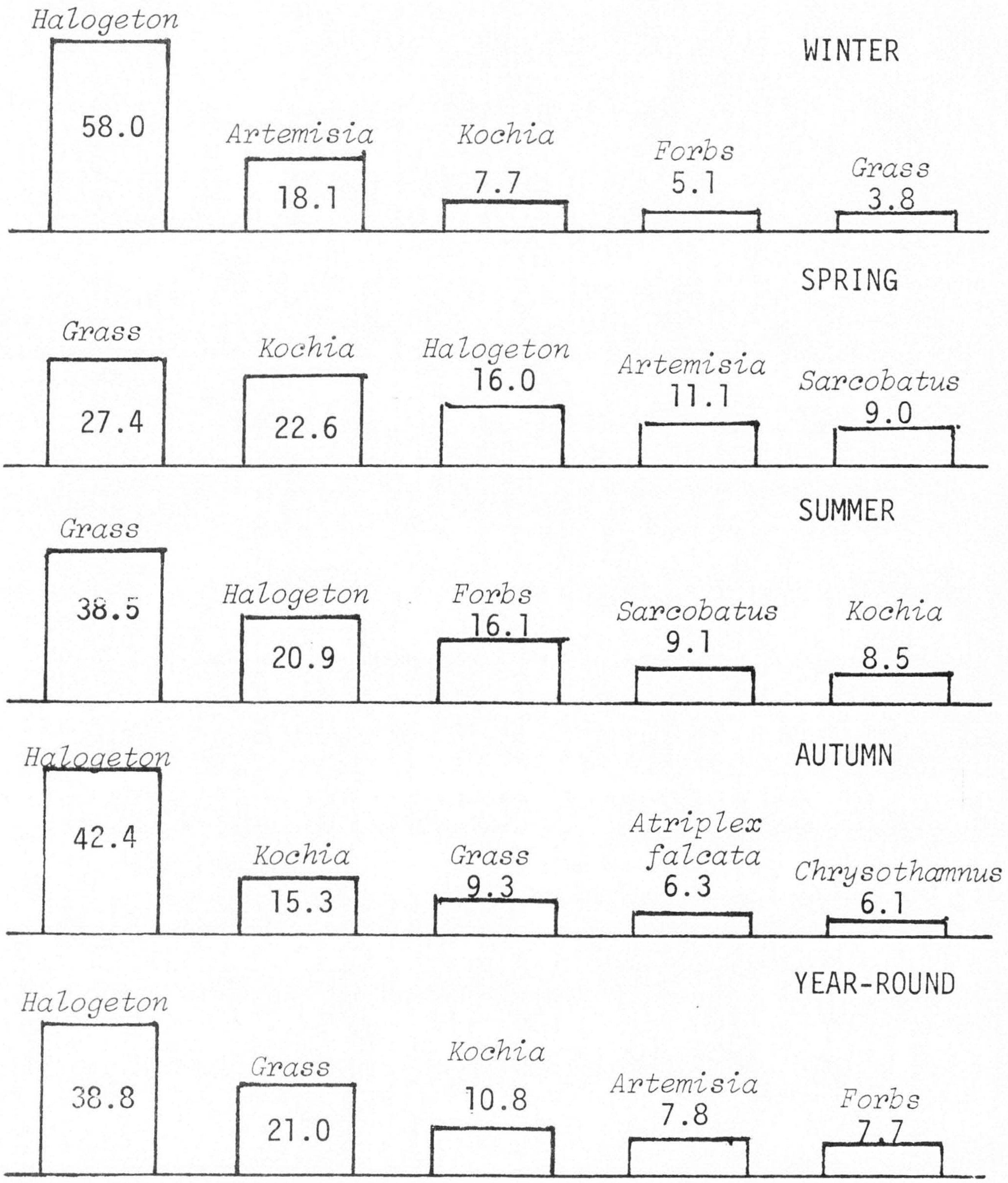


Figure 15. Mean percentages of the five leading taxa in the stomachs of jackrabbits shot away from wheatgrass seedings at each of four seasons, and year-round.

(3) *Atriplex confertifolia* and *Grayia* appear in the diet in autumn.

(4) *Chrysothamnus* is used in all seasons except spring, but particularly in autumn.

(5) *Kochia* is important throughout the year, but especially in spring and autumn.

(6) Grass is very important in spring and summer, less so in autumn and winter.

(7) *Halogeton* dominates the diet during autumn and winter, and is also important during spring and summer.

(8) Forbs other than *Halogeton*, and unknowns, are most important in spring and summer.

The data from the wheatgrass seeding (Table 12) support these patterns. *Chrysothamnus*, *Kochia* and *Halogeton* are all more important in autumn than summer, as they were away from the seeding; grass less. Grass (presumably *Agropyron*) is naturally most important in the diet. *Chrysothamnus*, which is abundant around the western rim of the seeding, also forms a high percentage of the diet.

These results generally agree with those obtained by other workers. Currie and Goodwin (1966) found that *Artemisia* was used from the beginning of dormancy in November until growth began during April. McKeever and Hubbard (1960) found that *Grayia* was highly preferred in comparison to *Artemisia*, *Chrysothamnus nauseosus*, and *C. viscidiflorus*. *Chrysothamnus* spp. were little eaten in that study; preferred plants besides *Grayia* were *Atriplex canescens* (Pursh) Nutt. and *Prunus andersonii* A. Gray, neither of which were found in my study area. Currie and Goodwin (1966), working in Curlew Valley, found that *Chrysothamnus* spp. were mainly used October-December. They found that perennial grasses appeared in the diet during April, were eaten almost exclusively during summer, and were replaced by shrubs by October. Forbs were used in the spring, but not during summer. They did not collect data on *Halogeton*.

The following features of the jackrabbit diet have not appeared in earlier studies: first, the extensive use of *Halogeton* year-round; and second, use of species (including *Halogeton*) with high salt content, and hence water content, during summer. Use of cactus during hot, dry periods has been reported (Vorhies and Taylor, 1933; Riegel, 1942; Brown, 1947).

Discussion

Null Hypothesis--Random Feeding

The simplest possible explanation of the diet is that it is the result of random feeding. If this were the case, foods would be taken in proportion to their availability. Figure 16 plots year-round percentage in the diet against availability. The correlation is statistically significant ($r_{12} = 0.77$, $P < .05$). The correlation coefficient implies that somewhat more than half (58 percent) of the variation in

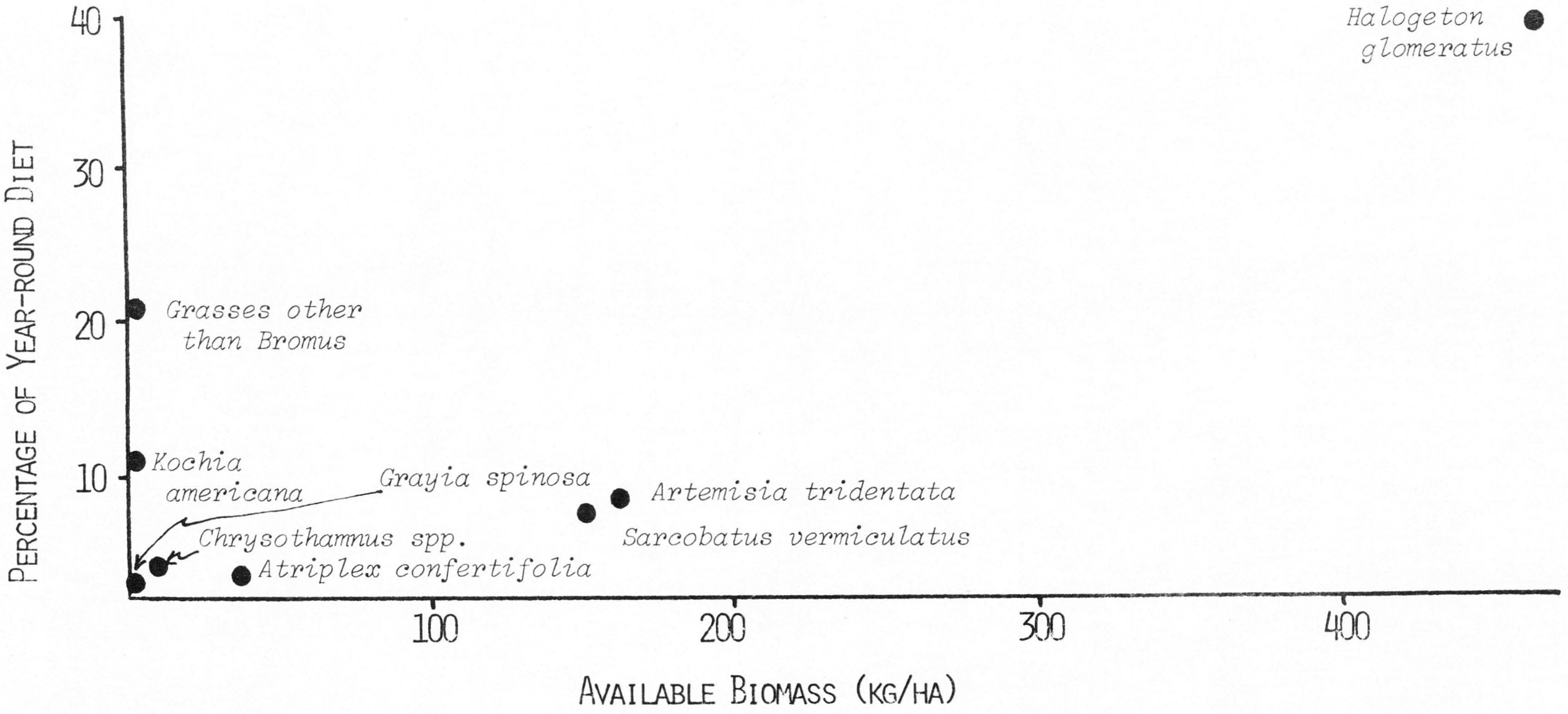


Figure 16. Relationship between consumption and availability of different plant taxa on a year-round basis.

year-round consumption between is associated with availability. Yet, nearly half of the variation is not associated with availability and therefore needs analysis.

Empirical Relationships between Nutrients and the Diet

From the evolutionary point of view, the most plausible reason why a food should be preferred is that it is more beneficial to the animal; i.e. it is nutritionally superior. It is difficult, though, to test formally the hypothesis that the diet is "nutritionally wise." The benefit obtained from a food depends on its content of digestible nutrients, and on the animal's need for each nutrient. Data on both needs and supplies are sparse. Even where the supply of one nutrient from a food is known, the benefit it gives will depend on how well the animal is supplied with other nutrients, from other foods. The best that can be done here is to present available data on the nutrient contents of foods, and to assess in general terms which seasonal changes in jackrabbit diets are reflected in the nutritional properties of the foods.

Energy, protein, and phosphorus

Available data on nutritional properties are presented in Figures 17, 18, and 19. These were developed by assembling all

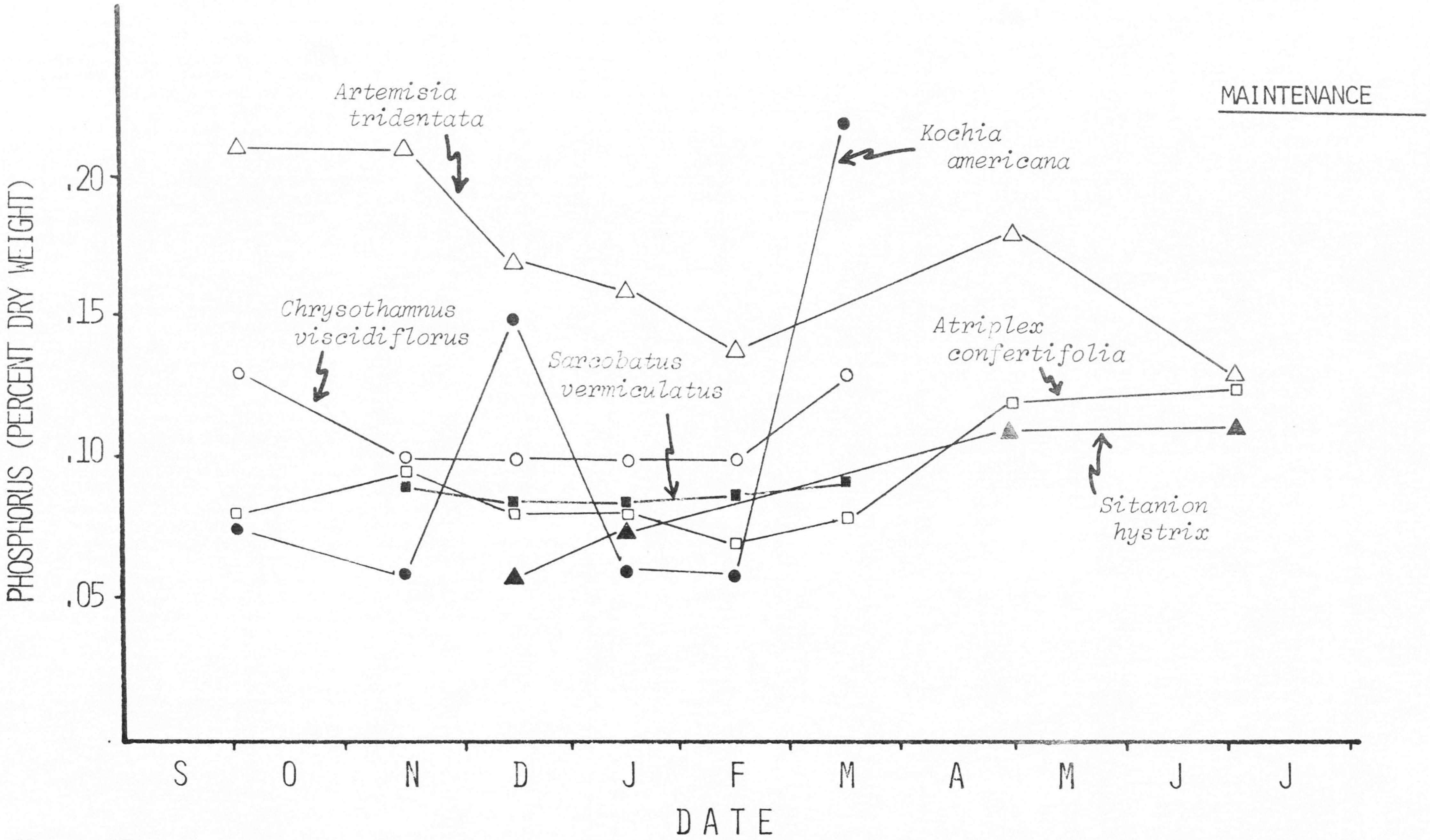
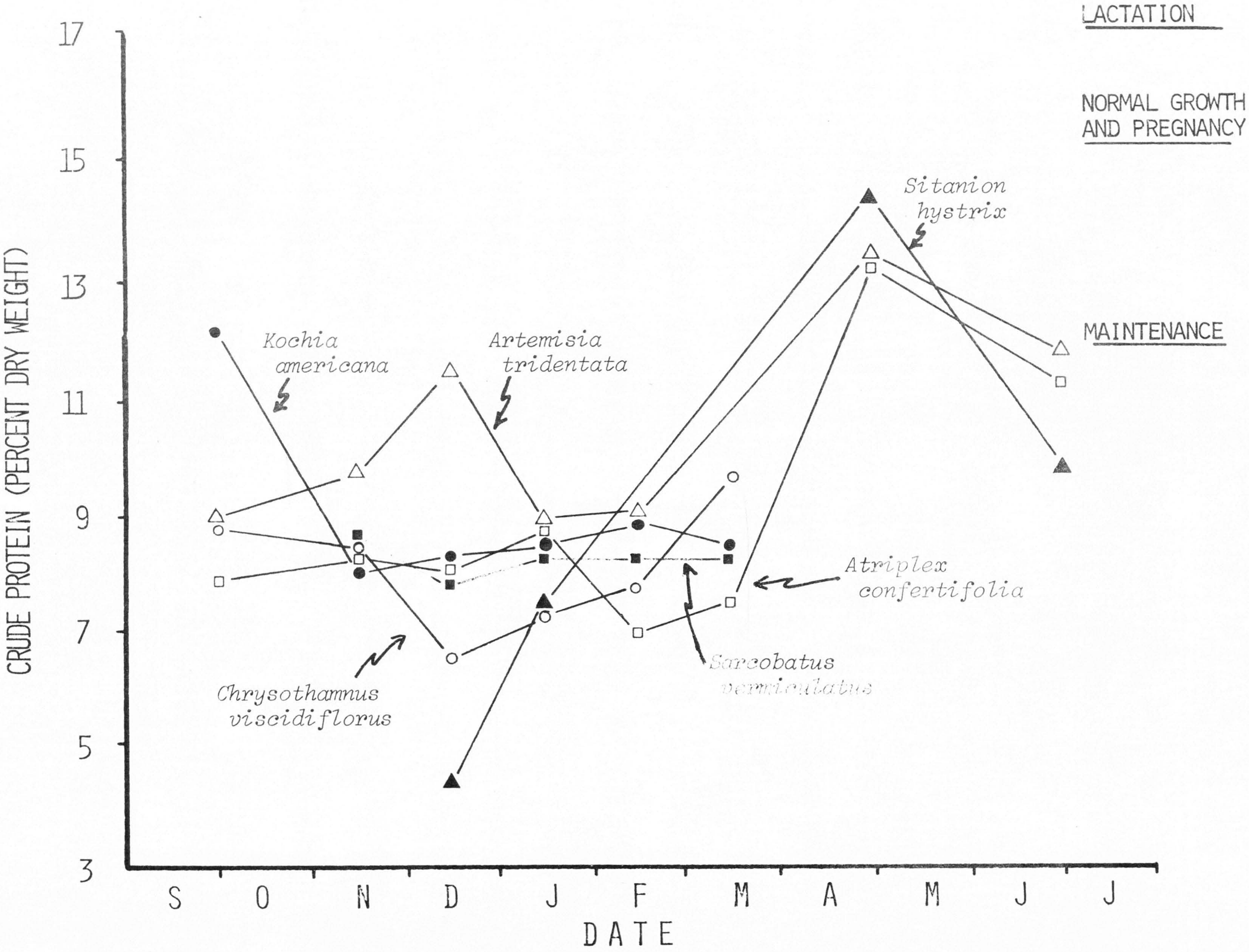


Figure 17. Seasonal changes in the phosphorus content of six plant species of the northern desert shrub biome. Also shown are the phosphorus requirements of domestic rabbits (NAS/NRC, 1966).


