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A QUANTITATIVE FOOD WEB ANALYSIS OF A SHORTGRASS COMMUNITY

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ABSTRACT

Several modes of analysis were imposed upon certain data sets contained in the U.S. IBP Grassland Biome central data bank. The first analysis resulted in a vector of food items occurring in the summer diet for each of 36 different consumer groups. These data were then collated to form a 36 × 112 dietary-composition matrix for the major consumer groups of a shortgrass prairie ecosystem. A second analysis produced a matrix of pairwise dietary-overlap values based upon the species composition of the observed diets. Finally, we attempted to estimate the relative importance of the various consumer groups by synthesizing the approximate densities, the number of active days per year, and the daily consumption rates.

Results indicate a clear dichotomy between herbivore and carnivore groups, but overlap values are as high as 100% within the two major groups. It also appears that at a modest stocking rate of one animal unit per 30 acres, domestic stock may account for as much as 68% of the annual aboveground energy transferral.

INTRODUCTION

Of vital imporatance to the success of any large integrated research program is the degree of data synthesis finally achieved. Even though this paper is no paradigm, it cuts across many disciplinary boundaries and hopefully provides a tie between the more disciplinary-oriented summaries such as the data synthesis project (French, 1971). This paper deals with the natural consumptive process in a shortgrass prairie ecosystem, and because the emphasis is on the process and not the processors, it treats all consumer groups for which we have data. Further, it indicates many of the data inequities and incongruities that will be found as greater and greater emphasis is placed upon this phase of the study.

The purpose, therefore, is threefold. First, we believe that only by trying to synthesize the work to date can the inadequacies be made explicit. This "taking-stock" is necessary for any prudent redirection of future work. Secondly, the modelling has advanced on several fronts to the extent that parameter values are urgently needed to validate many compartmental, process, and whole-system models. Hopefully, a synthesis such as this will help alleviate problems in this area. Finally, to our knowledge, no whole-system food web model has ever been produced. For the most part, ecologists quickly abdicated after the 20th or 30th arrow overcomplicated the food web picture. This report is, we feel, a modest advancement insofar as it represents quantification of many consumer relations. In some cases, we have had to use the literature and a certain degree of guesswork in generating the biomass-density and flow-rate vectors included at the end of the report.

It is trite to say that ecosystems are complex. Yet we have again encountered this stark reality in attempting to make sense of the overall data base. For example, a modest computer easily handles a matrix of the dimensions dealt with here. It taxes one's grasp, however, to mentally and pictorially integrate all of the groups identified. We cannot, in any meaningful sense, report the data for each of the 57 beetle families, the 20 grasshopper species, and the scores of other identified consumer groups. This is a resolution problem, and the chosen level of resolution necessitated some lumping as well as some omissions.

Causing equal disquietude is the problem of mentally evaluating the relations. Interpreting third and fourth trophic-level relations quickly recalls biometrics laboratories wherein one unravels third and fourth-degree interactions. The fact that Ferruginous Hawks consume weasels, which consume ground squirrels, which consume grasshoppers, which consume blue grama is not new. On the other hand, it boggles the mind to mentally picture the effect of the hawks on blue grama. When this is but one of many combinations of the 36 consumer groups finally considered, it is readily apparent that ecosystem analysis (at this level) is no simple task. Scientific names of all species considered are to be found in Table 1, alphabetized by code name within each major grouping.

While the dietary matrix (Table 2) combines most of the available data from the biome program and provides a reasonable representation of the aboveground consumer community on a shortgrass prairie, there are many obvious omissions. The cottontail (*Sylvilagus floridanus*) and prairie dog (*Cynomys* spp.) are among the more conspicuous vertebrates missing from the array. Similarly, there are no mammalian secondary consumers such as coyote (*Canis latrans*), weasel (*Mustela frenata*), mink (*Mustela vision*), fox (*Vulpes fulva*), or badger (*Taxidea taxus*) considered. Although the birds

Table 1. List of codes, scientific names, and common names for both the consumer (abscissa) and consumee (ordinate) axes of the dietary composition matrix given as Table 2.

