5-1988

Acquisition of Forgaging Skills by Lambs Eating Grass or Shrub

Enrique R. Flores
Utah State University

ACQUISITION OF FORAGING SKILLS BY LAMBS EATING GRASS OR SHRUB

by

Enrique R. Flores

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

of

DOCTOR OF PHILOSOPHY

in

Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1988

DEDICATION

To the memory of my father, the late Enrique.

ACKNOWLEDGEMENTS

A very special thanks is extended to Dr. Frederick Provenza for his patience, guidance and comments that provided the inspiration and culmination of this dissertation. To the Agricultural State University of La Molina for financial assistance and a leave of absence provided during my program.

Acknowledgement is made to the constructive comments and guidance provided by Dr. David Balph. A grateful thanks is also made to Dr. John Malechek, Dr. Ben Norton and Dr. Dave Turner of my Graduate Committee for their support in fulfilling this assignment. To the U. S. Sheep Experiment Station for their cooperation and for providing livestock.

To my mother for her moral and emotional support, I extend a son's gratitude.

Sincere appreciation goes to Debbie Brunson for preparing the final draft of this manuscript.

Finally to Lucrecia Aguirre for her patience and care that was so heartily given throughout this program.

Enrique Flores

TABLE OF CONTENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Acquisition of Forgaging Skills by Lambs
Eating Grass or Shrub

by

Enrique R. Flores, Doctor of Philosophy
Utah State University, 1988

Major Professor: Dr. Frederick D. Provenza
Department: Range Science

I studied the acquisition of foraging skills by lambs eating shrub or grass in three experiments. The general approach was to isolate those skills involved in prehending forage from those related to the acceptance of novel foods. Treatment lambs received 15 times more exposure to grass or shrub than did control lambs. Lambs were tested in 2.5 x 2.5 meter monocultures of shrub or grass 5 min/d, on two separate occasions. Height, bulk density and spatial arrangement of plant material were controlled during testing.

In Experiment 1, I studied the acquisition of foraging skills by lambs on monocultures of shrubs. I found that inexperienced lambs ingested less forage per unit time than experienced lambs because they had less developed prehension skills. Lambs were more successful at plucking individual leaves than breaking twigs from

branches or stripping leaves. Lambs emphasized prehension patterns that were most successful.

In Experiment 2, I explored the extent to which foraging skills gained on shrub or grass are specific to shrub or grass. Grass-experienced lambs were more successful at prehending and ingesting grass than were shrub experienced lambs. No statistical differences were observed between shrub- and grass-experienced lambs at prehending and ingesting shrub although numerical values were higher for shrub- than grass-experienced lambs. I hypothesize that a relationship exists between plant form, prehension pattern and foraging experience.

In Experiment 3, I studied the degree to which lambs experienced with grass or shrub vary in their ability to prehend and ingest vegetative and flowering grass. Grass- and shrub-experienced lambs ingested more flowering than vegetative grass per unit time. Grass-experienced lambs were more efficient than shrub-experienced lambs at prehending and ingesting vegetative and flowering grass. Shrub-experienced lambs experienced more difficulty at prehending flowering compared to vegetative grass while grass-experienced lambs did not.

(41 pages)

CHAPTER I

INTRODUCTION

Livestock production on rangelands is to a great extent a function of forage intake. Intake is a product of intake per bite, rate of biting and grazing time (Arnold and Dudzinski, 1978). Changes in these variables, as well as mastication and prehension, allow animals to compensate for changes in forage availability (Hodgson 1982).

Sward characteristics and prior experience affect forage intake. Considerable effort has been directed at investigating the relationship between forage structure and intake of grazing animals (Allden and Whitakker, 1970; Chacon and Stobbs, 1976; Hodgson, 1982; Black and Kenney, 1984; Penning, 1986). However, little research has been conducted to investigate the relationship between sward structure and the acquisition of foraging skills. This is probably in part due to difficulties associated with isolating the effects of experience and sward structure on intake rate, grazing time and prehension patterns.