LACTATION
NORMAL GROWTH AND PREGNANCY
MAINTENANCE
CRUDE PROTEIN (PERCENT DRY WEIGHT)
17
15
13
11
9
7
5
3
Kochia americana
Artemisia tridentata
Sitanion hystrix
Atriplex confertifolia
Sarcobatus vermiculatus
Chrysothamnus viscidiflorus
S
O
N
D
J
F
M
A
M
J
J
DATE

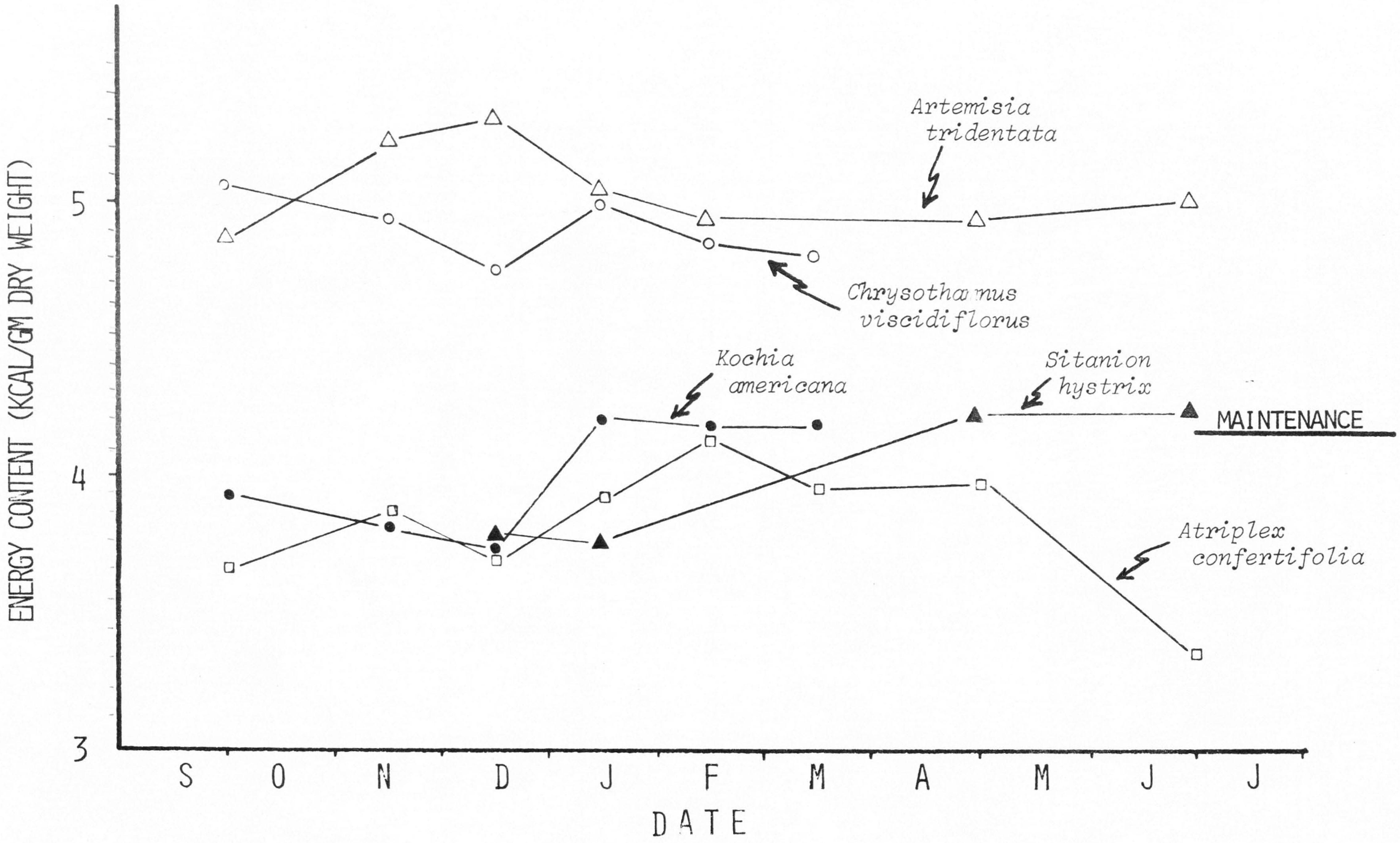


Figure 19. Seasonal changes in the energy content (gross, determined by Parr oxygen bomb calorimeter) of five plant species of the northern desert shrub biome. Also shown are the energy requirements of domestic rabbits (NAS/NRC, 1966).

values for the nutrient content of the current growth of plant species at definite dates, from Cook (1971), Cook et al. (1954, 1959), and Jameson (1952). Means were then taken for each month, and these values were plotted. Figure 17 gives data for phosphorus, Figure 18 for protein, and Figure 19 for energy. These nutrients were chosen because they were best documented; and because Cook et al. (1954) characterized nutritional problems for stock on these ranges as inadequate protein and phosphorus from grasses, versus inadequate energy from shrubs.

Most of the nutrition data are from the period October-April, because the main economic use of this vegetation is as winter range. On the same figures the requirements of domestic rabbits for the nutrients (NAS/NRC, 1966) are indicated. These requirements assume the digestibilities of commercial feeds; unfortunately the actual digestibilities of Curlew Valley plants to jackrabbits are unknown.

Artemisia seems to have a higher phosphorus content than other species during autumn, winter, and spring.

All species are low in protein during autumn and winter. Grass is much lower than the shrubs in this regard. Artemisia seems to be the best of the shrubs during winter. All species increase in protein content in spring, with grass increasing markedly. Given that grass has higher digestibility than shrubs (Cook and Harris, 1968), it is probably the best source of protein during spring, and perhaps summer too. Jackrabbit breeding in this area lasts from about January to July (Stoddart, 1972); the protein needs of females presumably increase during this period, relative to the nonbreeding season.

Artemisia and *Chrysothamnus* have a higher energy content than the other shrubs and *Sitanion* for all seasons when data are available. There is no conspicuous seasonal variation in energy content within species; the relative ranks of the different species are consistent.

Now I shall consider the list of eight features of the jackrabbit diet given earlier, to see which of them are intelligible in the light of these nutrient data.

Of the eight features listed (7), (8), and in part (3) cannot be considered, because we have no data on *Grayia*, *Halogeton* or forbs. Of the others:

(1) *Artemisia* is used mainly in winter and spring. However it ranks high in several attributes throughout the year. Why is it not used during summer and autumn? A possible explanation is that it is eaten only during its dormant period, November-April (Appendix A). Currie and Goodwin (1966) give the same dates. Nagy et al. (1964) found that the volatile oils of *Artemisia* reduced digestion efficiency in deer; it may be that the volatile oil content is lowered during dormancy.

(2) *Sarcobatus* is most important in spring and summer. It is unexceptional in protein and phosphorus content during winter, so would not be expected to be used then. No nutrient data for spring and summer are available.

(3) Atriplex confertifolia appears in the diet in autumn. It is consistently low-ranked in all the nutrients chosen, so its unimportance in the year-round diet is reasonable. Its use in autumn would not be predicted from these data, though.

(4) Chrysothamnus is used in all seasons except spring, particularly in autumn. It is ranked high in energy content, but not in phosphorus or protein. Its rankings do not change much seasonally. Its use may be explained by its energy content, but no reason appears for the seasonal changes in use.

(5) Kochia is important throughout the year, but especially in spring and autumn. On the whole it ranks low in all attributes. There are two exceptions; it is high in protein in early autumn, and increases sharply in phosphorus in early spring. But both of these high points result from single,high observations in the literature, and so must be regarded with caution. Overall, then, its importance in the diet seems inexplicable; but the seasonal pattern of use is reflected in the data.

(6) Grass is very important in spring and summer, less so in autumn and winter. It is ranked low in all attributes except protein during spring and summer. Supposing that, taking its high digestibility into account, it is the

best source of protein during spring and summer, and that the protein need is the most important over that period, its seasonal pattern of use seems reasonable. It seems more important overall in the diet than one would expect, though.

Water

Water is another nutrient known to be important to jackrabbits. All workers on jackrabbit diets agree that they select for "succulence" (Hansen and Flinders, 1969). The animal is quite small (ca 2 kg in weight) so that its heat load is large. It does not shelter underground from radiation. Thus, its thermoregulation has been a matter of great interest (Schmidt-Nielsen, 1964; Schmidt-Nielsen et al., 1965; Porter and Gates, 1969; Wathen et al., 1971). It must be solving its heat problem by evaporating water, which it obtains only from food.

In order to study quantitatively the needs of a jackrabbit for water, I built a simulation model. The program, named RABWAT, written in PL/I, is given in Appendix B. This model carries out the following calculations. It reads 24-hr maximum and minimum air temperatures for a series of days. It predicts the hourly course of air-temperature during each day by drawing a sine curve through the maximum and minimum. It takes 12 temperatures (at 2 hr intervals) from this curve, and uses them as independent variables in the function shown in Figure 20, which is taken from Figure 4 of Schmidt-Nielsen et al. (1965). By this means, an estimate of the total evaporative loss over the 24-hr period from a jackrabbit of 2100 gm body weight (Stoddart 1972) is obtained. To this a water loss in urine and feces, arbitrarily set at 6 gm/day, is added. The model then computes the mean daily water loss per week.

Next, the model estimates the daily dry-matter intake of the jackrabbit for the date under consideration. This is done by linear interpolation between the three values reported by Currie and Goodwin (1966) (97 gm at the beginning of September, 111 gm around December 20, and 61 gm around May 10). The production of metabolic water is estimated as .4 times the dry-matter intake. (This is obtained from .12 ml H_2O per kcal of digested energy (Brody 1945), times 4 kcal per gm dry matter, times an unknown digestion coefficient, estimated conservatively high at .8). Metabolic water is subtracted from the water expense as computed above. Then the net water expenditure is expressed as a percentage of the dry-matter intake. This gives a figure for the water content, as a percentage of dry weight, which the jackrabbit would require in its food in order to remain in water balance.

The values obtained by running the model with 1970 temperature data from the Snowville, Utah weather station

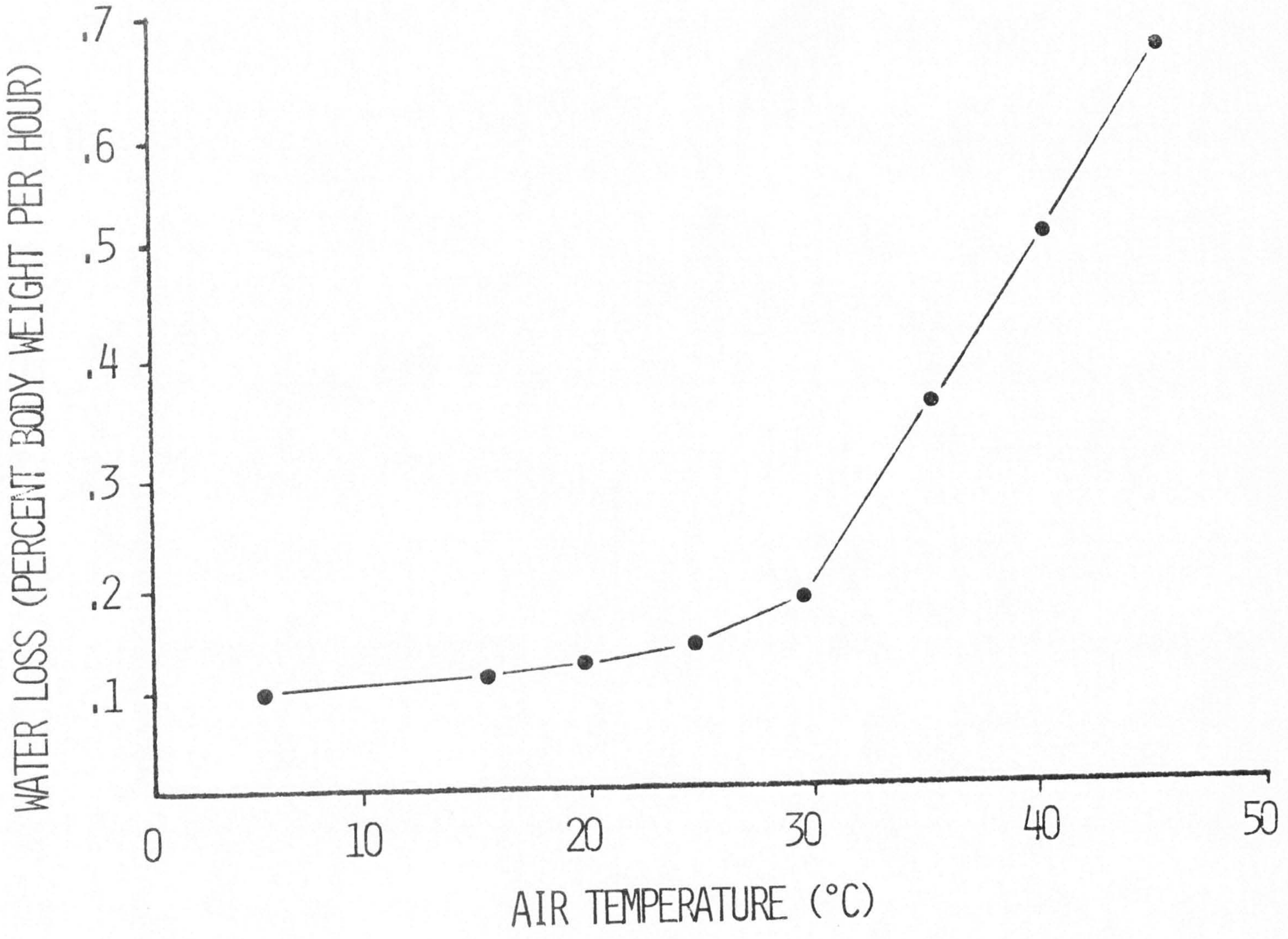
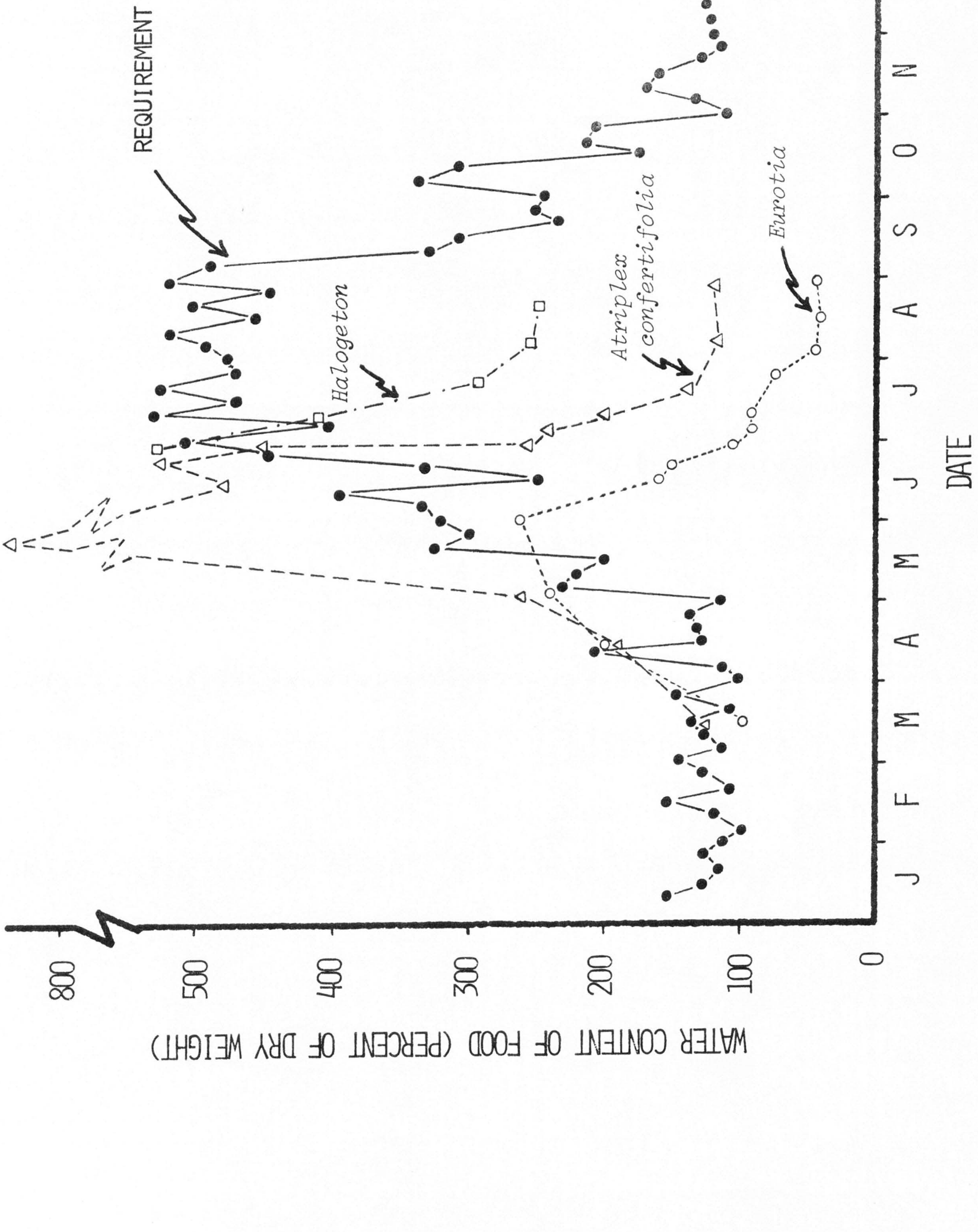


Figure 20. Function relating rate of water loss to air temperature for jackrabbits used in the model RABWAT (see text). Values obtained by linear interpolation between the points shown. Taken from Schmidt-Nielsen et al. (1965).

are plotted in Figure 21. Data for seasonal variation in water content of plants found in Curlew Valley are plotted on the same figure. Moisture content of the leaves of *Eurotia lanata* and of *Atriplex confertifolia* during 1970 were reported by Caldwell et al. (1971), and for the terminal inch of stems of *Halogeton* during 1957 by Cronin (1965).

Of these three species, *Eurotia* does not develop high salt concentrations; its water content is probably representative of most species. *Atriplex confertifolia* takes up salts readily, but extrudes them into vesicles on the leaf surface (Kenagy 1972); these in due course break, and the salts are leached off the leaves. Thus it has an exceptionally high water content during May, which decreases sharply during June and July.

Halogeton also takes up salts readily, but solves the resulting physiological problems by developing high oxalate concentrations (Cronin 1965). These make it poisonous to livestock when eaten in quantity. *Sarcobatus* also has high oxalate concentrations (Forbes and Skinner 1903, Fleming et al. 1928, Couch 1937). The water data given for *Halogeton* in Figure 21 are for the terminal inch of stems; note that *Halogeton* leaves contain more than twice as much oxalate as stems (Dye 1956), and presumably have correspondingly higher water content.


REQUIREMENT
Halogeton
Atriplex confertifolia
Eurotia
0
100
200
300
400
500
800
J
F
M
A
M
J
J
A
S
O
N
D
DATE
WATER CONTENT OF FOOD (PERCENT OF DRY WEIGHT)

This model suggests that during summer (June-August) jackrabbits in Curlew Valley would be in water stress eating most plants. They can overcome this by taking *Halogeton* or *Sarcobatus* during this period, assuming that the oxalate concentrations involved do not trouble them, and they can dispose of the salts without increasing urine volume.

The need for water during summer relates to features (2), (7) and (6) of the jackrabbit diet, as listed earlier.

(2) *Sarcobatus* is most important in spring and summer. Use in summer is reasonable for water. Spring and summer nutrieint data on *Sarcobatus* are lacking, but Forbes and Skinner (1903) give it a high protein content of 19.8 percent (date not reported). Perhaps it is used during spring as a source of protein.

(7) *Halogeton* dominates the diet during autumn and winter, and is also important during spring and summer. The water need provides a reason for its use during summer. There are no data for its content of nutrients at other seasons.

(6) Grass is very important in the diet in spring and summer. But dormant grasses have a low water content. Would this not be a reason to avoid grass during summer? Perhaps dry grass provides more moisture than would appear. Taylor (1968) found that some grasses which had water contents below 1 percent during the day, increased to more than 40 percent at night; and jackrabbits are nocturnal feeders.

I shall defer discussing the extent to which all the preceding supports or opposes the idea of nutritional wisdom until after the mechanisms involved in food selection have been considered.

Analysis of Mechanisms Influencing the Food Selected

The concept which range managers use to interpret food selection is "palatability." An operationally-defined measure of this is the Relative Preference Index (RPI) of Van Dyne and Heady (1965), variants of which were first used in fisheries work reviewed by Ivlev (1961). It relates relative availability (A_i) and relative consumption (C_i):

$$RPI_i = C_i/A_i \qquad [11]$$

The RPI, though, is a relative measure (NAS/NRC, 1962; Heady, 1964; Marten, 1969). It is not constant for a particular food and herbivore, even if phenophase and chemical race of the plant are specified, but depends on what other plants, in what abundance, are associated with the one being considered.