Code Name	Scientific Name	Common Name
	Grasses and Grasslike Plants	
AGCR	*Agropyron cristatum*	Crested wheatgrass
AGSM	*Agropyron smithii*	Western wheatgrass
ARFE4	*Aristida fendleriana*	Fendler three-awn
ARLO3	*Aristida longiseta*	Red three-awn
AVSA	*Avena sativa*	Oats
BOGR2	*Bouteloua gracilis*	Blue grama
BRTE	*Bromus tectorum*	Cheatgrass brome
BUDA	*Buchloe dactyloides*	Buffalo grass
CAREX	*Carex* spp.	Carex
DAGL	*Dactylis glomerata*	Orchard grass
ELCA4	*Elymus canadensis*	Canada wild rye
ELYMU	*Elymus* spp.	Wild rye
FEOC2	*Festuca octoflora*	Six-weeks fescue
ORHY	*Oryzopsis hymenoides*	Indian ricegrass
SIHY	*Sitanion hystrix*	Bottlebrush squirreltail
SPCR	*Sporobolus cryptandrus*	Sand dropseed
STCO4	*Stipa comata*	Needle and thread
TRAE	*Triticum aestivum*	Wheat
	Forbs and Shrubs	
AMGR	*Amaranthus graecizans*	Tumbleweed amaranth
ARFR4	*Artemisia frigida*	Fringed sagewort
ASTRA	*Astragalus* spp.	Locoweed
ATCA2	*Atriplex canescens*	Fourwing saltbrush
BAOP	*Bahioa oppositifolia*	Plains bahia
CHENO	*Chenopodium* spp.	Lambs-quarter
CHLE4	*Chenopodium lepthophyllum*	Slimleaf goosefoot
CHNA2	*Chrysothamnus nauseosus*	Rubber rabbit brush
CHVI6	*Heterotheca villosa*	Hairy golden aster
CIUN	*Cirsium undulatum*	Wavyleaf thistle
CLSE	*Cleome serrulata*	Bee spiderflower
CRMI5	*Cryptantha minima*	Cryptantha
CRYPT	*Cryptantha* spp.	Cryptantha
DEPI	*Descurainia pinnata*	Pinnate tansy mustard
EREF	*Erigonum effusum*	Common buckwheat
ERIOG	*Eriogonum* spp.	Wild buckwheat
ERMI	*Eriogonum microthecium*	Slenderbush buckwheat

Table 1 (continued).

Code Name	Scientific Name	Common Name
	Forbs and Shrubs (continued)	
FUNG	*Eumycophyta*	Fungus
GUSA2	*Gutierrezia sarothrae*	Broom snakeweed
HASP2	*Haplopappus spinulosus*	Ironplant goldenweed
HEAN3	*Helianthus annuus*	Common sunflower
KOSC	*Kochia scoparia*	Belvedere summer cypress
LAEU	*Lathyrus eucosmus*	Bush peavine
LAOC	*Lathyrus ochroleucus*	Cream peavine
LARE	*Lappula redowskii*	Redowski's stickseed
LATHY	*Lathyrus* spp.	Peavine
LEDE	*Lepidium densiflorum*	Prairie pepperweed
LICH	*Thallophyta*	Lichen
LIIN2	*Lithospermum incisum*	Gromwell
LIPU	*Liatris punctata*	Dotted gayfeather
MATA	*Aster tanacetifolius*	Tansyleaf aster
MESA	*Medicago sativa*	Alfalfa
MILI3	*Mirabilis linearis*	Four-o-clock
MUDI	*Musineon divaricatum*	Musineon
OECO2	*Oenothera coronopifolia*	Cutleaf evening primrose
OPPO	*Opuntia polyacantha*	Plains prickly pear
OXSE	*Oxytropia sericea*	Silky crazyweed
PLPAG	*Plantago purshii*	Woolly Indian wheat
POLYG	*Polygonium* spp.	Knotweed
PSTE3	*Psoralea tenuiflora*	Slimflower scurf pea
RACO3	*Ratibida columnaris*	Upright prairie coneflower
SAKAT	*Salsola kali tenuifolia*	Tumbling Russian thistle
SEED		Unidentified seeds
SEMU2	*Senicio multicapitatus*	Groundsel
SENEC	*Senecio* spp.	Groundsel
SETR2	*Senecio tridenticulatus*	Groundsel
SOSE4	*Sophora sericea*	Silky sophora
SPCO	*Sphaeralcea coccinea*	Scarlet globe mallow
TARAX	*Taraxacum* spp.	Dandelion
THME	*Thelesperma megapotamicum*	Greenthread
THTR	*Thelesperma trifidum*	Three-cleft greenthread
TROC	*Tradescantia occidentalis*	Prairie spiderwort
UNKF		Unknown forbs
UNKV		Unknown vegetation
YUGL	*Yucca glauca*	Small soapweed
	Arthropods	
ANTS	Hymenoptera	Ants
ARPS	*Arphia pseudonietana*	Grasshopper
BETL	Coleoptera	Beetles
BUGS	Hemiptera	True bugs

Table 1 (continued).