My dissertation focuses on the development of foraging skills and the relationship between plant form and experience. I isolated the effects of experience from those of sward structure by comparing inexperienced and experienced animals on pastures of similar height, bulk density and spatial arrangement of plant material. I conducted

three experiments. Chapter I presents results of studies on the acquisition of foraging skills by lambs on monocultures of shrub. Chapter II explores the extent to which foraging skills gained on shrubs or, alternatively grass are specific to shrubs or grass. Chapter III compares the ingestive behavior of shrub- or grass-experienced lambs on monocultures of vegetative and flowering grass. Chapter IV presents conclusions and recommendations for future research.

CHAPTER II

ROLE OF EXPERIENCE IN THE DEVELOPMENT OF FORAGING SKILLS OF LAMBS BROWSING THE SHRUB SERVICEBERRY

Summary

I studied the development of foraging skills in lambs to better understand why sheep foraging in an unfamiliar environment ingest less forage per unit time than sheep familiar with the environment. I hypothesized that inexperienced sheep are less efficient foragers in part because they lack the skills necessary to efficiently prehend and ingest forage. Twenty twin-lambs were assigned to either a treatment (experienced) or a control (inexperienced) group. Experienced lambs received 15 times more exposure to the shrub Amelanchier alnifolia than inexperienced lambs. This experimental design allowed me to test three predictions that stem from my hypothesis.

Prediction 1: Experienced lambs harvest forage more efficiently than do inexperienced lambs as forage becomes more difficult to harvest. Results showed that inexperienced vs. experienced lambs did not differ in ability to ingest pelleted (38 vs. 36 g/min) or chopped (6.7 vs. 7.4 g/min) shrub, but experienced lambs were more efficient ($P<.05$) at foraging from entire plants (4.1 vs. 4.7 g/min) in pen trials for 2 min duration on 2 occasions.

Prediction 2: Experienced lambs ingest forage more quickly than inexperienced lambs. We found the intake rate of experienced lambs was higher ($P<.05$) than for inexperienced lambs (5.0 vs. 4.3 g/min). Inexperienced lambs took larger ($P<.05$) bites (0.20 vs. 0.16 g/bite), but this did not compensate for the lack of prehension skill.

Prediction 3: Experienced lambs have better developed prehension skills than inexperienced lambs. I found that although both groups used similar prehension patterns during pasture trials, inexperienced lambs were less ($P<.05$) successful than experienced lambs at obtaining food by breaking twigs (56 vs. 77% success), stripping leaves (65 vs. 77% success), and plucking individual leaves (81 vs. 89% success).

Introduction

Sheep (Arnold, 1970; Arnold and Maller, 1977; Gluesing and Balph, 1980), goats (Provenza and Malechek, 1986) and cattle (Hodgson, 1971: Hodgson and Jamieson, 1981) in unfamiliar environments spend as much as 20% more time foraging, and hence more energy (Osuji, 1974), but ingest as much as 40% less food than animals foraging on known foods in familiar environments. These differences persisted for as long as trials were conducted, in some cases 10 months (Arnold, 1970). As a consequence, livestock moved from familiar to unfamiliar foraging environments may be less productive (Provenza and Balph, 1988).

At least two factors are associated with lack of experience and foraging behavior. First, animals placed in a new environment may be reluctant to accept novel foods, and second they may lack the skills

necessary to efficiently harvest novel foods (Provenza and Balph, 1987, 1988). These factors are related in that harvesting skills cannot be achieved unless an animal accepts unfamiliar food. These factors are also confounded in field studies. However, the relative importance of these variables should be known before designing conditioning programs for livestock (Provenza and Balph, 1987, 1988). Exposure early in life apparently need not be long for food acceptance to occur (reviewed by Chapple and Lynch, 1986), but harvesting skills may require exposure of longer durations to develop (Provenza and Balph, 1987, 1988).

This study sought to isolate those skills involved in harvesting forage from those related to the acceptance of novel foods in order to determine whether or not foraging skills are learned. The approach was first to familiarize all lambs with the shrub Amelanchier alnifolia and then to give half of the lambs more extensive experience with A. alnifolia. It was not my goal to assess the amount of experience required to reach a maximum level of foraging efficiency. I then tested three predictions related to the hypothesis that inexperienced lambs are less efficient foragers than experienced lambs because they lack the skills necessary to efficiently prehend and ingest forage. The predictions are:

1) Experienced lambs harvest forage more efficiently in pens than inexperienced lambs as forage becomes more difficult to harvest.
2) Experienced lambs ingest more forage per unit time than inexperienced lambs when grazing.