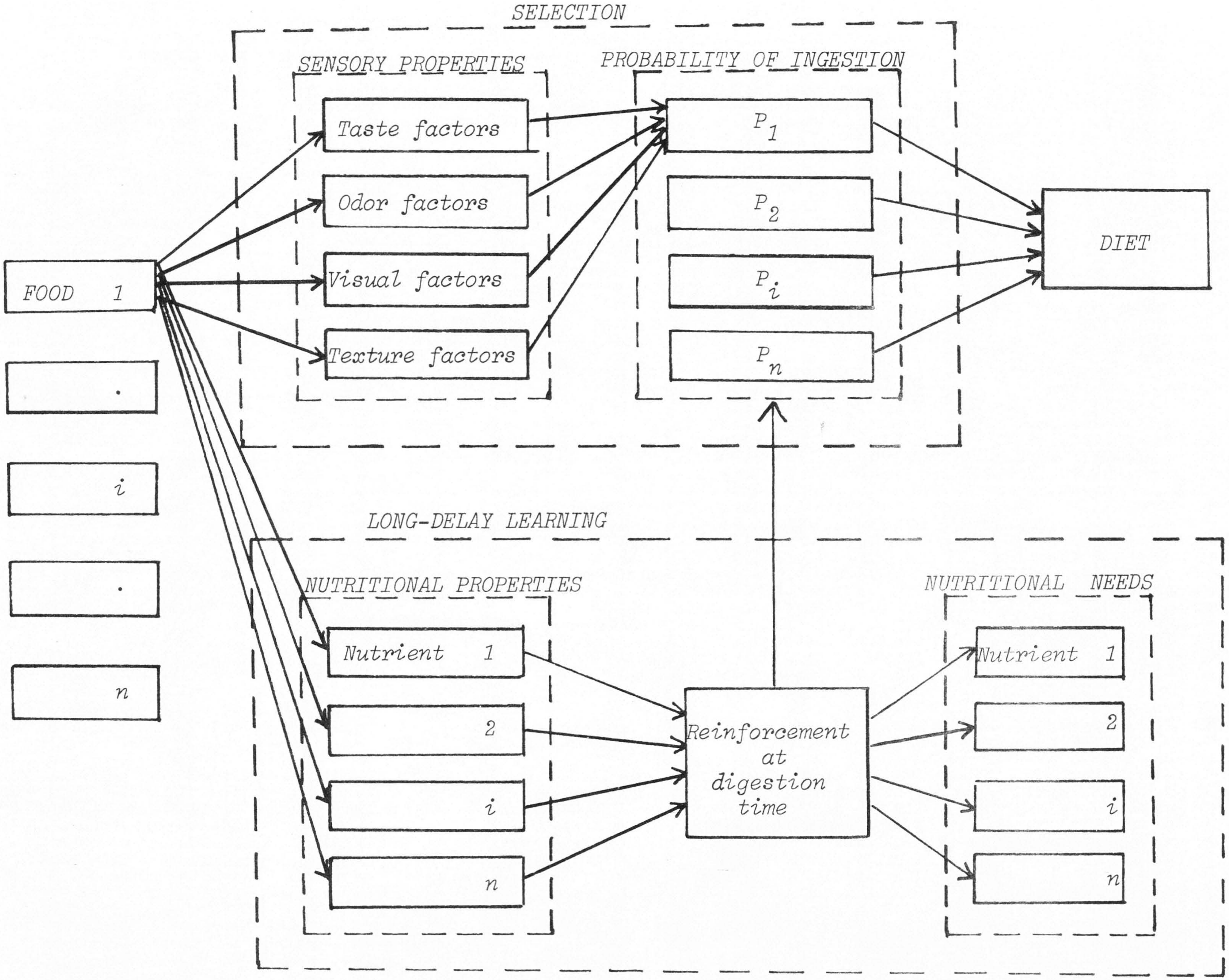
While useful a posteriori measures of selection, then, relative preference indices (there are several--"electivity" (Ivlev, 1961) was used earlier, and others (Krueger, 1972) incorporate frequencies of consumption and abundance) have little predictive power outside the circumstances where they were measured. The problem is that they are empirical measures which do not describe the real processes going on. If we can develop a good causal account of the processes involved in food selection, we will have a basis for predicting the diet of a herbivorous species when it is placed in a given vegetation.

I feel that enough is now known to warrant developing deductively a hypothesis about food selection mechanisms. Its implications can then be compared with existing food selection data.

The optimization-and-sampling hypothesis

Mechanisms. Figure 22 represents my understanding of the processes involved in food selection. Selection happens when a food item is examined by the herbivore, and is ingested or rejected. A food item has two logically distinct groups of properties. The first are those detectable before ingestion by an animal; these are the only properties which can be used in making the decision whether or not to ingest. The second are those detectable after ingestion; it is on the effects of these that natural selection acts. These will be called sensory and nutritional properties, respectively.

In Figure 22 the nutritional properties of foods do not directly affect the probability of ingesting an item with particular sensory properties. Their effect is via "long-delay learning." It is possible for feeding preferences to be changed by giving aversive stimuli (e.g. low levels of body X-irradiation) as much as 18 hours after ingestion of the food (Revusky and Garcia 1970). This behavior is in sharp contrast to the usual paradigm of operant behavior, in which reinforcement is much less effective if not delivered immediately after the behavior being reinforced. Apparently some record of the sensory properties of the food which was eaten is stored centrally


SELECTION
SENSORY PROPERTIES
Taste factors
Odor factors
Visual factors
Texture factors
PROBABILITY OF INGESTION
P_1
P_2
P_i
P_n
DIET
FOOD 1
.
i
.
n
LONG-DELAY LEARNING
NUTRITIONAL PROPERTIES
Nutrient 1
2
i
n
Reinforcement at digestion time
NUTRITIONAL NEEDS
Nutrient 1
2
i
n

(Rozin, 1969a; Revusky and Garcia, 1970) and compared with the account given by relevant proprioceptors at digestion time. Single trials can produce significant learning. The system seems unique to feeding behavior, and is a powerful and obviously adaptive tool for associating the nutritional value of a food, as measured by reinforcement at digestion time, with characters which enable the animal to identify it before ingestion (Revusky and Garcia, 1970; Rozin and Kalat, 1971).

If the long-delay learning mechanism is operating, preferences for particular sensory properties of foods should be very changeable. This is so. Figure 23 (after Arnold and Hill, 1972) shows the responses of an individual sheep to different taste solutions on five occasions, as an example.

The hypothesis. Food selection operates *via* the relations between the sensory properties of foods, and the probabilities of ingesting them. But these relations are changeable. Rather than try to predict them, we will do better to think of the act of selection as a black box, controlled by another black box, the long-delay learning mechanism. The two together would act to maintain consistent relations between the nutritional properties of foods and the diet chosen. These relations should be more predictable than the insides of either black box. What are they?

If it were possible to establish criteria for the levels which each chemical component (protein, carbohydrate, ash content, etc.) should reach in an ideal diet, one could formulate the problem of

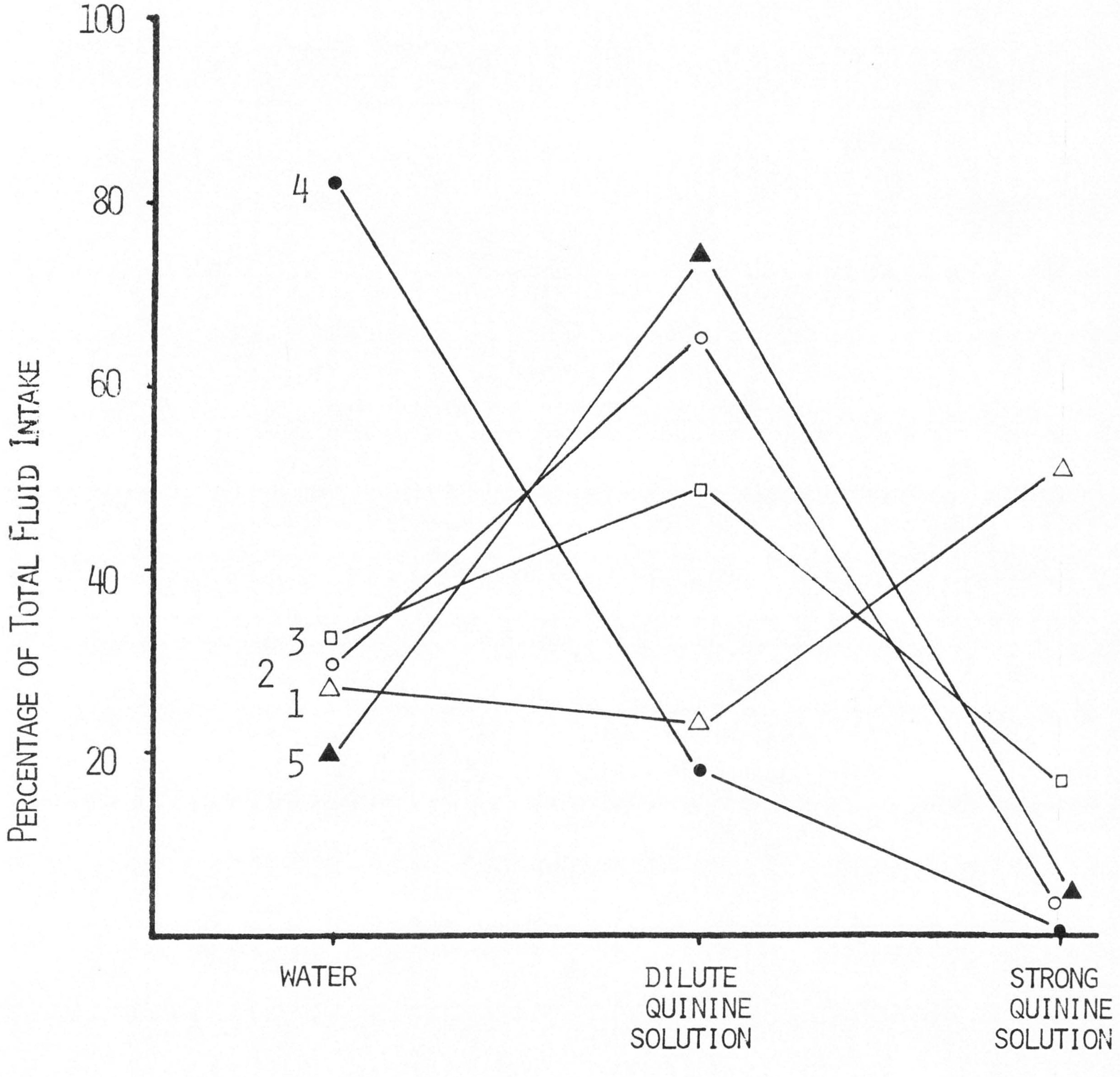


Figure 23. Preferences of one sheep given the same choice of three solutions on five occasions, spaced over four months. Choice was over 24 hours. The variability shown was similar for each of another five sheep and for choices involving glucose, sodium chloride and acetic acid (after Arnold and Hill, 1972).

selecting an optimal mixture of species as a linear program (Table 14). Animal nutritionists routinely do this when choosing feeding regimes for penned stock (Crampton and Lloyd, 1960).

In Table 14, x_j is the proportion of the jth food in the diet, and a_{ij} is the amount of the ith chemical property the animal will obtain from the jth food. Adding across the rows of the Table will give the overall chemical composition of the diet; that is

$$\sum_j a_{ij} . x_j = N_i \qquad [12]$$

The criteria of what the best overall chemical composition of the diet should be are set up, mostly as inequalities, on the right-hand-side (RHS) of Table 14. One (represented by an equal-sign) is known as the Objective Function. This is to be maximized within the constraints shown by the rest of the RHS. For example, one might maximize caloric content within the constraints that protein content must be greater than 15 percent and lignin less than 10 percent, and so on. If the a_{ij}'s (properties of the available foods) are known, the system of equations can be solved for the x_j's which best satisfy the criteria of the RHS; i.e., the best food composition of the diet can be selected.

This model will hereinafter be referred to as the "optimization" model. The diet it predicts will be called the "optimized"

Table 14. A diet optimization problem formulated as a linear program

	Food_1		Food_2		Food_3		Food_j	Constraint	RHS
Property 1 (percent protein)	$a_{1,1}x_1$	+	$a_{1,2}x_2$	+	$a_{1,3}x_3$	+	$a_{1,j}x_j$	$\geq$	15.0
Property 2 (percent fiber)	$a_{2,1}x_1$	+	$a_{2,2}x_2$	+	$a_{2,3}x_3$	+	$a_{2,j}x_j$	$\leq$	30.0
Property i (calorie content)	$a_{i,1}x_1$	+	$a_{i,2}x_2$	+	$a_{i,3}x_3$	+	$a_{i,j}x_j$	=	Maximum (Objective Function)

diet. The model has the following property. If a food increases in content of a beneficial nutrient, the contribution of the food to the optimized diet will increase only if that nutrient is limiting the Objective Function.

This pattern is clearly shown in Table 15 (after Marten, 1969), which summarizes the literature on the responses of preferences to nutritional properties of foods. Nutrients which are potentially beneficial either increase preference or do not change it. Chemicals which reduce food quality (e.g., fiber, cellulose, in Table 15) either reduce preference or do not change it.

The object (in evolutionary terms) of the long-delay learning mechanism is to improve diets. But when the animal eats meals of a mixture of species, how can the reinforcements be associated with particular foods? Foods chosen for particular meals would have to fit some pattern, or sampling procedure. Various sampling patterns could be imagined.

The simplest would be to take meals mainly from one food (a different one each time). Rats suffering from various possible mineral or vitamin deficiencies switch into a pattern of this kind (Rozin, 1969a,b). On the other hand Revusky and Bedarf (1967) and Shettleworth (1972) have shown that aversive consequences are associated selectively with novel foods. Thus one might hypothesize that individual meals in a sampling procedure would contain, not one food only, but only one novel food: successive meals would differ mainly in the proportion of one food.

Table 15. Reported relations between palatability and various nutritional properties of plants (after Marten, 1969)

Substance(s)	Relationship	References
Sugars and soluble carbohydrates	None	Warmke et al. (1952), Hardison et al. (1954), Reid & Jung (1965), Reid et al.(1966), O'Donovan et al (1967), Buckner et al. (1969), Rabas et al. (1969), Marten & Donker (1964).
	Positive	Cowlishaw & Alder (1960), Gangstad (1964), Bland & Dent (1962, 1964), Dent & Aldrich (1963), Heady (1964), Reid et al. (1967).
Protein or nitrogen	None	Archibald et al. (1943), Reid & Jung (1965), Reid et al. (1966), Reid et al. (1967), O'Donovan et al. (1967), Buckner et al. (1969).
	Positive	Hardison et al. (1954), Cook (1959), Blaser et al. (1960), Burton et al. (1964), Gangstad (1964), Heady (1964), Fontenot & Blaser (1965).
Proximate analysis	None	Brown (1961)

Table 15. Continued

Substance(s)	Relationship	References
	None	Leigh (1961), Reid et al. (1966, 1967).
Crude fiber, acid detergent fiber, or cell walls	Negative	Archibald et al. (1943), Hardison et al. (1954), Buckner (1955), Blaser et al. (1960), Gangstad (1964), Arnold (1964), Heady (1964), Fontenot & Blaser (1965).
Ether extract or fat	Positive	Hardison et al. (1954), Blaser et al. (1960), Gangstad (1964), Fontenot & Blaser (1965).
Minerals (individual or total ash)	None	Marten & Donker (1964, Reid & Jung (1965).
	Positive	Beaumont et al. (1933), Hardison et al. (1954), Ivins (1955), Cook (1959), Cowlishaw & Alder (1960), Leigh (1961), Gangstad (1964).
Cellulose	None	Brown (1961)
	Negative	Cook (1959)
Carotene	None	Buckner (1955).
	Positive	Archibald et al. (1943).
Vitamins	None	Hardison et al. (1954), Reid & Jung (1965).
Organic acids (silage)	Positive	Allen & Porter (1954).

Two general points: first, a sampling pattern would not have to be used at all times in an animal's life. It would only be useful when information on available foods had to be updated. Second, what is a "meal?" Imagine the material ingested as a continuous stream. Insofar as this stream can be cut into segments, each of which gives a distinguishable level of reinforcement indicating its nutritional properties, the segments are "meals." This is the sense in which the term has been used above.

What is proposed here is that to predict diets, both the act of selection and the long-delay learning mechanism should be treated as black boxes. Their internal functions, which are so variable, should be ignored. Their purpose, in evolutionary terms, is to maintain consistent relations between the diet and the nutritional properties of potential foods. These relations offer the best chance of predicting diets.

This is a "nutritional wisdom" hypothesis. The original nutritional wisdom hypothesis was given by Albrecht (1945) and Stapledon (1947). It stated that animals lacking particular nutrients developed "specific hungers" for them, and were able to detect them in foods. Range managers have looked on this theory as discredited, at least since Tribe's (1950) review. Actually, two things have been proven. First, grazing animals are not nutritionally infallible.

Second, most "specific hungers" do not operate via special senses which allow the animal to detect the nutrient before ingestion. (Exceptions are salt and sugar -- cf. Cabanac 1971.)

On the other hand animals generally obtain a diet better than random choice would give (Cook et al. 1956). By using the long-delay learning mechanism, they can often correct deficiencies even of nutrients they cannot sense in foods (Revusky and Garcia 1970).

This "fallible nutritional wisdom" hypothesis states that animals optimize their diets, subject to modification for necessary sampling, and to the fallibilities of the long-delay learning mechanism.