Code Name	Scientific Name	Common Name
	Arthropods (continued)	
BTFL	Lepidoptera	Butterflies
CRIK	Gryllidae	Crickets
DRFL	Anisoptera	Dragon flies
FLY	Diptera	Flies, mosquitoes
GHPR	Orthoptera	Unidentified grasshoppers
HANT	*Pogonomyrmex occidentalis*	Harvester ants
HOMO	Homoptera	Leafhoppers, aphids, etc.
LWNG	Heuroptera	Lace wings
MEIN	*Melanoplus infantilis*	Grasshopper
MISC		Misc. arthropods
OPOB	*Opeia obscura*	Grasshopper
PSDE	*Psolessa delicatula*	Grasshopper
RFLY	*Asilidae*	Robber fly
SPDR	Araneae	Spiders
THP	Thysanoptera	Thrips
TRKI	*Trachrachys kiowa*	Grasshopper
	Birds	
BAOW	*Tyto alba*	Barn Owl
BUOW	*Speotyto cunicularia*	Burrowing Owl
CSPR	*Calcarius ornatus*	Chestnut-collared Longspur
FHAK	*Buteo regalis*	Ferruginous Hawk
GEAG	*Aquila chrysaetos*	Golden Eagle
GHOW	*Bubo virginianus*	Great Horned Owl
HLRK	*Eremophila alpestris*	Horned Lark
KDER	*Charadnus vociferous*	Killdeer
LBUN	*Calamospiza melanocorys*	Lark Bunting
LBCR	*Numenius americanus*	Long-billed Curlew
LEOW	*Asio otus*	Long-eared Owl
MPLR	*Eupuda montana*	Mountain Plover
MSPR	*Rhynchophanes mccownii*	McCown's Longspur
RNPH	*Phasianus colchicus*	Ring-necked Pheasant
SHAK	*Buteo swainsoni*	Swainson's Hawk
UNKB		Unidentified bird
WMLK	*Sturnella neglecta*	Western Meadowlark
	Mammals and Reptiles	
ANTL	*Antilocapra americana*	Antelope
BISN	*Bison bison*	Bison
BJAC	*Lepus californicus*	Black-tailed jackrabbit
CATL	*Bos taurus*	Cattle
CRAB	*Sylvilagus floridanus*	Cottontail rabbit
DMSE	*Peromyscus maniculatus*	Deer mouse
FFF	Misc. animal material	Fur, feather, fin
GMSE	*Onychomys leucogaster*	Northern grasshopper mouse

Table 1 (continued).

Code Name	Scientific name	Common Name
	Mammals and Reptiles (continued)	
GOPH	*Thomomys talpoides*	Northern pocket gopher
GSQR	*Spermophilus tridecimlineatus*	Thirteen-lined ground squirrel
HMSE	*Rethrodontomys* spp.	Harvest mouse
JACK	*Lepus* spp.	Jackrabbit
KRAT	*Dipodomys ordii*	Ord's kangaroo rat
MRAT	*Ondatra zebethicus*	Muskrat
MUS	*Mus musculus*	House mouse
MVOL	*Microtus pennsylvanicus*	Meadow vole
PMSE	*Perognathus hispidus*	Hispid pocket mouse
PVOL	*Microtus ochrogaster*	Prairie vole
SHEP	*Ovis aries*	Sheep
UKSM		Unknown small mammal
UKSN		Unknown snake
VOLE	*Microtus* spp.	Vole
WEAS	*Mustela frenata*	Long-tailed weasel
WJAC	*Lepus townsendii*	White-tailed jackrabbit

Table 2. Percentages for dietary composition matrix for various consumers on the shortgrass plai
The 36 consumer groups listed down the ordinate axis represent the important consumers o
constituting greater than 0.5% of the consumer's diet.

Dietary Composition Matrix

Consumed Items

	HASP2	THTA	CRYPT	BRTE	LARE	SENEC	TARAX	PLPAG	LEDE	SEMU2	ARFR4	BOGR2	KOSC	SPCO	DECO2	PSTE3	STCO4	CHVI6	ARLO3	ASTRA
ANTELOPE	10	09	04	01	01	01	01	05	03	06	08	10	02	25						
CATTLE											01	44	01	05	02	05	10	01	03	01
SHEEP											01	34		26	02	01	03			
BISON												58		.02		.03			.04	
BLACK-TAILED JACKRABBIT												08	27	01						05
WHITE-TAILED JACKRABBIT								01				08	11	02	02					10
GRASSHOPPER-OPOB												95								
GRASSHOPPER-TRKI												97								
GRASSHOPPER-PSDE												98								
GRASSHOPPER-ARPS												70								
GRASSHOPPER-MEIN																				
COLEOPTERA											04	05			01	12	04	01	05	
DIPTERA											05									
HEMIPTERA											08	08				04		02	01	
HOMOPTERA											01	19			01	05		01	01	
[illegible]PTERA											02	01		05		08		02		
LEPIDOPTERA												04				04		08		
THYSANOPTERA											02	61					02			
GOPHER												10	03	27		02	02		02	
KANGAROO RAT												06	08							
HARVESTER ANT								12									01	01	09	
HORNED LARK														01						
LARK BUNTING																				
McCOWN'S LONGSPUR																				
CHESTNUT-COLLARED LONGSPUR																				
ROBBER FLY																				
GROUND SQUIRREL									02	01	09	01	03							01
DEER MOUSE											01	06	03							
GRASSHOPPER MOUSE											05	01	03							
GREAT HORNED OWL																				
BURROWING OWL																				
LONG-EARED OWL																				
BARN OWL																				
GOLDEN EAGLE																				
FERRUGINOUS HAWK																				
SWAINSON'S HAWK																				