What are these fallibilities? They stem from the fact that the animal depends on differential reinforcement at digestion-time to select foods. Figure 24 shows some different ways reinforcement might depend on the animal's need for the chemical. Sugar (A) shows a continuous response of reinforcement to need. Poison (C) is aversive at any time, if the animal survives. Some minerals and vitamins (B), such as thiamine (Rozin 1967), are not detectable when

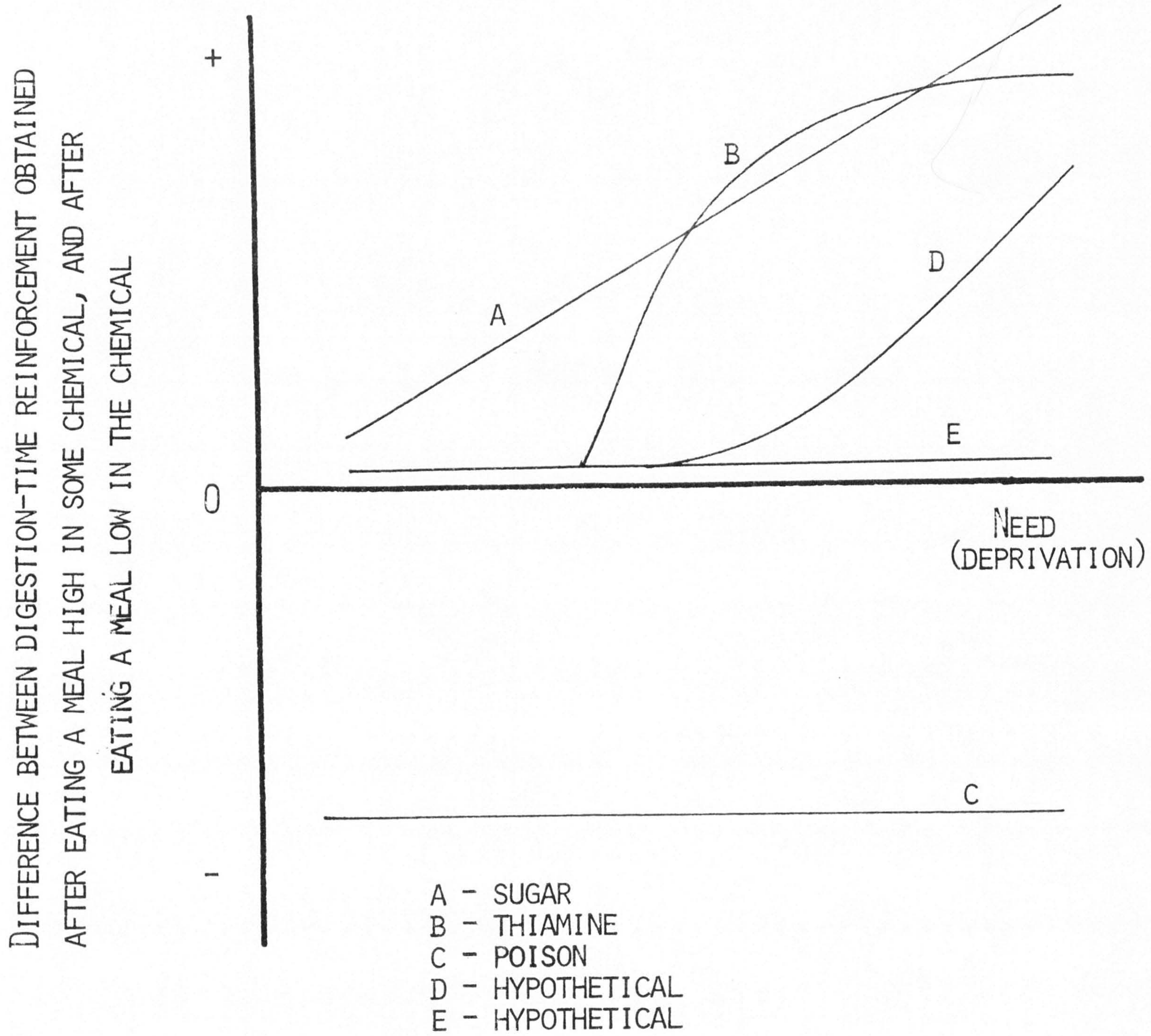


Figure 24. The degree to which chemicals are detectable at digestion time, depending on the degree of deprivation of the chemical. Shown are the general shapes of some possible curves for the difference between reinforcement from a meal high in the chemical, and reinforcement from a meal low in the chemical, plotted against the animal's need for, or degree of deprivation of, the chemical. The sources for these curves are Cabanac (1971) for sugar, Rozin (1967) for thiamine. The poison curve is by definition and D and E are hypothetical.

the animal is not deficient, but meals without them cause nausea when the animal is deficient. Other possible responses are D -- an indistinct threshold -- perhaps protein; and E -- no response.

Using the linear programming approach to reproduce the optimization, we can simulate the effect of many curves of type B, and one of type A (the Objective Function) on the RHS.

From these curves we can see that long-delay learning allows the following kinds of "nutritional unwisdom":

(1) Deficiencies of nutrients with type-E curves;

(2) Failure to maximize intake of nutrients with type-B or type-C curves;

(3) Failure to avoid poisonous plants that kill;

(4) Overeating of nutrients with type-A curves.

This last case is particularly interesting. Gordon and Tribe (1951), in a study often cited as evidence against nutritional wisdom, offered pregnant ewes ad lib. access to various foods, including a carbohydrate concentrate. The ewes selected a diet with a higher carbohydrate/protein ratio than was good for them. At first they became fat, then listless, and did not feed properly. Most miscarried.

The voluntary intake of sheep is largely controlled by gut-fill (Weston 1966) rather than by blood-sugar. They therefore have no protection against overeating energy concentrates. Of course, ruminants would not have needed such protection during evolution.

How widely in the animal kingdom might the "optimization-and-sampling" model apply? First, the mechanisms involved are only valuable to "generalist", rather than "specialist", herbivores -- those that take a large and variable spectrum of foods. Second, long-delay learning should be most important where the sensory properties are poor correlates of the nutritional properties of the foods, as for range plants. Third, food quality will be more important than availability when digestion-time, rather than search- or pursuit-time, is limiting. This will be so for large herbivores such as equines, ungulates and lagomorphs.

On these grounds the theory ought to be most applicable to "large generalist herbivores." Much turns on whether these animals have and exercise long-delay learning mechanisms. The direct evidence for the long-delay learning comes mainly from rats, with some work on birds and man. Do domestic stock (for example) also show it? There are three indirect arguments that they do. First, they show great variability in the response to particular sensory properties (Figure 23). Second, they show nonlinearities in the response to nutritional properties (Table 15). Third, faced with foods of such variable quality, they need it.

Against this, there are two arguments that they do not have it. First, there is no direct evidence that they do. Second, what would a "meal" be for a polygastric animal?

In discussing the optimization model to this point, foods have been called simply "available" or "unavailable." One of the ecologically important predictions by which the theory must be judged is what happens when one food becomes progressively less common in either time or space. The optimization model supposes that foods are chosen largely on grounds of chemical qualities, rather than how hard they are to obtain. This means that the diet should be conservative in response to availability; the proportion of a food in the diet should not vary with availability over most of the range. Clearly, though, consumption must fall to zero at zero availability.

(Clearly, too, consumption must rise to 100 percent as relative availability reaches 100 percent. But this is logically the result of unavailability of other foods, rather than high availability of the one. This effect will not be considered further here.)

The optimization model therefore predicts a response to availability of the form shown in Figure 25 . At what level (shown by X) does decreasing availability prevent a food from forming part of the optimized diet? The highest answer is given by assuming that the animal must be able to take a meal made entirely of the food, to learn to include it in the optimal diet. What level of food availability would allow this? Consider a range sheep, travelling 12 km a day (Squires, Wilson and Daws 1972), and searching a band 20 cm wide. With such a pattern it examines .24 ha per day.

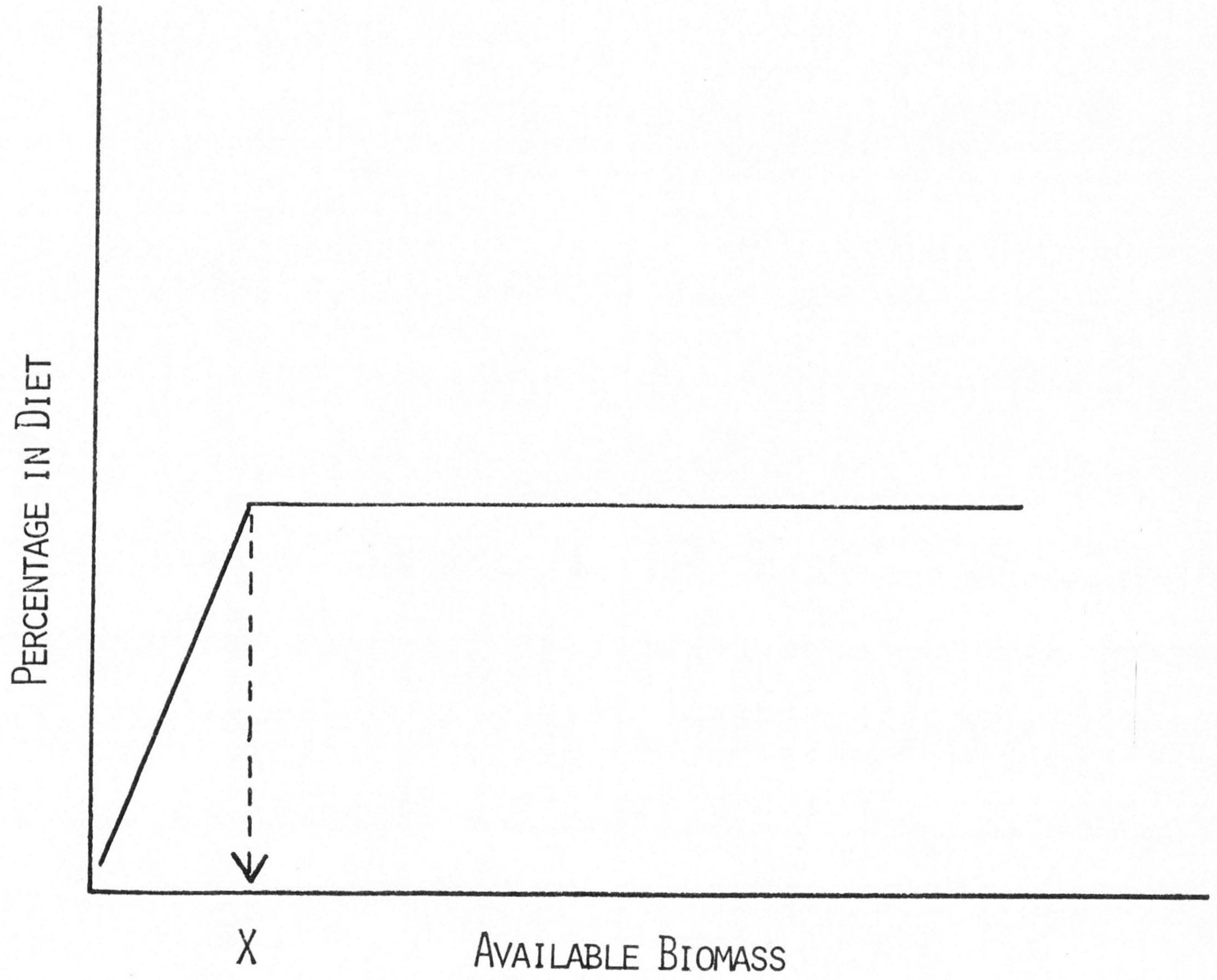


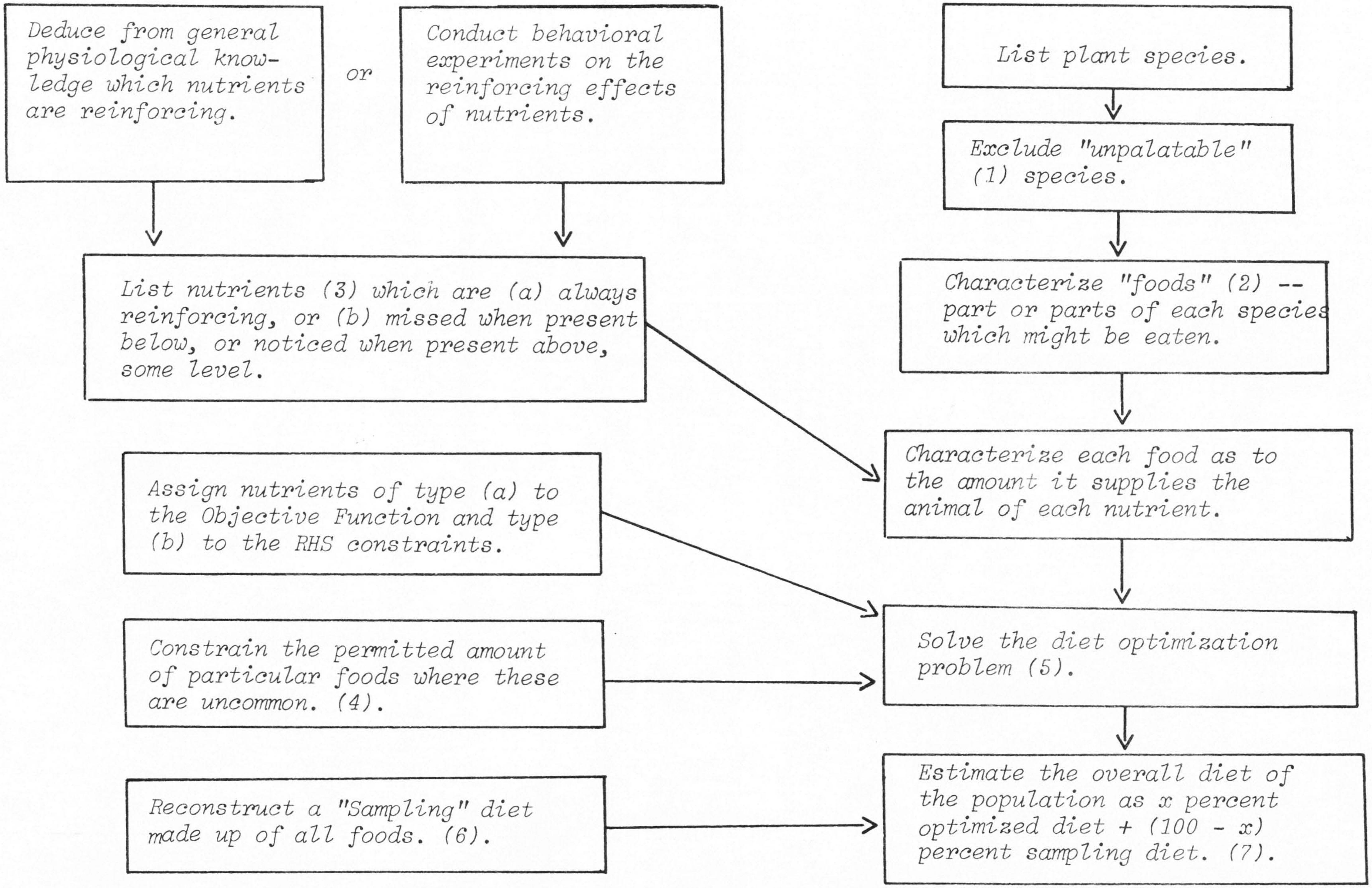
Figure 25. Expected changes in the percentage of a food in the diet as its availability decreases. Point X is estimated to be at not more than 10 kg/ha for range sheep.

If it takes 2 kg dry weight of food per day, it will be able to take its meal entirely from one food if the food is available at more than 8-10 kg/ha. (Probably a sheep is only looking for food during 4-5 of those km; on the other hand, it probably searches a strip more than 20 cm wide. I believe the calculation estimates the point X conservatively high, if anything.)

If total available food is 300 kg/ha, the calculation implies that the sheep is taking about one item in 30 examined. If most herbivores select at least as intensively as the sheep, X will lie similarly low on the scale of availability for them. The optimization model implies that their diet composition will not be affected by availability as long as the major components of the diet occur at densities above about 10 kg/ha.

If the amount consumed from a plant species is independent of its availability, the percentage utilization (consumption/availability) will tend to be higher the lower the availability. This will be so both between species, and for the same species at different locations.

If the account which has been given of mechanisms controlling diet selection in large generalist herbivores is realistic, it should be possible in principle to predict diets *de novo*. Necessary steps in making predictions are flow-diagrammed (Figure 26). Number superscripts in the figure indicate problems which will be commented on now:



Deduce from general physiological knowledge which nutrients are reinforcing.

or

Conduct behavioral experiments on the reinforcing effects of nutrients.

List nutrients (3) which are (a) always reinforcing, or (b) missed when present below, or noticed when present above, some level.

Assign nutrients of type (a) to the Objective Function and type (b) to the RHS constraints.

Constrain the permitted amount of particular foods where these are uncommon. (4).

Reconstruct a "Sampling" diet made up of all foods. (6).

List plant species.

Exclude "unpalatable" (1) species.

Characterize "foods" (2) -- part or parts of each species which might be eaten.

Characterize each food as to the amount it supplies the animal of each nutrient.

Solve the diet optimization problem (5).

Estimate the overall diet of the population as x percent optimized diet + (100 - x) percent sampling diet. (7).

(1) "Palatable" is here being used as a qualitative term. Unpalatable species are those with unavoidable thorns, or strong chemical repellents. Perhaps some animals "know" genetically to avoid some poisonous plants.

(2) A "food" is a category of palatable material such that the animal cannot select within it. Jaw morphology and feeding posture of the animal determine this.

(3) "Nutrient" is here being used as a general term for any property of the food which affects the welfare of the animal.

(4) As discussed, availability does not affect percentage consumption at levels above about 10 kg/ha. The exact nature of the response below this is unknown, but the curve must pass through (0 percent, 0 kg/ha). The simplest assumption would be a straight line, as shown in Figure 25.

(5) Only the simplest kind of optimization procedure has been presented here. Many sophistications of it are available (Wagner 1969). Two which might add realism are goal programming (establishing an order in which objectives should be met), and making the Objective Function non-linear.

(6) The nature of the sampling component of the diet would depend on the sampling pattern used. A simple assumption would be equal proportions of all foods.

(7) I have no basis for determining x, the relative contribution of the optimized diet to the whole. It would be adaptive for it to vary, sampling becoming more important when the nutritional properties of foods are changing rapidly.

Goodness-of-fit between the optimization-and-sampling hypothesis and the jackrabbit data. Two aspects of the jackrabbit data can be assessed as to how well they correspond with the optimization-and-sampling hypothesis. First, are the jackrabbits on the whole nutritionally wise; i.e., are their diets intelligible in terms of the nutritional properties of the food plants? This has been discussed in detail above. Second, are diets conservative in relation to availability; i.e., does the proportion of a taxon in the diet follow the curve predicted in Figure 25?

The discussion of whether features of the jackrabbit diets were nutritionally wise was inconclusive. Subjectively, I would say that perhaps 40 percent of the features discussed could plausibly be said to be wise, 20 percent seemed unwise, and on 40 percent there were no data either way. Features which seemed wise included the seasonal pattern of grass use, and *Halogeton* and *Sarcobatus* use during summer. The high year-round use of *Kochia* was an example of apparently unwise feeding. On the heavy use of *Halogeton* during autumn and winter, for example, there were no nutritional data.

When a case is found of a food being eaten which is apparently not nutritionally desirable, at least three kinds of conclusions can be drawn:

(1) The data either on consumption or on nutritional quality of the food are in error;

(2) The food is nutritionally useful for some unstudied reason;

(3) The nutritional wisdom hypothesis is wrong.

As remarked, about 40 percent of the features of the jackrabbit diet seemed nutritionally wise. This seems higher than would happen at random. My own inclination would be to try to exclude conclusions (1) and (2), above, before rejecting the nutritional wisdom hypothesis.

Some of the jackrabbit stomach data allow the response to availability to be examined. Exact locations where stomachs were shot were recorded between April and September of 1972. For each plant taxon I chose dates during this period when that taxon averaged more than 10 percent of the diet. The food was assumed to be part of the "optimized diet," rather than the "sampling diet." on these dates. The stomach from each animal shot on these dates could be said to come from one of three cover-classes (availability-classes) of each taxon, using the distribution maps (Figures 7 to 13). These cover-classes are called I, II and III, in order of increasing cover. This procedure gave populations of values for the percentage composition in individual stomachs of four taxa, from three cover-classes each. These values were divided by 100 so that they were in the range 0-1, subjected to arcsine transformation, and examined by analysis of variance. Results of comparisons are presented in Table 16. F_s values for three-group anovas were not significant, so an attempt to correlate consumption with availability across the full range would have failed. When cover-class I was compared with cover-classes II and III, it was significantly less for *Kochia* and for grass, but not for *Artemisia* or for *Sarcobatus*. Cover-classes II and III were not significantly different for any taxon.

Class I for *Kochia* and for grass represents lower availabilities than for *Artemisia* and for *Sarcobatus*. These data indicate that consumption of particular foods is constrained by availability only at cover values below about 0.5 percent. These might represent biomass values of 5-10 kg/ha. This result fits the prediction of the optimization model that availability does not affect consumption over most of the range, but only constrains it at very low values.

PART III. IMPACT OF JACKRABBITS ON THE VEGETATION

Introduction

The response of vegetation composition to the impact of a grazing animal depends on several related phenomena:

(1) The extent and nature of grazing activity on the individual plants of each species.