	CAREX	SPCR	AGSM	LIIN2	GUSA2	FEOC2	CIUN	BUDA	AGCR	MESA	SAKAT	MILI3	SOSE4	UNKV	TRAE	AVSA	HEAN3	UNKF	CHNA2	CLSE
ANTELOPE																				
CATTLE	14	01	07	01																
SHEEP	18	01	04		05	01	01													
BISON	05	03	18			01	01	04												
BLACK-TAILED JACKRABBIT	03	06	09			04			06	08	01	02	02	01	04	02	01			
WHITE-TAILED JACKRABBIT	07	02	29			11	01		01		01	02	02	01	07		01			
GRASSHOPPER-OPOB	01	03																		
GRASSHOPPER-TRKI		03																		
GRASSHOPPER-PSDE	02																			
GRASSHOPPER-ARPS	26		04															14		
GRASSHOPPER-MEIN	32		54																07	02
COLEOPTERA	01				25		10												02	05
DIPTERA					36		10					02		01					02	01
HEMIPTERA	01		02		30		09													
HOMOPTERA			11		12		13					01					01		08	
[illegible]PTERA					03		20										08			16
LEPIDOPTERA					12		54													
THYSANOPTERA			07				07										02			
GOPHER		03	13											08						
KANGAROO RAT		01								03	02									
HARVESTER ANT						01		03				03		04						
HORNED LARK														02		03				
LARK BUNTING				05											05	02	03			
McCOWN'S LONGSPUR				01				06						02			01			
CHESTNUT-COLLARED LONGSPUR																				
ROBBER FLY													01				01	04		
GROUND SQUIRREL	01	01					01													
DEER MOUSE																				
GRASSHOPPER MOUSE			01																	
GREAT HORNED OWL																				
BURROWING OWL																				
LONG-EARED OWL																				
BARN OWL																				
GOLDEN EAGLE																				
FERRUGINOUS HAWK																				
SWAINSON'S HAWK																				

	LIPU	DEPI	ATCA2	SIHY	BAOP	OPPO	THME	SETR2	YUGL	RACO3	TROC	SEED	FUNG	EMEF	[illegible]
ANTELOPE															
CATTLE															
SHEEP															
BISON															
BLACK-TAILED JACKRABBIT															
WHITE-TAILED JACKRABBIT															
GRASSHOPPER-OPOB															
GRASSHOPPER-TRKI															
GRASSHOPPER-PSDE															
GRASSHOPPER-ARPS															
GRASSHOPPER-MEIN	01	02	04	01	01	01									
COLEOPTERA	02		07				05								
DIPTERA	01	01	02	06	01	12	01	02							
HEMIPTERA															
HOMOPTERA			03	01	06		01	01							
[illegible]PTERA			03		01	01		02	04						
LEPIDOPTERA	04	04	04	04											
THYSANOPTERA			05		02			07		02					
GOPHER			07			24									
KANGAROO RAT											01	64	03		
HARVESTER ANT				02	11	01								24	0
HORNED LARK															
LARK BUNTING															
McCOWN'S LONGSPUR															
CHESTNUT-COLLARED LONGSPUR															
ROBBER FLY			01			01					01	12	08		
GROUND SQUIRREL			01									23	03		
DEER MOUSE												03	01		
GRASSHOPPER MOUSE															
GREAT HORNED OWL															
BURROWING OWL															
LONG-EARED OWL															
BARN OWL															
GOLDEN EAGLE															
FERRUGINOUS HAWK															
SWAINSON'S HAWK															

of the Pawnee National Grassland (U.S. IBP Grassland Biome site) of northeastern Colorado. the community, while the 112 dietary items along the abscissa represent all food items

CHENO	LAOC	ERMI	CRMIS	DAGL	ELCAA	ELYMU	ERIOG	LATHY	OXSE	MUD1	LAEU	POLYG	ORHY	ARFE4	AMGR	CHLE4	LICH	GHPR	ANTS
05	03	03	01	01	01	01	01	01	01	01									
												01	01		02	01		72	04
												06	05	07				19	11
												08	01	13				18	13
														46				17	
										01	01							26	12
																	01	07	03
																	01	04	
																	01	17	01
																		01	