(2) The physiological and morphological effect of this grazing on each plant.

(3) The population responses of each plant species to these effects. These population responses collectively add up to the change in vegetation composition which results from the activities of the herbivore.

These are plant autecological and synecological problems beyond the scope of this study. But with a knowledge of vegetation composition, and with estimates of the amount of material of each plant species consumed by jackrabbits, it is now possible to estimate the proportion of each species consumed by jackrabbits. This is equivalent to the mean percentage utilization of each species by jackrabbits. Percentage utilization is the best single predictor of the regrowth response of plant populations under grazing (Stoddart and Smith 1955). Using the estimates, then, we can propose hypotheses on how jackrabbits have affected vegetation. A number of jackrabbit-proof exclosures exist in Curlew Valley, and this makes it possible to test these hypotheses.

Methods

Utilization Estimates

Utilization was estimated indirectly for all taxa. Consumption was estimated as jackrabbit density, times per capita consumption, times the percentage of each taxon in the diet as estimated in Part II. Availability was estimated in Part I. Utilization is then the ratio of consumption and availability.

In addition utilization was estimated directly for *Artemisia tridentata* and *Chrysothamnus viscidiflorus*. In February 1972,200 individual *Artemisia* plants were chosen by a wandering quarter method (Catana 1963) and examined. Numbers of clipped and unclipped twigs were counted for each plant.

In June 1972,120 individual *Chrysothamnus viscidiflorus* plants at four locations were tagged. Utilization was estimated by eye. The plants were reexamined in September 1972, when they were all positively identified as *C. viscidiflorus*. (The original objective of this work was to see if *Gutierrezia sarothrae* (Pursh) Britton & Rusby could be told from *C. viscidiflorus* in the vegetative state.) Utilization was estimated again. Height and two crown diameters were measured. The differences between the pairs of utilization estimates for each plant formed a population whose mean was not significantly different from zero ($t_s = 1.09$; df = 101; $P > .2$). The average of the two utilization estimates was therefore used as the best estimate for each bush.

Vegetation of Jackrabbit-Proof Exclosures

Biomass estimates for Kochia were described in Part I. Four of the transects were either inside or outside an exclosure which has been effectively jackrabbit-proof since 1958 (E.H. Cronin, pers. comm.).

In the area marked "range research area" in Figure 1, a variety of exclosures are to be found. These have been put up by previous researchers with the objective of protecting their studies on various plant species against distortion by grazing effects. The histories of these exclosures are summarized in Table 17. Exclosures with the prefix CO were used by Cook (1971); with the prefix CT, by Coyne (1969) and Trlica (1971); and those with the prefix B by Bjerregaard (1971). All of these exclosures were kept effective from the date of their establishment up to 1969 (C.W. Cook, pers. comm.).

To assess how effective they had been against jackrabbits since that date, I measured the standing crop of identifiable jackrabbit pellets inside and outside each exclosure during April 1973. Eight randomly placed circular quadrats of .25 m^2 area were sampled inside and outside each exclosure.

Table 17. History and characteristics of some exclosures in Curlew Valley

Vegetation type.	Exclosure name	Sheep-proof since	Pellets per m^2 (with 95% confidence limits) Inside	Outside	Dates definitely rabbit-proof
Atriplex confertifolia	C01	1957	34 ± 28	155 ± 148	Never
	CT1	1966	29 ± 17	28 ± 13	Never
	B1	1968	1 ± 1	29 ± 37	1968-1973
Artemisia nova	C02	1957	24 ± 31	30 ± 39	1958-1969
Artemisia tridentata	C03	1957	29 ± 26	92 ± 52	Never
Atriplex confertifolia and perennial grasses	C04	1957	73 ± 52	57 ± 31	1958-1969
	CT2	1966	53 ± 52	54 ± 49	Never
Atriplex nuttallii	C05	1957	19 ± 11	125 ± 51	1958-1973
	CT3	1966	99 ± 31	131 ± 90	Never
Eurotia[a] lanata	C06	1957	0 ± 0	155 ± 148	1958-1973
	CT4	1966	70 ± 17	90 ± 47	Never
	B2	1968	3 ± 4	92 ± 34	1968-1973

[a] Sheep grazing in this community stopped in 1969.

Means and 95 percent confidence limits of the pellet standing crop are given in Table 17.

It was found on the drive-count area (Westoby and Wagner, in press) that the standing crop of pellets was 2-3 times as great as a yearly deposition rate which can be calculated from literature values. Therefore it is assumed here that the standing crop of pellets can reasonably be used as a crude estimator of jackrabbit grazing pressure at a location over the last 2-3 years. If the 95 percent confidence limits of pellet density inside and outside an exclosure do not overlap, the exclosure has probably provided effective protection since 1969. (Non-overlap of confidence limits is of course a conservative test for the difference between means.) The two peaks of jackrabbit density in Curlew Valley during the history of these exclosures have been in 1959-1961 and in 1970-1972. From the data presented in Table 17 it is possible to decide which exclosures were rabbit-proof during those peaks.

It might be thought that exclosures which had been protected against sheep grazing but not made rabbit-proof would be subject to heavier jackrabbit use than the community at large; but the pellet counts show no evidence of this. However, a higher rate of pellet deposition may have been counteracted by a higher rate of decomposition inside the exclosures, resulting from a more uneven (less trampled) soil surface and a denser herb layer (cf. Flux 1967).

The vegetation of the range research area was divided into locations. Nineteen locations were described between 6-12 May 1973. These were: the interiors of the 12 exclosures described in Table 17; a location outside exclosures for each of the subjectively-defined plant communities listed in Table 17; and a second outside location for the *Atriplex confertifolia* community, which occurs in two separate parts of the area.

Each location was analysed in the following way. Four 100-ft transects were laid out. Along each transect 20 quadrats were placed at 5-ft intervals. These quadrats were 20 x 50 cm (1/10 m^2). For each quadrat the following information was recorded:

(1) Percentage cover of shrubs and half-shrubs, by species;

(2) Rooting density of shrubs and half-shrubs, by species;

(3) Rooting density of annual species in each of two subsidiary quadrats of 1/40 m^2, at each end of the larger quadrat;

(4) Size (expressed as an equivalent percent cover) of all individuals of perennial grass species which were centered in the quadrat. Seedlings were described as having 1 percent cover.

(5) Percentage of the ground surface covered by bare soil, litter (including plant bases), cryptogams (including algal crust), and rock (stones with diameter greater than 2 cm);

(6) Type of surface struck by each of the four legs of the quadrat.

Special Study on an Agropyron desertorum Seeding

Black-tailed jackrabbits commonly invade cultivated or managed fields during the nocturnal feeding period (Lewis 1946, Bronson and Tiemeier 1958). They appear to favor habitats which provide an interspersion of tall cover with open spaces (Taylor, Vorhies and Lister 1935, Phillips 1936, Orr 1940, Taylor and Lay 1944, Lechleitner (1958a). Hence there may be a tendency for jackrabbit grazing to be concentrated near the edges of seedings. If such an effect could be quantified, implications might become apparent for the sizes and shapes of seeding which would most effectively limit jackrabbit use.

A count of the standing crop of pellets per unit ground area was used as an estimator of jackrabbit grazing pressure at each location. All pellets that were still recognizable as such were counted within .25 m^2 circular quadrats; eight such quadrats were positioned randomly at each location. Locations were placed at intervals of 160 m along arbitrarily chosen transects oriented perpendicularly into the seeding from its edge. Transects were also situated along roads leading away from the seeding; in these cases the eight quadrats were placed after walking 50 paces to one side of the road. A further transect was run through the drive-count area.

All pellet counts were completed between March 25 and April 10, 1972.

Results

Vegetation Consumption

The highest and lowest mean jackrabbit densities in Curlew Valley since 1963 have been 1.03/ha and 0.12/ha, at the autumn censuses of 1970 and 1967 respectively (Gross et al., in press). The mean year-round density is probably at least 10 percent less than the autumn density (F.H. Wagner, pers. comm.). Accordingly consumption is here estimated for a high population of 0.93/ha. A high density persisted until the summer of 1972.

A number of estimates exist in the literature for the daily forage consumption of individual Lepus californicus (Table 18). Using from this Table a value of 110 gm/day, we estimate that the jackrabbit population ingests 0.93 x .11 x 365 = 37 kg/ha/yr of forage (dry-weight).

Table 18. Estimates by various authors of daily forage consumption by individual Lepus californicus

Source	Consumption (gm)	Material
Vorhies & Taylor (1933)	128.1 (28.8 - 125.0)	Air-dry alfalfa
" " " "	307.4 (146.5 - 653.1)	Green feed
Arnold (1942)	132 ± 9	"Native air-dry forage"
Arnold & Reynolds (1943)	145 ± 14	" " "
Haskell & Reynolds (1947)	123	Alfalfa and barley
Currie & Goodwin (1966)		
Fall	97.3 Clipped forage	Salt desert shrub vegetation.
	196.4 Field pen trials[a]	
Winter	111.4 Clipped forage	
	200.8 Field pen trials[a]	
Spring	61.2 Clipped forage	
	153.9 Field pen trials[a]	

[a] Includes wastage.

This total may be subdivided into consumption for each plant species by using the diet break-down of Part II (Table 12). The mean year-round percentage of the diet occupied by each taxon is reproduced in Table 19, Column A. In Column B, it is multiplied by 37/100 to give an estimated consumption in kg/ha/yr for each taxon.

Table 19. Mean consumption (estimated) of various plant taxa by jackrabbits in Curlew Valley on a year-round basis

Taxon	A	B	C	D
	Percentage of year-round diet (Table 12)	Year-round consumption (kg/ha/yr) (A x 37/100)	Available biomass (kg/ha) (Table 6)	Percent Utilization (B/C x 100)
Artemisia tridentata	7.8	2.9	162.3	1.8
Sarcobatus vermiculatus	6.7	2.5	152.1	1.6
Chrysothamnus spp.	2.1	0.8	10.2	7.8
Grayia spinosa	0.6	0.2	0.5	40.0
Atriplex confertifolia	1.6	0.6	36.3	1.7
Kochia americana	10.8	4.0	2.3	173.9
Bromus tectorum	0.2	0.1	-	-
Grasses other than Bromus	21.0	7.8	3.7	210.8
Halogeton glomeratus	38.8	14.4	465.0	3.1
Forbs beside Halogeton	7.7	2.8	-	-
Unknowns	1.9	0.7	-	-

Vegetation Utilization

Indirect estimates

The available biomass figures of Part I, Table 6, are reproduced in Column C of Table 19. In Column D percentage utilization is estimated as consumption/availability x 100.

There has been scope for many kinds of error in the estimates which contributed to these indirect utilization estimates. Logically, none of the estimates should be above 100 percent. But when consumption is large relative to available biomass, the latter seriously underestimates current growth, and so percentage utilization is overestimated.

The utilization estimates have been obtained using data for the consumption of each taxon by the jackrabbits. But sometimes more may be removed from the plants than is ingested. Some wastage is associated with any feeding activity. But it becomes serious when plant parts other than stem or leaf tips are selected. The most obvious cases that I have noticed are for *Artemisia* and *Sarcobatus* during winter. Twigs are clipped in the second-year wood, 10-20 cm back from the tip, turned round and chewed. As much as 10 cm may be discarded. Currie and Goodwin (1966) report this kind of wastage of *Artemisia*, and Hayden (1966) reports it of *Larrea divaricata* Cav., attributing it to avoidance of phenolics in the new growth. In these special cases the utilization estimate should be markedly increased -- perhaps as much as doubled.

Measurements

Utilization was estimated directly on *Artemisia tridentata* and *Chrysothamnus viscidiflorus*. These data can serve as an independent test of the the indirect estimates.

The weighted mean utilization (percentage of twigs clipped) of *Artemisia* was 12.1 percent. Mean utilization of C. *viscidiflorus* at the four locations was 15.6, 18.6, 4.2 and 4.7 percent, respectively.

These results indicate that the indirect utilization estimates are of the right order of magnitude.

Conclusions on impact

Certain patterns in the utilization figures are apparent. The three dominant full shrubs, *Artemisia*, *Sarcobatus*, and *Atriplex confertifolia*, all have low levels of use. Perennial grasses and the suffrutescent shrub, *Kochia*, are under severe pressure. The subdominant full shrub *Grayia* is subject to significant use. Use of *Chrysothamnus*, while not high on average, may be significant for local populations of *C. viscidiflorus*. Of the annuals, *Halogeton* is used mostly after it has set seed in autumn; this presumably has no effect on its abundance. If the "unknowns" in the stomachs are mainly less common herbaceous species, as seems likely, 3-4 kg/ha are being taken from forbs other than *Halogeton*. This may constitute severe pressure. Whether their abundance would be affected is unclear. A figure for mean utilization probably indicates little about the effect of grazing on a population of annuals.

A range management rule-of-thumb is that perennials will generally accept 50 percent utilization without decreasing sharply in abundance or vigor (Stoddart and Smith 1955). On this basis high populations of jackrabbits in this area apparently exert damaging pressure on _Kochia_ and perennial grasses, to a lesser degree on _Grayia_, and perhaps locally on _Chrysothamnus viscidiflorus_.

Vegetation of Jackrabbit-Proof Exclosures

Mean biomass of _Kochia_ inside the _Kochia_ exclosure (Transects 1 and 2) was 14.5 kg/ha, while outside (Transects 3 and 4) it was 0.4 kg/ha (Part I, Table 3). This exclosure has been reliably proof against both jackrabbits and sheep since 1959. Apparently grazing by one or both of these has greatly reduced _Kochia_ outside the exclosure over that period.

For the exclosures in the range research area, the comparisons which will show the effect of jackrabbit grazing are those between the interior of an exclosure from which only sheep have been excluded, and the interior of an exclosure in a similar plant community from which both sheep and jackrabbits have been excluded. Three such comparisons are possible in the set of exclosures described in Table 17; between exclosures CT1 and B1, CT3 and CO5, and CT4 and B2. Tables 20, 21 and 22 show the results of comparing the parameters measured at each location between these pairs

Table 20. Vegetation parameters in two exclosures within a community dominated by *Atriplex confertifolia*; one has excluded sheep and jackrabbits for 5 years, the other sheep only for 7 years. P is the probability that the two means come from the same population

Parameter	Mean (per m^2 for density)		P
	Without jackrabbits	With jackrabbits	
	B1	CT1	
Percent cover			
Atriplex confertifolia	18.6	19.6	>.75
Rooting density			
Atriplex confertifolia	4.6	0.3	<.25
Bromus tectorum	180.4	49.6	<.0005
Lepidium perfoliatum	3.2	446.4	<.0005
Halogeton glomeratus	112.8	16.8	<.0005
Descurainia spp.	25.6	17.6	<.25
Cryptantha spp.	24.8	2.4	<.0005
Camilina microcarpa [a]	1.2	0.0	<.1
Percent cover			
Sitanion hystrix	3.4	4.1	>.5
Bare Soil	33.8	37.4	<.5
Litter	19.5	24.1	<.25
Cryptogam	46.5	37.0	<.05

[a] *Camilina microcarpa* Andrz.

Table 21. Vegetation parameters in two exclosures within a community dominated by Atriplex falcata; one has excluded sheep and jackrabbits for 7 years, the other sheep only for 13 years. P is the probability that the two means come from the same population

Parameter	Mean (per m^2 for density)		P
	Without jackrabbits	With jackrabbits	
	C05	CT3	
Percent cover			
Atriplex falcata	15.0	22.2	<.005
Rooting density			
Atriplex falcata	28.0	41.9	<.0005
Descurainia spp.	3.2	4.0	<.5
Bromus tectorum	372.8	66.8	<.0005
Malcolmia africana[a]	0.0	250.0	<.0005
Halogeton glomeratus	0.0	20.4	<.01
Cryptantha spp.	2.8	16.4	<.0005
Lepidium montanum[a]	0.0	0.4	<.5
Percent cover			
Sitanion hystrix	4.3	0.2	<.01
Bare Soil	48.5	47.3	>.5
Litter	14.8	9.1	<.05
Cryptogam	32.3	42.8	<.01

[a] Malcolmia africana (L.) R. Br.; Lepidium montanum Nutt.

Table 22. Vegetation parameters in two exclosures within a community dominated by *Eurotia lanata*; one has excluded sheep and jackrabbits for 5 years, the other sheep only for 7 years. P is the probability that the two means come from the same population

Parameter	Mean (per m^2 for density)		P
	Without jackrabbits	With jackrabbits	
	B2	CT4	
Percent cover			
Eurotia lanata	29.1	21.1	<.005
Artemisia tridentata	0.1	1.1	<.25
Rooting density			
Eurotia lanata	26.6	23.4	<.25
Artemisia tridentata	0.3	0.5	>.5
Bromus tectorum	5.6	44.4	<.025
Malcolmia africana	22.4	6.8	<.0005
Cryptantha spp.	3.2	2.8	>.75
Descurainia spp.	1.2	7.2	<.0005
Halogeton glomeratus	1.6	19.6	<.005
Ranunculus testiculatus[a]	0.0	0.4	<.5
Percent cover			
Sitanion hystrix	6.2	3.2	<.25
Oryzopsis hymenoides	0.6	0.4	>.5
Bare Soil	64.3	78.5	<.0005
Litter	9.3	7.9	>.5
Cryptogam	25.9	13.6	<.0005

[a] *Ranunculus testiculatus* Crantz.

of sites. The probability that the means are from different populations is given (test of equality of means assuming heterogeneity of variance, Sokal and Rohlf 1969). Many of the differences between pairs of locations are significant ($P < .05$).

However, there is no consistent pattern of increase or decrease in particular plant species in different communities when jackrabbits are excluded from the vegetation, as can be seen from Table 23. Any changes ensuing on the exclusion of sheep are seemingly not affected by whether or not jackrabbits are also excluded, at least over a 5-7 year time-span.

Special Study on an *Agropyron desertorum* Seeding

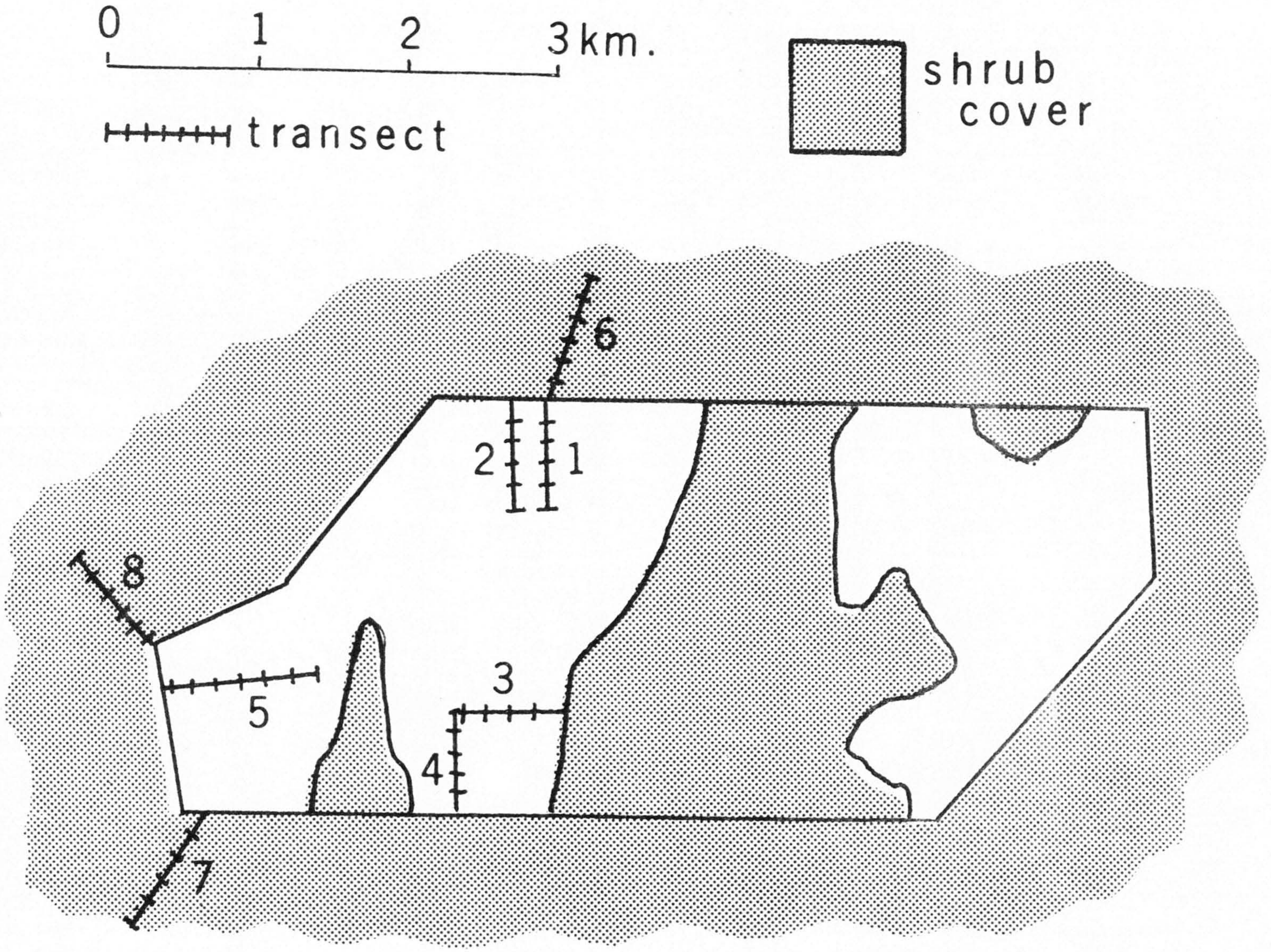
Spatial distributions of jackrabbits in vicinity of seeding

Locations of the transects taken are shown in Figure 27. Transects 1-4 show a similar pattern, and these results have been pooled. The trend of pellet density with distance into the field for these pooled results is shown by line A in Figure 28. Under the conditions represented by these transects about 70 percent of the total pressure of jackrabbit use on the field is concentrated in a 300 meter band around its edge.

Transect 5 represents a different situation (line B in Figure 28). This transect occurs close to a corner of the field, and at its end reaches the tip of a tongue of invading shrubs, so hares feeding at locations more than about 400 m along this transect would have access

Table 23. Increase (+) or decrease (-) or no change (0) in vegetation parameters as a result of excluding jackrabbits for 5-7 years, in three subjectively-defined plant communities. Blanks indicate the taxon was absent from both exclosures in a community. Increases and decreases defined at $P < .05$

Parameter	Plant Community		
	Atriplex falcata	*Atriplex confertifolia*	*Eurotia lanata*
Percent cover			
Atriplex falcata	-		
Atriplex confertifolia		0	
Eurotia lanata			+
Artemisia tridentata			0
Rooting density (m^{-2})			
Atriplex falcata	-		
Atriplex confertifolia		0	
Eurotia lanata			0
Artemisia tridentata			0
Descurainia spp.	0	0	-
Bromus tectorum	+	+	-
Malcolmia africana	-		+
Halogeton glomeratus	-	+	-
Cryptantha spp.	-	+	0
Lepidium montanum	0		
Lepidium perfoliatum		-	
Camilina microcarpa		0	
Ranunculus testiculatus			0
Percent cover			
Sitanion hystrix	+	0	0
Oryzopsis hymenoides			0
Bare Soil	0	0	-
Litter	+	0	0
Cryptogams	-	+	+


0
1
2
3km.
transect
shrub cover
6
2
1
8
5
3
4
7

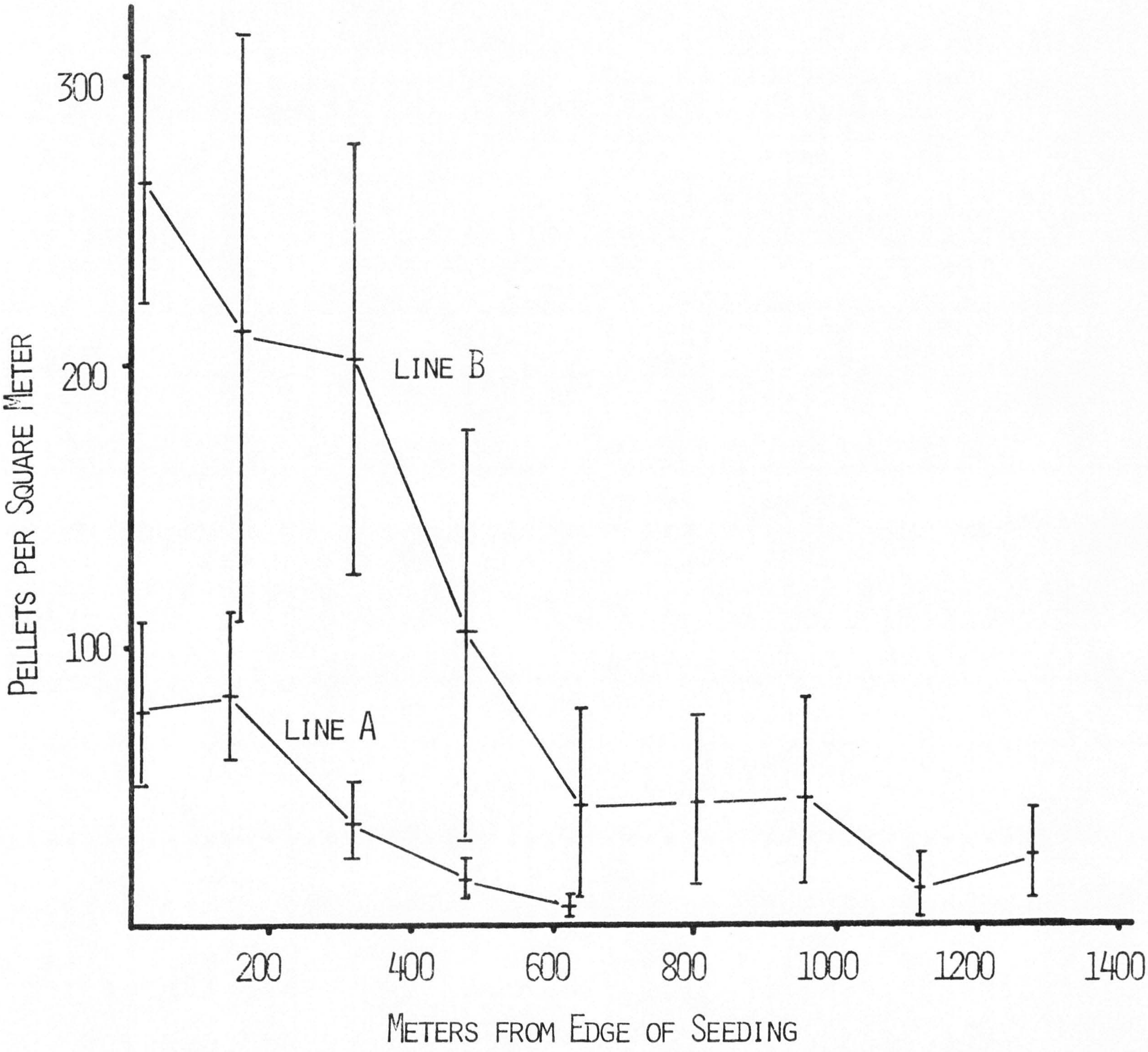


Figure 28. Number of pellets per m^2 (mean and 95 percent confidence limits) at various distances into an Agropyron desertorum seeding. Pooled results from transects 1-4 (line A), and results from transect 5 (line B).

to cover closer than the beginning of the transect. This presumably accounts for the failure of the pellet density to fall to near-zero values. The absolute densities of pellets may be higher because hares are entering the field from more than one direction. There is no evidence of a higher population in the native vegetation adjacent to this particular transect; that is, transect 8 does not show higher pellet counts than transects 7 and 6 (Table 24).

There is no obvious trend toward higher populations in the native vegetation immediately adjacent to the seeding, compared to that up to 900 m away.

Three assumptions are necessary to the calculations which follow.

The first is that the pellets found represent at least one whole year's history of pellet deposition. This assumption is necessary because the calculations which follow compare the drive-count area, where jackrabbits are present year-round, to the seeding, which they use seasonally; the calculations would be wrong if the pellet counts in the seeding were heavily weighted by any one season. Arnold and Reynolds (1943) give an average daily pellet count of 531 ± 27 for a jackrabbit, irrespective of age, sex, size or species. Cochran and Stains (1961) found comparable values for cottontails (*Sylvilagus audubonii*) on natural diets, ranging down to 100 on various artificial diets. The value of 531 is probably near the upper end of the likely

Table 24. Number of pellets per m^2 (mean and 95 percent confidence limits) at various distances along transects leading away from a wheatgrass seeding

Transect Number	Distance (m) Along Transect from Seeding's Edge						
	16	160	320	480	640	800	960
6	69 ± 32	49 ± 20	82 ± 39	240 ± 113	154 ± 52	155 ± 35	
7	123 ± 108		66 ± 36		104 ± 87		83 ± 64
8	101 ± 47		104 ± 62		86 ± 41		

range. In the autumn of 1971 there were estimated to be 691 hares per square mile, or 2.7/ha, on the drive-count area (Gross et al., in press). If each animal is depositing 531 pellets/day, this implies a yearly deposition of about 52 pellets/m^2. This yearly deposition rate is well below the actual measured density of 143 ± 76/m^2, so that pellets are apparently persisting for at least a year after deposition.

Secondly we assume that the number of pellets found at a location is proportional to the pressure of the jackrabbits on the vegetation there. This can be divided into three subsidiary assumptions. First, animals on a natural diet produce pellets predominantly while feeding, and at a reasonably constant rate (Lechleitner 1957, Flux 1967). Second, pellets are not moved after deposition over distances (hundreds of meters) great enough to account for the distributions observed. There is no evidence of movement by wind or water; pellets are not found in aggregations against natural wind-breaks, and the absence of any system of channels shows that there is little net water movement on the study area. Third, any variation in the rate at which pellets disintegrate and become unrecognizable is insufficient to account for the distribution pattern observed. Flux (1967) has observed a six- to ten-fold variation in that rate, but the variation was strongly correlated with an altitudinal gradient. In his opinion, pellets do not normally break up until they are overgrown by vegetation. If so, there should be little systematic variation in the rate of disappearance of pellets inside the field. The difference between the rate inside the field and that in shrub vegetation should not be great, since the species composition of the herb layer, the elevation, and probably precipitation and temperature, are similar for the two situations.

A third assumption is that jackrabbits waste little or no material when eating the leaves of perennial grasses (Vorhies and Taylor 1933, Arnold 1942, Currie and Goodwin 1966). This is in contrast to their behavior when eating shrubs or tall crops, when they may waste as much as, or more than, they actually consume. Serious wasting of grass leaves could occur if a situation arose in which the bases of stems or leaves remained green and succulent while the leaves were dry.

Estimation of impact

All samples from transect 9, situated on the jackrabbit demography research area, have been pooled. The mean number of pellets per square meter is 143 ± 76 (95 percent confidence limits).

Assuming as before that *Lepus californicus* consume 110 gm/day of forage, 2.7 individuals/ha, working year-round, would consume about 108 kg/ha/yr. This is the situation which is found on the drive-count area (Figure 1), where the pellet density is $143/m^2$. If we can assume that pellet density is

The estimates show a basic pattern of heaviest impact on scarest plants. This is true between plant taxa, and also for the same taxon at different locations. This pattern is a reflection of the fact that consumption is only partially proportional to availability (see Figure 16 and Table 16). It therefore does not conflict with the nutritional optimization model of diet selection, which predicts that the diet is not affected by changes in availability over most of the range.

General ecological theory (e.g. MacArthur 1972) suggests that a natural herbivore community will be in equilibrium with its plant community. Given a vegetation (a spectrum of resources), the herbivorous species (exploiters) should, by competitive exclusion, arrange their exploiting activity across the spectrum so that each resource is exploited at a level which just maintains its abundance in the community. If any herbivore had regularly overexploited any plant, the plant, and possibly the herbivore, would not be there now.

Kochia, native perennial grasses, and population cycles of jackrabbits were part of this hypothetical equilibrium state. Yet the _Kochia_ exclosure results indicate that _Kochia_ has markedly decreased since the 1950's, and the utilization estimates suggest that jackrabbits could have been involved. _Kochia_ apparently formed quite widespread pure communities at the beginning of the century in the Intermountain area (Kearney et al., 1914). Many of these communities have now disappeared, although old root crowns can often be found. The sites are now typically occupied by Halogeton. They are unsuitable for many desert shrubs due to their characteristically high salt content in the second foot of soil (Cook 1961, Clarke and West 1969). Kearney et al. (1914) reported that after Kochia was reduced by grazing, it recovered, although slowly; the community was not invaded by other species.

What new element in the situation could have caused a decrease in Kochia? Stocking densities of domestic animals reached high levels in the Intermountain area before the turn of the century (Walker, 1964), so domestic stock do not seem likely candidates. I suspect the new element was Halogeton. This was first reported in America in 1935 (Zappetini,1953); it arrived in Curlew Valley in the early 1950's (N. E. West, pers. comm.). Whereas before its arrival Kochia could recover from temporary overgrazing by jackrabbits or stock, afterwards the biological space in the overgrazed community was invaded by Halogeton, and the Kochia did not recover.

The perennial native grasses, too, are apparently subjected to intermittent heavy pressure from jackrabbits. Since jackrabbits probably can select individual green leaves from a grass bunch, their impact may be greater than the results of clipping a given percentage would indicate. Is this pressure sufficient to reduce grass abundance further? I cannot answer this question. The data from exclosures

(Table 23) suggest that the presence or absence of jackrabbits does not affect the recovery rate of perennial grasses after the exclusion of sheep for a 5-7 year period. The correlation of utilization with scarcity discussed above suggests that jackrabbit pressure on grasses may have increased after the introduction of domestic stock, which had the effect of reducing perennial grass abundance in the vegetation (Christensen and Johnson 1964).

In the aftermath of the drought and the rodent control programs of the 1930's, there was much interest in the relations of rodents and lagomorphs to range succession. It was concluded (Bond 1945, Norris 1950, Ellison 1960) that jackrabbit populations increased on overgrazed ranges (Phillips 1936), due to increased supplies of either or both forbs and shrub cover. These increased populations might then retard the recovery of perennial grasses on overgrazed ranges. But jackrabbits would not themselves cause overgrazing.

Note that in that argument any retarding effect of jackrabbits on range recovery is attributed to increased populations. This report gives an additional reason why they should retard range recovery: that the percentage utilization they inflict will increase on plant species which become scarce.

Thus two kinds of new element can be distinguished which can disturb the equilibrium in a natural community of plants and herbivores. First, a new plant species such as Halogeton can disrupt the balance of competition between plants. Second, herbivores with artificial population dynamics, such as domestic stock, can drastically change the availabilities of plant foods. Then the pressure exerted by native herbivores on each food changes too.

Any community of plants is subject to oscillation in the abundance of its component species. A predator which "switches" (Murdoch 1969) its food preferences, concentrating on the most abundant species, would tend to damp such oscillations (Elton 1927). The jackrabbits studied here, on the contrary, did not change their diets in response to availability. As a result the pressure they exert would decrease on increasing species, and increase on decreasing species. If anything, the jackrabbits would amplify and encourage any changes in the plant community.

SUMMARY

(1) The interrelations of black-tailed jackrabbits with the desert shrub vegetation on which they were feeding were studied in Curlew Valley, northern Utah. Studies centered on a "shooting route" -- a set of roads along which jackrabbits were shot for stomach analysis.

(2) The percentage cover by perennial plants of the shooting route was described at 36 step-point transects. The unstandardized transect data, when subjected to principal components analysis, yielded a description of the vegetation of the shooting route as a three-cornered continuum, the three corners being types dominated by *Artemisia tridentata*, *Atriplex confertifolia* and *Sarcobatus vermiculatus*. Bray-Curtis ordination of the vegetation showed essentially the same pattern.

(3) This ordination did not show much clustering of sites. Accordingly, no classification was attempted. The principal species were mapped into 2-4 cover-classes, using the step-point transect data, supported by ground truth work.

(4) The available biomass in each cover-class was estimated by calibrating biomass against cover for each species. Data allowing this calibration were acquired by destructive sampling for *Kochia americana* and *Chrysothamnus viscidiflorus*. For other species data collected by other workers were used. The mean estimated available biomass for each species in each cover-class was weighted by the

proportion of the shooting-route occupied by that cover-class, to estimate the mean available biomass ("availability") of the plant taxon over the shooting route as a whole.

(5) Jackrabbit stomach contents were analysed by identification of plant fragments under the microscope. During a period of learning this technique, known mixtures were presented to the analysts. Deviation of estimated from actual composition was characterized by measures derived from vegetation analysis. Good results have been obtained with this method in analysing the diets of grassland herbivores, but its accuracy in this study was poor. This was thought to be mainly because the ratio of reliably identifiable tissues to all ingested tissues was low, and varied greatly, both between plant taxa, and seasonally within plant taxa. Accuracy of the method may be unavoidably low in desert shrub vegetation.

(6) Features of the jackrabbit diet (naming plant taxa in decreasing order of year-round importance in the diet) were as follows. Halogeton was eaten year-round, but especially during autumn and winter. Perennial grasses were mainly eaten during spring and summer. Kochia was used year-round, but with increased emphasis in spring and autumn. Artemisia was eaten during late autumn, winter, and early spring. Forbs were eaten during spring and summer, as was Sarcobatus. These results show the same general pattern

as has been found in other studies -- a grass-forb diet in spring and summer, and a shrub diet in autumn and winter. The intense (compared to its availability) use of Kochia, and the great importance of Halogeton, particularly in the autumn-winter diet, have not been reported from other vegetation types.

(7) There was a poor correlation between consumption and availability, so the hypothesis that foods are eaten solely because they are available was rejected. "Palatability" was rejected as an explanation because it is circular, and hence scientifically unprofitable. An attempt was made to explain the diet in terms of its nutritional quality. Data on the protein, phosphorus and energy contents of foods were collected, and a simulation model of the jackrabbit's water budget was built.

Results were inconclusive. The use of perennial grasses during spring and summer was reasonable in terms of protein supply. The water budget model predicted use of Halogeton and Sarcobatus during summer. On the other hand no reason appeared for the high use of Kochia. On many problems, such as autumn and winter use of Halogeton, there were no nutritional data.

(8) Diet selection by large generalist herbivores (those for which digestion-time, rather than search- or pursuit-time, is limiting) was analysed theoretically. It was suggested that they select for nutritionally beneficial

diets, but that they do so _via_ learning (long-delay reinforcement at digestion-time). This mechanism supplies them with imperfect information on the nutritional value of foods. Thus while they are on the whole nutritionally wise, they are by no means nutritionally infallible.

When digestion-time, rather than search- or pursuit-time, is limiting, the optimal diet is the mix of species, within a fixed total intake, which has the best net nutrient content. This problem can be formulated as a linear program. The model has the property that the relation of relative preference to content of a nutrient for any one food is nonlinear.

(9) When optimization of nutrient content dominates diet selection, availability will not affect consumption until enough of a food cannot be found during the normal day's search. The response to availability should not be continuous, but rather a cut-off at very low availability. This pattern was found in the spatial variation of jackrabbit diets. It is an important pattern because it implies that as plants become rarer in the vegetation,percentage utilization of them will increase.