BTFL	LMNG	BETL	SPDR	MISC	FLY	BUGS	BUOW	HOMO	DRFL	CRIK	MUS	CRAB	PVOL	HLRK	UKSN	FFF	PHSE	DMSE	HRAT
01		10		02															
01		29	01		02	01	01												
01		29		02	02	02		01											
02		25			03	04		03											
05	02	04			35	03		13	01										
06		26		01												01			
09		19	02	03	01											08			
03		55	03	01	01											07			
												86						01	10
		03		02			07			03	01	42	13		03		04	18	
												67						07	
												14	20				03	10	
												27							
												24		01					
							02					11		04	02			02	

WEAS	HMSE	GMSE	GOPH	MVOL	KRAT	UNKB	JACK	UKSM	GSQR	LBUN	WALK	LBCR	VOLE	NMPH	KDER	MPLR
03																
						03										
	02	03	11			10										
		02	40	04	04	01					02					
							70	02	01							
01			13				43	01	13		04	01				
			32		01	13	02	01	15	09	13		01	03	01	01

are reasonably well represented, one of the most common raptors, the Marsh Hawk (*Circus hudsonicus*), is not included. Of possibly greater importance is the striking lack of belowground consumer data. Therefore, although a step in the right direction, this report will point out that our consumer work is far from complete.

BACKGROUND AND METHODS

Although the original intent of this synthesis was to integrate one season's consumer data for the U.S. IBP Grassland Biome Intensive or Pawnee Site, it was soon apparent that this was inconsistent with a larger goal--that of evaluating the total consumptive process. Therefore, dietary data collected from wide-ranging species such as hawks and eagles were included, even though only a small proportion of the diet may have been obtained from the actual study area. Similarly, since a recent pocket gopher study had been conducted on the contiguous Pawnee National Grassland, we chose to include those data.

The summer of 1970 was chosen as the time interval of analysis since the greatest degree of data overlap occurred during this time. Yet, because certain dietary studies were conducted in 1969 and terminated in 1970, we could not achieve complete temporal synchrony. Finally, along with spatial and temporal discontinuities, the methodological procedures varied greatly. A full compilation of the data type and sources, time and location of study, and sample size appears in Table 3.

The methods used to develop the dietary matrix varied, as dictated by the available data. For this reason a brief description of each data type, as well as the method used to obtain the dietary proportions, is included

Table 3. Acknowledgement of the data sources utilized to compile the dietary and other matrices reported herein. Since the time, location, and methodology of all studies were not directly comparable, the specifics are given for each important consumer group.

Consumer Group	Source and Relevant Reference	Time of Study or Data Utilized	Location	Data Type	Sample Size
Antelope	Central data bank J. Hoover, personal communication; Hoover (1970); Nagy and Hoover (1971).	June 1970	Pawnee Site	Weight-adjusted bite count	12
Cattle	Central data bank R. Rice, personal communication; Rice and Vavra (1971).	June-Aug. 1970	Pawnee Site	Esophageal sample	113
Sheep	Central data bank R. Rice, personal communication.	June-Aug. 1970	Pawnee Site	Esophageal sample	11
Bison	Central data bank D. Peden, personal communication; Peden (1971).	July-Aug. 1970	Pawnee Site	Esophageal sample	2 animal days
Black-tailed jackrabbit White-tailed jackrabbit	Central data bank R. Hansen and J. Flinders, personal communication; Flinders and Hansen (1971).	June-Aug. 1969	Pawnee National Grassland	Stomach analysis	77 77

Table 3 (continued).

Consumer Group	Source and Relevant Reference	Time of Study or Data Utilized	Location	Data Type	Sample Size	
Grasshoppers	R. Lavigne and L. Rogers, personal communication.	June-Aug. 1970	Pawnee Site	Gut analysis (20 fields/ slide)	Grasshopper OPOB	5
					Grasshopper TRKI	17
					Grasshopper PSDE	9
					Grasshopper ARPS	16
					Grasshopper MEIN	6
Small mammal	Central data bank Flake (1971*a*,*b*); Cwik (1970).	June-Aug. 1969	Pawnee National Grassland	Gut analysis	Ord's kangaroo rat	99
					Thirteen-lined ground squirrel	86
					Deer mouse	182
					Northern grasshopper mouse	86
Insects	Central data bank V. Yount, personal communication; Yount (1971).	June-Aug. 1970	Pawnee Site	Frequency of occurence on various plant species	Beetles	720
					True bugs	200
					Ants	132
					Thrips	41
					Flies, mosquitos	42
					Leafhoppers, aphids, etc.	548
					Butterflies	24

Table 3 (continued).

Consumer Group	Source and Relevant Reference	Time of Study or Data Utilized	Location	Data Type	Sample Size	
Pocket gopher	Vaughan (1967).	June-Aug. 1962	Pawnee National Grassland	Stomach analysis (1 slide/animal 20 fields/slide)		75
Harvester ant	Central data bank Lavigne and Rogers (1970); Lavigne, Rogers, and Chu (1971).	June-Sept. 1970	Pawnee Site	Frequency of transported items	Individuals	578
Four species of birds	Central data bank P. Baldwin, personal communication; Baldwin et al. (1969); Creighton (1971).	June-July 1969 (May 1969 only for McCown's Longspur)	Pawnee National Grassland	Crop analysis	Horned Lark Lark Bunting Chestnut-collared Longspur McCown's Longspur	38 121 2 24
Robber flies	R. Lavigne and L. Rogers, personal communication; Lavigne and Rogers (1970); Lavigne et al. (1971).	1970	Pawnee Site	Frequency of items eaten (non-weight-adjusted)		250
Owls	R. Ryder, personal communication; Marti (1969).	June-Aug. 1969	Pawnee National Grassland	Percent/weight of pellet analysis	Great Horned Owl Long-eared Owl Burrowing Owl Barn Owl	11 10 61 173

Table 3 (continued).

Consumer Group	Source and Relevant Reference	Time of Study or Data Utilized	Location	Data Type	Sample Size	
Golden Eagle	Manuscript by M. Good (unpublished); Ryder, personal communication.	Mar.-Apr. 1970	Pawnee National Grassland	Weight-adjusted frequency pellet analysis	Pellets	25
Swainson's Hawk	R. Olendorff, personal communication.	June-July 1970-1971	Pawnee National Grassland	Weight-adjusted frequency of nest litter		89
Ferruginous Hawk		May-July 1971 June-July 1970				104

in this section. The dietary proportions reported are our best estimate of the relative importance of food items on a biomass basis.

The antelope dietary data used were from weight-adjusted, bite count sampling. The proportions of the antelope diet estimated by this method were used directly in the dietary matrix.

Diets of cattle, sheep, and bison were determined from esophageal-fistulated animals. These esophageal samples were dried and examined by microscopic slide inspection. Frequencies of various food species obtained in this manner were converted to proportions of the diet by the method described in Sparks and Malechek (1969).

The diets of jackrabbits, grasshoppers, and rodents were determined by analysis of stomach samples. Slides of these samples were microscopically examined to determine relative frequency and density (Cavender and Hansen, 1970; Sparks and Malechek, 1969) of dietary items.

For want of specific data, insect diets were inferred from data collected on the frequency of occurrence of particular insect species as observed on particular plant species. The assumption here, of course, is that the consumption of plants was proportional to the frequency of occurrence on the plants. Although of unproven validity, these frequencies (converted to proportions) were used directly in the dietary matrix.

Harvester ant diets were considered to be proportional to the relative frequency of occurrence of food items transported into the colony. As indicated for the other insects above, these proportions were used directly in the dietary matrix.

Robber fly diets were determined directly on the relative frequency of prey items which robber flies were observed eating.

Passerine bird diet data were derived from crop analysis. The items in the crop were separated into taxonomic categories and weighed to determine the proportions of the diet which each category represented.

Diets of owls and Golden Eagles were determined from the analysis of regurgitated pellets found in or near active nests. The proportions of the diet were based on weight-corrected estimates of the contents of these pellets. Swainson's Hawk and Ferruginous Hawk diets were based on frequency of prey items appearing in the litter in or near active nests. The species observed were assigned weights per individual based on the experience of the observer. These weights were then multiplied by the respective frequencies to yield proportions of the diet.

RESULTS AND DISCUSSION

The major objective, and result, of this exercise is a dietary composition matrix (Table 2). As mentioned in the introduction, we have lumped beetles at the ordinal level while considering other similar organisms at the species level (e.g., certain grasshoppers). There is no logically consistent rationale for this other than the adequacy of sample size and a presumed importance in the overall process. The matrix consists of elements representing the proportion of 112 consumed groups in the 1970 summer diet of 36 consumer groups. For simplicity, the elements have been rounded to the nearest one percent, and thus dietary items constituting less than one-half of one percent have been excluded. Footnotes describing the data source and peculiarities constitute a table in themselves and are given as such (Table 3), while the code names listed in the matrix are given along with their common and scientific name equivalents in Table 1.

Despite the depauperate number of non-zero elements in the matrix (413 ≈ 10% of potential), there exists a very high degree of overlap between certain consumers. To evaluate this, pairwise overlap values have been generated using a modification of Morisita's index (Horn, 1966). The matrix of overlap values is of the order 36 × 36 representing just the consumers and is triangular since the similarity of group 1 with group 2 is identical to that of group 2 with group 1 (Table 4).