(10) It was suggested that the diets of large generalist herbivores can in principle be predicted as the resultant of two processes: optimization of nutrient intake, modified by low availabilities; and sampling to obtain learned information on the nutritional value of foods.

(11) Jackrabbit consumption of each plant taxon was estimated as jackrabbit density (the peak value was used), times yearly food consumption per individual, times mean percentage of the plant taxon in the year-round diet. Mean utilization was estimated as consumption divided by availability of each taxon. Utilization was also measured directly on two species. The measurements agreed reasonably well with the indirect estimates, which are therefore probably of the right order despite the many sources of error involved in the estimation.

The basic pattern was of higher utilization of rarer species. This follows from the failure of consumption to be proportional to availability, as predicted and documented. Specifically, _Kochia_, perennial grasses, and perhaps _Grayia_ were intensely used; _Chrysothamnus_ less so; and _Artemisia_, _Sarcobatus_ and _Atriplex_ _confertifolia_ were lightly used.

These utilization levels would apply at high jackrabbit densities, for 3-4 consecutive years; there would follow 6-8 years at utilizations one-eighth to one-ninth those of the high (assuming no change in the diet).

(12) _Kochia_ had almost disappeared from outside, but remained inside, a sheep- and jackrabbit-proof exclosure since the 1950's. In other exclosures, the presence or absence of jackrabbits seemed to have made no difference to any changes in the vegetation over 5-7 years after the exclosure of sheep.

(13) Standing crop of identifiable jackrabbit pellets was sampled along transects leading into a wheatgrass seeding. Density fell off sharply away from the edge, 70 percent of the total being within 300 m of the seeding's boundary. Using the assumption that standing crop of pellets is proportional to feeding activity, and literature figures for yearly food consumption of jackrabbits, the pellet count was calibrated against forage removal in an area of known jackrabbit density. Forage removal in the 300 m band around the edge of the seeding apparently was in the order of 60 kg/ha/yr.

LITERATURE

Albrecht, W.A. 1945. Discrimination in food selection by animals. Sci. Month. 60:347-352.

Allen, R.S., and A.R. Porter. 1954. Effect of added ground corn on the consumption and palatability of stacked legume-grass silage. J. Dairy Sci. 37:658.

Archibald, J.G., E. Bennett, and W.S. Ritchie. 1943. The composition and palatability of some common grasses. J. Agr. Res. 66:341-347.

Arnold, G.W. 1964. Some principles in the investigation of selective grazing. Proc. Aust. Soc. Anim. Prod. 5:258-271.

__________., and J.L. Hill. 1972. Chemical factors affecting selection of food plants by ruminants. p. 72-101. in J. Harborne (ed.), Phytochemical Ecology, Academic Press, New York.

Arnold, J.F. 1942. Forage consumption and preferences of experimentally fed Arizona and antelope jackrabbits. Univ. Arizona Agr. Expt. Sta. Tech. Bull. 98:49-86.

__________., and H.G. Reynolds. 1943. Droppings of Arizona and antelope jackrabbits and the pellet census. J. Wildl. Manage. 7:322-327.

Beals, E. W. 1973. Ordination: mathematical elegance and ecological naivete. J. Ecol. 61:23-36.

Beaumont, A.B., R.E. Stitt, and R.S. Snell. 1933. Some factors affecting the palatability of pasture plants. J. Amer. Soc. Agron. 25:123-128.

Bjerregaard, R.S. 1971. The nitrogen budget of two salt desert shrub plant communities of western Utah. Unpub. Ph.D. Diss., Utah State Univ., Logan, Utah. 100 p.

Bland, B.F., and J.W. Dent. 1962. Animal preference in relation to chemical composition and digestibility with varieties of cocksfoot. J. Brit. Grassl. Soc. 17:157-158.

__________________. 1964. Animal preference in relation to the chemical composition and digestibility of varieties of cocksfoot. J. Brit. Grassl. Soc. 19:306-315.

Blaser, R.E., R.C. Hammes, Jr., H.T. Bryant, W.A. Hardison, J.P. Fontenot, and R.W. Engel. 1960. The effect of selective grazing on animal output. Proc. 8th Intern. Grassl. Congr. :601-606.

Blydenstein, J., C.R. Hungerford, G.I. Day, and R.R. Humphrey. 1957. Effect of domestic livestock exclusion on vegetation in the Sonoran desert. Ecology 38:522-526.

Bond, R.M. 1945. Range rodents and plant succession. Trans. North Amer. Wildl. Conf. 10:229-233.

Brody, S. 1945. Bioenergetics and Growth. Reinhold, New York. 1023 p.

Bronson, F.H., and O.W. Tiemeier. 1958. Notes on crop damage by jackrabbits. Trans. Kansas Acad. Sci. 61:226-229.

Brown, H.L. 1947. Coaction of jackrabbits, cottontails and vegetation in mixed prairie. Trans. Kansas Acad. Sci. 50:28.

Brown, J.A.M. 1961. Evaluation of certain morphological and chemical characteristics in relation to palatability in reed canarygrass (Phalaris arundinacea L.). Ph.D. Thesis, Purdue University. 180 p.

Buckner, R.C. 1955. Breeding in tall fescue for palatability. Ph.D. Thesis, University of Minnesota. 87 p.

____________, J.R. Todd, P.B. Burrus, II, and R.F. Barnes. 1967. Chemical composition, palatability and digestibility of ryegrass-tall fescue hybrids, 'Kenwell', and 'Kentucky 31' tall fescue varieties. Agron. J. 59:345-349.

____________, P.B. Burrus, and J.R. Todd. 1969. Morphological and chemical characteristics of inbred lines of tall fescue selected for palatability to cattle. Crop Sci. 9:581-583.

Buechner, H.K., and H.C. Dawkins. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. Ecology 42:752-766.

Burton, G.W., F.E. Knox, and D.W. Beardsley. 1964. Effect of age on the chemical composition, palatability and digestibility of grass leaves. Agron. J. 56:160-161.

Cabanac, M. 1971. Physiological role of pleasure. Science 174:1103-1107.

Caldwell, M.M., N.E. West, and P.J. Goodman. 1971. Autecological studies of Atriplex confertifolia and Eurotia lanata. US/IBP Desert Biome Research Memo. RM 71-13. 16 p.

Catana, A.J. 1963. The wandering quarter method of estimating population density. Ecology 44:349-360.

Christiansen, E.M., and H.B. Johnson. (1964). Presettlement vegetation and vegetational change in three valleys in Central Utah. Brigham Young Univ. Science Bull., Biol. Ser. Vol. 4, No. 4. 16 p.

Clarke, L.D., and N.E. West. 1969. Germination of Kochia americana in relation to salinity. J. Range Manage. 22:286-287.

Cochran, G.A., and H.J. Stains. 1961. Deposition and decomposition of fecal pellets by cottontails. J. Wildl. Manage. 25:432-435.

Cook, C.W. 1959. The effect of site on the palatability and nutritive content of seeded wheat grasses. J. Range Manage. 12:289-292.

_________. 1961. Seeding response and soil characteristics on adjacent sagebrush and desert molly soils. J. Range Manage. 14:134-138.

_________. 1971. Effects of season and intensity of use on desert vegetation. Utah Agr. Exp. Sta. Bull. 483. 57 p.

_________, L.A. Stoddart, and L.E. Harris. 1954. The nutritive value of winter range plants in the Great Basin. Utah State Agr. Exp. Sta. Bull. 372. 56 p.

_______________________________________. 1956. Comparative nutritive value and palatability of some introduced and native forage plants for spring and summer grazing. Utah Agr. Exp. Sta. Bull. 385. 39 p.

_______________________________________. 1959. The chemical content in various portions of the current growth of salt-desert shrubs and grasses during winter. Ecology 40:644-651.

Cook, C.W., and L.E. Harris. 1968. Nutritive value of seasonal ranges. Utah State Univ. Agr. Exp. Sta. Bull. 472. 55 p.

Couch, J.F. 1937. The chemistry of stock-poisoning plants. J. Chem. Educ. 14:16-30.

Cowlishaw, S., and F. Alder. 1960. The grazing preferences of cattle and sheep. J. Agr. Sci. 54:257-265.

Coyne, P.I. 1969. Seasonal trends in total available carbohydrates with respect to phenological stage of development in eight desert range species. Unpub. Ph.D. Diss., Utah State Univ., Logan, Utah. 164 p.

Crampton, E.W., and L.E. Lloyd. 1960. Fundamentals of Nutrition. W.H. Freeman, San Francisco. 494 p.

Cronin, E.H. 1965. Ecological and physiological factors influencing chemical control of Halogeton glomeratus. U.S. Dept. Agric. Tech. Bull. No. 1325. 65 p.

Currie, P.O., and D.L. Goodwin. 1966. Consumption of forage by black-tailed jackrabbits on salt-desert ranges of Utah. J. Wildl. Manage. 30:304-311.

Dent, J.W., and D.T.A. Aldrich. 1963. Soluble carbohydrate content of varieties of tetraploid ryegrass. Nature 198:905.

Dye, W.B. 1956. Chemical studies of Halogeton glomeratus. Weeds 4:55-60.

Ellison, L. 1960. Influence of grazing in plant succession of rangelands. Bot. Rev. 26:2-66.

Elton, C.S. 1927. Animal Ecology. MacMillan, New York. 207 p.

__________. 1966. The Pattern of Animal Communities. Methuen, London. 409 p.

Fitch, H.S., and J.R. Bentley. 1949. Use of California annual plant forage by range rodents. Ecology 30:306-321.

Fleming, C.E., M.R. Miller, and L.R. Vawter. 1928. The greasewood (Sarcobatus vermiculatus) a range plant poisonous to sheep. Nevada Agr. Exp. Sta. Bull. 115. 22 p.

Flux, J.E.C. 1967. Hare numbers and diet in an Alpine basin in New Zealand. Proc. N.Z. Ecol. Soc. 14:27-33.

Fontenot, J.P., and R.E. Blaser. 1965. Symposium on factors influencing voluntary intake of herbage by ruminants: selection and intake of grazing animals. J. Anim. Sci. 24:1202-1208.

Forbes, R.H., and W.W. Skinner. 1903. Range forages. Arizona Agr. Exp. Sta. Report 14:348-350.

Freund, J.E. 1962. Mathematical Statistics. Prentice-Hall, New Jersey. 390 p.

Gangstad, E.O. 1964. Physical and chemical composition of grass sorghum as related to palatability. Crop Sci. 4:269-270.

Gauch, H.G., and R.H. Whittaker. 1972. Coenocline simulation. Ecology 53:446-451.

Glover, J. 1963. The elephant problem at Tsavo. E. African Wildl. J. 1:1-10.

Goodall, D.W. 1970. Statistical plant ecology. Ann. Rev. Ecol. Syst. 1:99-124.

Gordon, J.G., and D.E. Tribe. 1951. The self-selection of diet by pregnant ewes. J. Agric. Sci. 41:187-190.

Gross, J.E., L.C. Stoddart, and F.H. Wagner. 1973 Demographic analysis of a northern Utah black-tailed jackrabbit population. Wildl. Monog.: In Press.

Hansen, R.M., and J.T. Flinders. 1969. Food habits of north American hares. Colorado State Univ. Range Sci. Dept. Science Series No. 1. 18 p.

Hardison, W.A., J.T. Reid, C.M. Martin, and P.G. Woolfolk. 1954. Degree of herbage selection by grazing cattle. J. Dairy Sci. 37:89-102.

Haskell, H.S., and H.G. Reynolds. 1947. Growth, developmental food requirements and breeding activity of the California jackrabbit. J. Mammal. 28:129-136.

Hayden, P. 1966. Food habits of black-tailed jackrabbits in southern Nevada. J. Mammal. 47:42-46.

Heady, H.F. 1964. Palatability of herbage and animal preferences. J. Range Manage. 17:76-82.

Hinds, D.S. 1970. A comparative study of thermoregulation and water balance in hares and rabbits of the Sonoran Desert. Ph.D. Thesis, Univ. Arizona, Tucson, Arizona. 164 p.

Holmgren, A.H., and J.L. Reveal. 1966. Checklist of the vascular plants of the Intermountain region. U.S. Forest Service Res. Paper INT-32. 160 p.

Holmgren, R.C., and S.S. Hutchings. 1971. Salt desert shrub response to grazing use. pp 153-164 in "Wildland Shrubs -- Their Biology and Utilization", USDA For. Serv. General Technical Report INT-1.

Hull, A.C.Jr., and G.J. Klomp. 1966. Longevity of crested wheatgrass in the sagebrush-grass type in southern Idaho. J. Range Manage. 19:5-11.

Hutchings, S.S., and G. Stewart. 1953. Increasing forage yields and sheep production on Intermountain winter ranges. USDA Circ. 925. 63 p.

Ivins, J.D. 1955. The palatability of herbage. Herbage Abstr. 25:75-79.

Ivlev, V.S. 1961. Experimental Ecology of the Feeding of Fishes. Yale Univ. Press, New Haven. (transl. from Russian). 302 p.

Jameson, D.A. 1952. The chemical composition and utilization of greasewood and other browse species as related to some aspects of cattle nutrition on winter ranges in southeastern Montana. M. S. Thesis, Univ. of Montana, Missoula. 77 p.

Kearney, T.H., L.J. Briggs, H.L. Shantz, J.W. McLane, and R.L. Piemeisel. 1914. Indicator significance of vegetation in Tooele Valley, Utah. J. Agric. Res. 1: 365-417.

Kenagy, G.J. 1972. Saltbush leaves: excision of hypersaline tissue by a kangaroo rat. Science 178:1094-1096.

Krueger, W.C. 1972. Evaluating animal forage preference. J. Range Manage. 25:471-475.

Lechleitner, R.R. 1957. Reingestion in the black-tailed jackrabbit. J. Mammal. 38:481-485.

_________________. 1958. Certain aspects of behavior of the black-tailed jackrabbit. Amer. Midl. Natur. 60:145-155.

Leigh, J.H. 1961. The relative palatability of various varieties of weeping lovegrass (Eragrostis curvula (Schrad.) Nees). J. Brit. Grassl. Soc. 16:135-140.

Leopold, A., L.K. Sowls, and D.L. Spencer. 1947. A survey of overpopulated deer ranges in the United States. J. Wildl. Manage. 11:162-177.

Lewis, J.H. 1946. Planting practice to reduce crop damage by jackrabbits. J. Wildl. Manage. 10:277.

MacArthur, R.H. 1972. Geographical Ecology. Harper and Row, New York. 269 p.

Marten, G.C. 1969. Measurement and significance of forage palatability. Proc. Nat. Conf. on Forage Quality Evaluation and Utilization. 55 p.

__________, and J.D. Donker. 1964. Selective grazing induced by animal excreta. II. Investigation of a causal theory. J. Dairy Sci. 47:871-874.

McKeever, S., and R.L. Hubbard. 1960. Use of desert shrubs by jackrabbits in northeastern California. Calif. Fish and Game 46:271-277.

Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monog. 39:335-354.

Nagy, J.G., H.W. Steinhoff, and G.M. Ward. 1964. Effects of essential oils on deer rumen microbial function. J. Wildl. Manage. 28:785-790.

Nelson, L. Jr. 1970. Effects of sublethal, cerebral X-irradiation on movement and home-range patterns of black-tailed jackrabbits. M.S. Thesis, Utah State Univ., Logan, Utah. 70 p.

Norris, J.J. 1950. Effect of rodents, rabbits and cattle on two vegetation types in semidesert range land. New Mexico Agr. Exp. Sta. Bull. 353. 23 p.

O'Donovan, P.B., R.F. Barnes, M.P. Plumlee, L.V. Packett, and G.O. Mott. 1967. Soluble and structural components of alfalfa (Medicago sativa L.) and selected reed canarygrass (Phalaris arundinacea L.) clones. Agron. J. 59:478-481.

Orr, R.T. 1940. The rabbits of California. Occa. Papers Calif. Acad. Sci. 109:1-97.

Palmer, T.S. 1897. Jackrabbits of the United States. USDA Biol. Surv. Bull. 8:1-88.

Phillips, P. 1936. The distribution of rodents in overgrazed and normal grassland of central Oklahoma. Ecology 17:673-679.

Pielou, E.C. 1969. An Introduction to Mathematical Ecology. Wiley, New York. 286 p.

Porter, W.P., and D.M. Gates. 1969. Thermodynamic equilibria of animals with environment. Ecol. Monog. 39:227-244.

NAS/NRC. 1962. Methods of studying vegetation. Chapter 3 in "Range Research", NAS/NRC Pub. 890.

_______. 1966. Nutrient requirements of rabbits. NAS/NRC Pub. 1194, 17 p.

Rabas, D.L., A.R. Schmid, and G.C. Marten. 1969. Relationships of HCN, total sugars, dry matter, and morphological characteristics to palatability in sorghum species and crosses. Agron. Abstr. :61.

Reid, R.L., and G.A. Jung. 1965. Influence of fertilizer treatment on the intake, digestibility of tall fescue hay. J. Anim. Sci. 24:615-625.

__________________________, and S.J. Murray. 1966. Nitrogen fertilization in relation to the palatability and nutritive value of orchardgrass. J. Anim. Sci. 25:636-645.

____________________________, and C.M. Kinsey. 1967. Nutritive value of nitrogen-fertilized orchardgrass pasture at different periods of the year. Agron. J. 59:265-271.

Revusky, S., and E.W. Bedarf. 1967. Association of illness with prior ingestion of novel foods. Science 155:219-220.

___________, and J. Garcia. 1970. Learned associations over long delays. pp 1-84, in The Psychology of Learning and Motivation, Vol. 4, (ed.) G.H. Bowers. Acad. Press, New York.

Riegel, A. 1942. Some observations of the food coactions of rabbits in western Kansas during periods of stress. Trans. Kansas Acad. Sci. 45:369-375.

Rozin, P. 1967. Specific aversions as a component of specific hungers. J. Comp. Physiol. Psychol. 64:237-242.

________. 1969a. Central or peripheral mediation of learning with long CS-US intervals in the feeding system. J. Comp. Physiol. Psychol. 64:421-429.

________. 1969b. Adaptive food sampling patterns in vitamin deficient rats. J. Comp. Physiol. Psychol. 69:126-132.

________, and J.W. Kalat. 1971. Specific hungers and poison avoidance as adaptive specializations of learning. Psychol. Rev. 78:459-485.

Saul, W.E. 1972. Food habits of northern rodents and jackrabbits. US/IBP Desert Biome Research Memo. RM 72-28. 4 p.

Schmidt-Nielsen, K. 1964. Desert Animals: Physiological Problems of Heat and Water. Oxford Univ. Press, London. 277 p.

__________________, T.J. Dawson, H.T. Hammel, D. Hinds, and D.C. Jackson. 1965. The jackrabbit -- a study in desert survival. Hvalradets Skrifter 48:125-142.

Shettleworth, S.J. 1972. The role of novelty in learned avoidance of unpalatable "prey" by domestic chicks (*Gallus gallus*). Anim. Behav. 20:29-35.

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

Sørensen, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Biol. Skr. K. Dansk. Vidensk. Selsk. 5:1-34.

Sparks, D.R., and J.C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. J. Range Manage. 21:264-265.

Smith, A.D. 1965. Determining common use grazing capacities by application of the key species concept. J. Range Manage. 18:196-201.

Squires, V.R., A.D. Wilson, and G.T. Daws. 1972. Comparisons of the walking activity of some Australian sheep. Proc. Aust. Soc. Anim. Prod. 9:376-380.