Whereas a high degree of dietary similarity exists between certain groups, several important incongruities arise. First, since the dietary determinations were usually made on taxonomic grounds, more overlap may be reflected than actually exists in nature. For example, different consumers may utilize entirely different parts of the plant and therefore obviate competition, while a taxonomic classification of dietary items would show a high degree of overlap. Secondly, the diets of many groups shift from season to season, and an analysis of only one season's data probably does not fairly represent the mean annual relations. Seemingly of much greater importance is the strikingly different biomass density of the various consumers and their highly variable consumption rates. Whereas cattle and bison only consume about 3% (dry forage) of their body weight per day, certain insect groups may consume two orders of magnitude more per unit body weight (i.e., 3 × body wt) per day (Waldbauer, 1967).

To provide a perspective on these latter two points, several ancillary vectors are provided (Table 5). One is a vector of biomass density believed to occur on the area. These elements represent our best estimate based upon the data at hand and our empirical conclusions where no data exist. A second vector of approximate consumption rates has been compiled largely from

Table 4. Pairwise dietary-overlap matrix of the 36 consumer groups considered in this report. Index limits are 0.0 and 1.0, with zero representing no commality of dietary species and 1.0 implying identical dietary proportions of all food items.

	Dietary Overlap Matrix of 36 Consumer Groups																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
(1) ANTELOPE	1.0																																			
(2) CATTLE	.34	1.0																																		
(3) SHEEP	.61	.85	1.0																																	
(4) BISON	.26	.92	.74	1.0																																
(5) BLACK-TAILED JACKRABBIT	.15	.29	.24	.27	1.0																															
(6) WHITE-TAILED JACKRABBIT	.13	.37	.33	.41	.64	1.0																														
(7) GRASSHOPPER--OPOB	.19	.74	.58	.86	.15	.14	1.0																													
(8) GRASSHOPPER-TRKI	.18	.73	.57	.86	.15	.14	1.0	1.0																												
(9) GRASSHOPPER--PSDE	.18	.73	.57	.85	.14	.14	1.0	1.0	1.0																											
(10) GRASSHOPPER--ARPS	.21	.87	.73	.91	.20	.24	.91	.91	.91	1.0																										
(11) GRASSHOPPER--MEIN	.00	.26	.24	.28	.22	.65	.01	.00	.01	.22	1.0																									
(12) INSECTS--BEETLES	.08	.21	.22	.14	.04	.04	.10	.09	.09	.11	.01	1.0																								
(13) INSECTS--FLIES, MOSQUITOS	.03	.00	.10	.00	.00	.01	.00	.00	.00	.00	.00	.84	1.0																							
(14) INSECTS--TRUE BUGS	.12	.22	.26	.20	.07	.11	.14	.14	.14	.17	.05	.86	.86	1.0																						
(15) INSECTS--LEAFHOPPERS, APHIDS, ETC.	.26	.56	.48	.54	.24	.41	.36	.35	.35	.42	.23	.68	.51	.66	1.0																					
(16) INSECTS--ANTS	.13	.06	.12	.04	.02	.04	.02	.02	.02	.02	.00	.45	.36	.34	.44	1.0																				
(17) INSECTS--BUTTERFLIES	.02	.07	.09	.08	.02	.04	.06	.06	.06	.06	.00	.44	.42	.42	.45	.72	1.0																			
(18) INSECTS--THRIPS	.25	.88	.69	.96	.22	.26	.90	.88	.88	.90	.09	.16	.04	.23	.56	.12	.18	1.0																		
(19) NORTHERN POCKET GOPHER	.56	.35	.56	.32	.24	.36	.18	.18	.17	.21	.24	.11	.03	.28	.26	.14	.03	.26	1.0																	
(20) ORD'S KANGAROO RAT	.03	.08	.06	.08	.11	.05	.08	.08	.08	.08	.00	.01	.00	.02	.04	.00	.01	.09	.02	1.0																
(21) HARVESTER ANTS	.03	.02	.00	.02	.01	.02	.00	.00	.00	.00	.00	.06	.00	.04	.08	.01	.01	.01	.06	.00	1.0															
(22) HORNED LARK	.01	.00	.01	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.01	.00	.00	1.0														
(23) LARK BUNTING	.00	.00	.00	.00	.02	.02	.00	.00	.00	.00	.00	.00	.00	.00	.00	.02	.00	.00	.00	.00	.00	.50	1.0													
(24) McCOWN'S LONGSPUR	.00	.00	.00	.01	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.01	.00	.00	.01	.00	.02	.48	.94	1.0												
(25) CHESTNUT-COLLARED LONGSPUR	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.35	.61	.70	1.0											
(26) ROBBER FLIES	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.52	.44	.42	.26	1.0										
(27) THIRTEEN-LINED GROUND SQUIRREL	.17	.25	.24	.22	.11	.09	.16	.16	.16	.20	.03	.06	.02	.08	.18	.06	.04	.22	.14	.32	.00	.24	.71	.68	.37	.21	1.0									
(28) DEER MOUSE	.09	.04	.06	.02	.16	.06	.02	.02	.02	.02	.00	.01	.01	.01	.02	.02	.00	.02	.08	.56	.00	.15	.48	.46	.26	.15	.87	1.0								
(29) NORTHERN GRASSHOPPER MOUSE	.06	.08	.08	.08	.04	.04	.08	.08	.08	.08	.01	.01	.00	.02	.04	.01	.01	.08	.06	.06	.00	.41	.78	.76	.52	.25	.74	.57	1.0							
(30) GREAT HORNED OWL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	1.0						
(31) BURROWING OWL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.02	.06	.06	.03	.02	.05	.04	.06	.74	1.0					
(32) LONG-EARED OWL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.94	.83	1.0				
(33) BARN OWL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.25	.44	.41	1.0			
(34) GOLDEN EAGLE	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.35	.28	.35	.10	1.0		
(35) FERRUGINOUS HAWK	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.40	.39	.46	.34	.87	1.0	
(36) SWAINSON'S HAWK	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.20	.26	.37	.72	.12	.44	1.0