Stapledon, R.G. 1947. The palatability and nutritive value of herbage plants. J. Min. Agric. 53:427-431.

Stoddart, L.A., and A.D. Smith. 1955. Range Management. 2nd edn. McGraw-Hill, New York. 433 p.

Stoddart, L.C. 1972. Population biology of the black-tailed jackrabbit (*Lepus californicus*) in Northern Utah. Ph. D. Diss., Utah State Univ., Logan, Utah. 134 p.

Taylor, C.R. 1968. Hygroscopic food: a source of water for desert antelopes? Nature 219:181-182.

Taylor, W.P. 1930. Methods of determining rodent pressure on the range. Ecology 11:523-542.

Taylor, W.P., C.T. Vorhies, and P.B. Lister. 1935. The relations of jackrabbits to grazing in southern Arizona. J. For. 33:490-498.

___________, and D.W. Lay. 1944. Ecological niches occupied by rabbits in eastern Texas. Ecology 25:120-121.

Tribe, D.E. 1950. The behaviour of the grazing animal: A critical review of present knowledge. J. Brit. Grassl. Soc. 5:209-224.

Trlica, M.J. Jr. 1971. Defoliation and soil moisture regime effects on plant regrowth and carbohydrate reserve utilization and storage in eight desert range species. Ph.D. Diss., Utah State Univ., Logan, Utah. 122 p.

Van Dyne, G.M., and H.F. Heady. 1965. Botanical composition of sheep and cattle diets on a mature annual range. Hilgardia 36:465-492.

Vorhies, C.T., and W.P. Taylor. 1933. The life histories and ecology of jackrabbits, *Lepus alleni* and *Lepus californicus* sp. Arizona Agr. Exp. Sta. Tech. Bull. 49:471-587.

Wagner, H.M. 1969. Principles of Operations Research. Prentice-Hall, N.J. 935 p.

Warmke, H.E., R.H. Freyre, and M.P. Morris. 1952. Studies on palatability of some tropical legumes. Agron. J. 44:517-520.

Wathen, P., J.W. Mitchell, and W. Porter. 1971. Theoretical and experimental studies of energy exchange from jackrabbit ears and cylindrically shaped appendages. Biophys. J. 11:1030-1047.

Westoby, M., and F.H. Wagner. 1973. Use of a crested wheatgrass seeding by black-tailed jackrabbits. J. Range Manage: In Press.

Weston, R.H. 1966. Factors limiting the intake of feed by sheep. I. The significance of palatability, the capacity of the alimentary tract to handle digesta and the supply of glucogenic substrate. Aust. J. Agric. Res. 17: 939-954.

APPENDICES

Appendix A

Detailed Stomach Content Data

Table 25 presents the mean percentage of each plant taxon, including distinguishable "unknowns", in the jackrabbit stomachs shot away from the *Agropyron* seeding, at each sampling date. These data were the basis for calculating the seasonal and year-round averages (Table 12). They indicate more precisely the exact dates when certain changes occurred in the diets. For example, *Artemisia tridentata* increases in the diet in mid-autumn, and decreases in mid-spring. Similar data for stomachs from animals shot near the seeding are given in Table 26.

Data from stomachs analysed at Utah State University were tentatively "corrected" by applying the correction regressions (Table 17) developed during the learning period. Corrected figures for the subset of Table 25 which was corrected are given in Table 27. They show no major qualitative differences from the original data.

Table 25. Stomach contents of Lepus californicus shot away from a wheatgrass seeding

Plant Taxon	Percent of Stomach Content by Date													
	1971					1972								1973
	5-20	9-8	10-4	11-2	11-8	2-23	4-3	5-15	6-12	7-15	8-29	9-27	11-2[c]	1-25[c]
Artemisia tridentata	15.9	2.9	0.0	0.0	10.1	22.1	14.8	1.6	0.0	0.0	0.0	0.4	0.9	4.9
Sarcobatus vermiculatus	0.0	4.0	0.5	2.4	0.3	4.5	13.9	13.6	4.0	17.8	6.5	14.7	0.0	0.0
Chrysothamnus spp.	0.0	20.7	0.0	0.0	4.3	1.2	0.0	2.0	2.0	0.0	8.3	3.2	1.1	10.3
Grayia spinosa	0.0	9.0	2.3	3.1	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
C4 *Atriplex confertifolia*	0.0	1.8	0.0	12.6	1.0	0.7	3.4	0.0	0.0	0.0	0.0	5.6	11.1	0.0
C4 *Atriplex falcata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	43.0	0.0
C4 *Kochia americana*	40.0	29.6	26.7	12.5	13.5	6.0	7.0	20.7	7.3	19.4	0.0	2.7	0.0	13.3
Bromus tectorum[a]						0.0	0.0	0.4	2.4	0.0	0.0	0.0	1.1	0.0
Grasses other than Bromus[a]	20.5	0.2	0.0	0.0	10.6	4.8	26.7	35.8	43.0	49.7	24.1	12.6	35.6	0.5
C4 *Halogeton glomeratus*	4.3	21.9	68.9	67.1	54.3	54.1	30.7	12.6	9.4	8.7	43.2	44.9	5.7	71.0
Descurainia spp.	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mentzelia albicaulis	0.0	0.2	0.0	0.0	0.0	6.6	0.0	7.0	15.3	4.4	0.6	6.9	0.0	0.0
C4 *Salsola kali*	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 25. Continued

Plant Taxon	Percent of Stomach Content by Date													
	1971					1972								1973
	5-20	9-8	10-4	11-2	11-8	2-23	4-3	5-15	6-12	7-15	8-29	9-27	11-2[c]	1-25[c]
Lappula redowskii[b]	2.3	0.0	0.0	0.0	0.0	0.0	3.4	0.0	4.0	0.0	0.0	0.0	0.1	0.0
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.6	0.0	0.0	16.8	0.0	0.0	0.0
Lepidium perfoliatum	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Opuntia polyacantha	0.0	1.7	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erigeron pumilus[b]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0
Unknown[d]	16.8	2.9	1.7	2.3	2.1									
Unknown A[d]						0.0	0.0	0.0	10.9	0.0	0.0	0.0	0.0	0.0
Unknown E[d]						0.0	0.0	0.0	0.4	0.0	0.5	3.9	0.0	0.0
Number of stomachs	10	15	11	8	13	10	10	9	9	8	9	11	10	3

[a] During 1971 Bromus tectorum was lumped with the other grasses.

[b] Lappula redowskii (Hornem.) Greene; Erigeron pumilus Nutt.

[c] On these two dates the animals were not taken from the shooting route.

[d] During 1971 all Unknowns were grouped; afterwards they were separated as far as possible.

Table 26. Stomach contents of Lepus californicus shot near a wheatgrass seeding, during 1971

Plant Taxon	Percent of Stomach Contents by Date				
	6-15	9-22	10-4	10-19	10-26
Artemisia tridentata	0.1	0.8	12.7	0.0	0.0
C4 *Atriplex confertifolia*	5.1	0.3	0.0	4.3	0.3
Chrysothamnus spp.	0.3	36.5	0.0	11.4	42.5
C4 *Kochia americana*	0.1	20.6	25.5	3.3	1.0
Grass[a]	85.3	38.7	62.0	65.3	48.8
C4 *Halogeton glomeratus*	6.4	2.4	0.1	15.6	6.4
Descurainia spp.	0.1	0.0	0.0	0.0	1.1
Mentzelia albicaulis	0.2	0.0	0.0	0.0	0.0
Sphaeralcea spp.	0.2	0.5	0.0	0.2	0.0
Unknown	1.8	0.0	0.0	0.1	0.1
Number of stomachs	23	15	1	30	12

---

[a] Presumably mainly Agropyron desertorum.

Table 27. Stomach contents of *Lepus californicus* on various dates, as corrected by correction regression. Correction was only carried out for dates after the learning period when the correction regressions were obtained, and for taxa for which they were obtained. Because the regressions were applied independently to each taxon, results do not add to 100 percent for each date

Plant Taxon	Corrected Percent Stomach Content by Date								
	1972								1973
	2-23	4-3	5-15	6-12	7-15	8-29	9-27	11-2	1-25
Artemisia tridentata	18.9	13.8	4.5	3.3	3.3	3.3	3.6	3.3	6.8
Sarcobatus vermiculatus	14.9	20.4	20.2	14.6	22.7	16.1	20.9	12.2	12.2
Chrysothamnus spp.	8.5	7.8	8.0	9.0	7.8	13.0	9.8	8.5	14.3
Atriplex confertifolia	6.7	8.3	6.3	6.3	6.3	6.3	9.6	12.9	6.3
Atriplex falcata	1.0	1.0	1.0	1.0	1.0	1.0	1.0	17.1	1.0
Kochia americana	5.4	6.0	13.6	6.1	12.9	2.1	3.6	2.1	9.5
Grasses other than *Bromus*	6.9	18.3	23.0	26.8	30.3	16.9	11.0	22.9	4.7
Halogeton glomeratus	45.7	25.5	13.7	11.3	10.7	37.3	38.6	8.4	58.7
Sphaeralcea spp.	0.0	0.0	1.2	0.0	0.0	2.7	0.0	0.0	0.0
Descurainia spp.	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
Opuntia polyacantha	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8

Appendix B

Listing of the Computer Program RABWAT

```
*****************************************************************************************************
*
*                         P L / I   C A R D   I M A G E   L I S T I N G
*
*                                         RABWAT3
*
*                                                                                       (120772)
*   0.0.122              SATURDAY   --   MAR. 10 1973   --   15:03:16
*
*****************************************************************************************************

   00001          RABWAT3: PROC OPTIONS(MAIN);
   00002          DCL SPREAD (12) INIT (600,0,1000,0,1000,0,1000,0,1000,0,1000,0);
   00003          DCL DUMMY INIT (0);
   00004          DCL N_BODY_WEIGHT_FUNCTION_PTS  INIT (2);
   00005          DCL MEAL_SIZE FLOAT DEC;
   00006          DCL N_MEAL_SIZE_FUNCTION_PTS INIT (3);
   00007          DCL OUTPUT_INTERVAL FIXED BIN INIT (5);
   00008          DCL N_EVAPORATION_FUNCTION_PTS INIT (8);
   00009          DCL START_DAY FIXED BIN INIT (1);
   00010          DCL STOP_DAY FIXED BIN INIT (365);
   00011          DCL RADIAL_FREQUENCY INIT (0.262);
   00012          DCL LOTEMP FIXED BIN;
   00013          DCL OUTPUT_OPTION FIXED BIN INIT (1);
   00014          DCL (DAY,HOUR) FIXED BIN;
   00015          DCL URINE_LOSS INIT (5);
   00016          DCL FAECES_LOSS INIT (1);
   00017          DCL INPUT_OPTION INIT (2);
   00018          ACQUIR: BEGIN;
   00019          DCL MEAL_SIZE_FUNCTION(2,N_MEAL_SIZE_FUNCTION_PTS) FLOAT DEC;
   00020          GET LIST (MEAL_SIZE_FUNCTION);
   00021          DCL EVAPORATION_FUNCTION(2,N_EVAPORATION_FUNCTION_PTS) FLOAT DEC;
   00022          GET LIST (EVAPORATION_FUNCTION);
   00023          DCL BODY_WEIGHT_FUNCTION(2,N_BODY_WEIGHT_FUNCTION_PTS) FLOAT DEC;
   00024          GET LIST (BODY_WEIGHT_FUNCTION);
   00025          HITEMP=0;
   00026          LOTEMP=0;
   00027          ACC=0;
   00028          DAYS: DO DAY=START_DAY TO STOP_DAY;
   00029          BODY_WEIGHT=CURVE(DAY,BODY_WEIGHT_FUNCTION(1,*),
   00029                                BODY_WEIGHT_FUNCTION(2,*));
   00030          IF INPUT_OPTION=2 THEN DO;
   00032          GET EDIT (X1     ,X2     ) (COL(9),F(3,0),COL(15),F(3,0));
   00033          IF X1¬=999 THEN HITEMP=X1;
   00035          IF X2¬=999 THEN LOTEMP=X2;
   00037          AVERAGE=(HITEMP+LOTEMP)/2;
   00038          AMPLITUDE=(HITEMP-LOTEMP)/2;
   00039          END;
   00040          DAYS_EVAPORATION=0;
   00041          HOURS: DO HOUR=2 TO 24 BY 2;
   00042          IF INPUT_OPTION=2 THEN DO;
   00044          AIR_TEMP=AVERAGE+AMPLITUDE*SIN(RADIAL_FREQUENCY*HOUR);
   00045          END;
   00046          IF INPUT_OPTION=1 THEN DO;
   00048          GET EDIT (AIR_TEMP) (COL(11),F(3,0));
   00049          AIR_TEMP=(AIR_TEMP-32)*5/9;
   00050          END;
   00051          EVAPORATION_RATE=CURVE(AIR_TEMP,EVAPORATION_FUNCTION(1,*),
```

```
     RABHAT3                                    PL/I CARD IMAGE LISTING (120772)   ---   PAGE 0002

                                              EVAPORATION_FUNCTION(2,*));
     EVAPORATION=2*BODY_WEIGHT*EVAPORATION_RATE/100;
     DAYS_EVAPORATION=DAYS_EVAPORATION+EVAPORATION;
     END HOURS;
     OUTGO=DAYS_EVAPORATION+URINE_LOSS+FAECES_LOSS;
     MEAL_SIZE=CURVE(DAY,MEAL_SIZE_FUNCTION(1,*),
                         MEAL_SIZE_FUNCTION(2,*));
     OUTGO=OUTGO-.4*MEAL_SIZE;
     WATER_NEED=100*OUTGO/MEAL_SIZE;
     ACC=ACC+WATER_NEED;
     IF MOD(DAY,OUTPUT_INTERVAL)=0 THEN
     DO;
     AVE=ACC/OUTPUT_INTERVAL;
     ACC=0;
     CALL PRTPLT(DAY,AVE,DUMMY,DUMMY,DUMMY,DUMMY,DUMMY,SPREAD);
     END DAYS;
    /*                                                                   */
    /*********************************************************************/
    /*                                                                   */
    /*      GRAPHING PROCEDURE                                           */
    /*                                                                   */
    /*********************************************************************/
    /*                                                                   */
    PRTPLT:
            PROC (Y,X1,X2,X3,X4,X5,X6,BOUNDS) ;
            DCL BOUNDS (*) FLOAT DEC ;
            DCL HEADING CHAR (40) VAR INIT (
             'WATER BUDGET OF JACKRABBITS');
            DCL YLABEL (6) CHAR (10) VAR INIT
       ('DEFIC','DUMMY','DUMMY','INWT','FOODW','LOSS');
            DCL XLABEL CHAR (10) VAR INIT ('DAY ') ;
            DCL ALINE CHAR (70) ;
            DCL SYMB (6) CHAR (1) INIT ('D','O','O','I','F','L') ;
            DCL K FIXED BIN ;
            DCL XV (6) FLOAT DEC ;
            DCL NDIV (6) FIXED BIN (31,0) ;
            DCL DIV (6) FLOAT DEC STATIC ;
            DCL FIRST_PASS BIT (1) STATIC INIT ('1'B) ;
               IF K=1 THEN
               FIRST_PASS='1'B ;
               IF FIRST_PASS THEN
                  DO ;
                  FIRST_PASS = '0'B ;
    /*      HEADING                                                      */
                  PUT EDIT (HEADING) (COL(33),A) ;
                  PUT SKIP (3) EDIT ('SYMBOL','MINIMUM','GRAPHING',
                  'MAXIMUM') (COL(19),A,COL(33),A,COL(59),A,COL(92),A) ;
                     DO I = 1 TO 6 ;
                     J = 2 * I ;
                     PUT SKIP EDIT (SYMB(I),BOUNDS(J),YLABEL(I),'.VS.',
                     XLABEL,BOUNDS(J-1)) (COL(21),A, COL(31),E(15,5),COL(
                     51),A,COL(64),A,COL(71),A,COL(90),E(15,5)) ;
                     END ;
                  PUT SKIP(2) EDIT (XLABEL,YLABEL(1)) (COL(5),A,COL(19),A)
```

```
    RABWAT3                          PL/I CARD IMAGE LISTING (120772)  ---  PAGE 0003

               ;
               PUT SKIP (2) ;
/*        SCALE                                                          */
                  DO I = 1 TO 6 ;
                  J = 2 * I ;
                  DIV(I) = (BOUNDS(J-1)-BOUNDS(J))/70 ;
                  END ;
               END ;
/* END FIRST_PASS SECTION */
         XV(1) = W1 ;
         XV(2) = W2 ;
         XV(3) = W3 ;
         XV(4) = W4 ;
         XV(5) = W5 ;
         XV(6) = W6 ;
         ALINE = '                                                 '||
         '                                         ' ;
         SUBSTR(ALINE,1,1)='.' ;
         SUBSTR(ALINE,70,1)='.' ;
            DO I = 1 TO 6 ;
            J = 2 * I ;
            NDIV(I) = (XV(I)-BOUNDS(J))/DIV(I) + 0.5 ;
               IF NDIV (I) <= 1 THEN
               NDIV(I) = 1 ;
               IF NDIV (I) > 70 THEN
               NDIV(I) = 70 ;
            SUBSTR(ALINE,NDIV(I),1)=SYMB(I) ;
            END ;
         PUT EDIT (X,XV(1),ALINE) (COL(4),F(4,0),COL(12),E(15,5),COL(31)
         ,A) ;
         RETURN ;
         END PRTPLT ;
CURVE : PROC(X,XVAL,YVAL) RETURNS (FLOAT DEC);
/*                                                                       */
/***********************************************************************/
/*                                                                       */
/*   INTERPOLATION PROCEDURE.                                            */
/*                                                                       */
/***********************************************************************/
/*                                                                       */
DCL I FIXED BIN INTERNAL, X FLOAT DEC;                                   00000200
DCL XVAL(*), YVAL(*);                                                    00000300
NDIM=DIM(XVAL,1);                                                        00000400
    IF X<=XVAL(1) THEN                                                   00000500
    RETURN (YVAL(1));                                                    00000600
    IF X>=XVAL(NDIM) THEN                                                00000700
    RETURN (YVAL(NDIM));                                                 00000800
    DO I=1 TO NDIM;                                                      00000900
       IF XVAL(I)>X THEN DO;                                             00001000
          AM=(YVAL(I)-YVAL(I-1))/(XVAL(I)-XVAL(I-1));                    00001100
          C=YVAL(I)-AM*XVAL(I);                                          00001200
          RETURN (AM*X+C);                                               00001300
          END;                                                           00001400
    END;                                                                 00001500


    RABWAT3                          PL/I CARD IMAGE LISTING (120772)  ---  PAGE 0004

END CURVE;
 END ACQUIR;
 END RABWAT3;
```

VITA

Mark Westoby

Candidate for the Degree of
DOCTOR OF PHILOSOPHY

Dissertation: Impact of Black-Tailed Jackrabbits (*Lepus californicus*) on Vegetation in Curlew Valley, northern Utah.

Major Field: Ecology.

Biographical Information:

Personal Data: Born at Hayes, Middlesex, England, September 21, 1947, son of Jack Westoby and Florence Westoby.

Education: Attended primary schools in Hayes, Middlesex; Geneva, Switzerland; and Rome, Italy; secondary education at Caterham School, Caterham, Surrey, England; received Bachelor of Science degree in Ecological Science, with First Class Honours in Ecology, from the Department of Forestry and Natural Resources, Edinburgh University, Scotland, in 1970.

Professional Experience: 1970-1973, Research Assistant with the Systems Modelling Group of th US/IBP Desert Biome, Ecology Center, Utah State University; summer 1969, Research Assistant (termite ecology) with the Royal Geographical Society South Turkana (Kenya) Expedition.