Table 5. Vectors of the major aboveground consumers on the Pawnee shortgrass range and their estimated summer density and consumption rates. Density estimates are derived from Grassland Biome data sets and personal communication with many investigators. Food consumption rates were derived by applying interspecies homeotherm requirement equation (2) 70 $kg^{0.75}$ (Craighead and Craighead, 1969, and personal communication).

Consumer Group	Number (N/ha)	and Individual Wt (kg)	Density (kg/ha) Wet Wt	Dry Food Consumption (kg/kg/day)	Amount Transferred (kg/ha/day)	Active Days/Year	Amount Transferred (kg/ha/yr)	Percent of Total Transfer
Antelope	.012	4.5×10	0.520	.04	0.208	365	75.920	12.6
Cattle, sheep, and bison	.082	4.5×10^{2}	37.333	.03	1.120	365	408.800	68.1
Jackrabbits	.058	6.0×10^{-1}	0.035	.04	0.001	365	.365	0.1
Rodents	4.50	5.4×10^{-2}	0.243	.06	0.015	325	4.875	0.8
Passerine birds	3.450	3.8×10^{-2}	0.132	.10	0.013	365	4.745	0.8
Raptors	3.2×10^{-2}	7.4×10^{-1}	0.003	.04	0.000	365	0.046	0.0
Grasshoppers	1.7×10^{4}	2.8×10^{-5}	0.487	.60	0.292	180	52.574	8.8
Beetles	3.3×10^{4}	1.2×10^{-5}	0.390	.60	0.234	180	42.120	7.0
Leafhoppers	2.6×10^{4}	1.5×10^{-6}	0.040	.60	0.024	180	4.432	0.7
Ants	5.0×10^{4}	1.2×10^{-6}	0.060	.60	0.036	180	6.480	1.1
							$\Sigma = 600.357$	

the literature. The element-by-element multiplication of these two vectors is given as a vector of amounts of dry food consumed per day, per consumer group.

Multiplication of this vector by the number of active days per year for each group considered yields a final vector of amounts of dry food consumed per year. Summation of these and division of each element by the total reflects upon the importance of each group relative to the whole.

The major points of discussion regarding this exercise have been alluded to or explicitly stated above. The first point is in defense of the approach. We do not think the mass, energy, or nutrient flow concepts are necessarily any better than several other approaches; however, it logically follows from the classical food web approach. We do not believe that a group's importance or "role" in the total functioning system is necessarily reflected by its percentage of total transferral. It cannot be denied, however, that this type of exercise is important from the production-ecology or pedagogical standpoints.

Another major point of concern involves the much larger question of whether or not the whole gamut of consumption is important in ecosystems. We do not wish to address this point except to say that until man satiates his desire for certain proteins, it is! Secondly, if the aboveground net primary production figure of 1420 kg/ha is accepted (Sims and Singh, 1971), it will be noted that the consumer groups listed consume over 40% of the net production since a very high percentage of the consumption listed is primary productivity.

We have not included belowground consumers in our consideration, and we do not know if their importance below ground is greater or less than that of those above ground. Some would argue that it is greater.

Finally, a major motive for the exercise was to illustrate the primordial nature of our knowledge. Reiterating incongruities; the data were collected in different years, in different areas, and by grossly different methods. We have little, if any, appreciation of the data accuracy or precision, and we have no numbers on many groups. The food consumption rates of the invertebrates are largely speculative and clearly need serious study.

Despite the incongruities and lack of certain data, we are convinced of the efficacy of this process type analysis vs. the more classical disciplinary approach. We are begging a verification or refutation of these figures.

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