3) Experienced lambs have better prehension skills than inexperienced lambs when grazing.

Materials and Methods

Ten range-experienced ewes, each with twin lambs, were used in this study. Lambs from each ewe were tagged at birth and randomly assigned to either a treatment (experienced) or a control (inexperienced) group. During the first 8 weeks of life, I restricted the dietary experience of the lambs to mother's milk, concentrate pellets, and alfalfa pellets. When the lambs were 2-3 months old, all were exposed for 10 minutes on two occasions with their mothers to Amelanchier alnifolia shrubs in pelleted, chopped, and whole form to familiarize them with the test food. Treatment lambs were subsequently exposed to A. alnifolia for 2 hr/d for 15 d in a 2.5 x 4.8 m pasture to gain foraging skills. The experimental area was prepared daily during training by placing shrubs growing in pots in 8 regularly-spaced positions. Exposures took place in the mornings after an overnight fast to insure the animals fed actively. I assumed that brief exposure to A. alnifolia with the mother was sufficient for control lambs to accept the shrub as food (Chapple and Lynch, 1986; Provenza and Balph, 1987, 1988), but too brief to develop the skills necessary to efficiently harvest forage from the shrub.

One week after the treatment lambs finished exposures, I conducted two trials to test foraging performance of all lambs. Trial 1 tested prediction 1, while trial 2 tested predictions 2 and

3. Except during trials, all animals remained in pens and were fed a maintenance ration of alfalfa pellets in the morning and evening.

Trial 1: Feeding Response to Harvesting Difficulty

Three structural classes of A. alnifolia, pellets (P), chopped branches with leaves (C), and entire plants (EP), were compared. Pellets were 1.2 cm long and 2.7 cm in diameter, chopped branches were 18 cm long and had an average of 8 leaves, and entire plants were 65 cm tall and had an average of 158 leaves. I assumed that the three forms represent an increasing gradient of harvesting difficulty. Sheep were offered a similar amount of forage for 2 min/d for 2 d in individual pens. After each 2-d period, the type of forage offered to individual animals was changed. The forage classes were given in increasing order of structural complexity, P-C-EP, to individual lambs early in the mornings after an overnight fast. Feeding efficiency was defined as the amount eaten per unit time. I used a paired T-test (Dowdy and Wearden, 1983) to compare feeding efficiency of control and treated lambs.

Trial 2: Ingestive Behavior on Pasture

Lambs' foraging skills were subsequently tested by offering A. alnifolia for 5 min/d on two days during the summer of 1986. Four similar plants were offered to lambs from both groups in a 2.5 x 2.5 m plot. The experimental area was prepared daily by placing the four potted plants in holes at regular intervals. Shrubs were considered similar if they had the same height, volume, and number of leaves. This procedure allowed me to control for differences in plant

architecture and leaf availability during testing. I used focal sampling (Altmann, 1974), the continuous observation of lamb's ingestive behavior, to determine bites per minute. Observations were taken from a distance of less than 1 m. Bite rate was then calculated from records of the total number of bites that occurred during a test. The difference between leaf and stem weight before and after browsing was used to estimate the amount ingested. The weight of leaf material ingested was determined by multiplying the number of leaves harvested by the average weight per leaf. Stem consumption was estimated using a regression equation that related twig weight (W) to twig diameter at the browsing point (D) ($\log W = -1.93 + 3.55 \log D$; $R^2 = 0.97$). Intake per bite was the ratio of intake rate (g/min) to bite rate (bites/min). Analysis of variance was used to detect differences in bite rate, bite size, leaf:stem ratios, and intake rate. There were 10 blocks (ewe with 2 lambs) and two treatments (experienced vs. inexperienced) and each trial was repeated twice.

Three prehension modes were examined: plucking individual leaves, breaking twigs (i.e. gripping a branch with the teeth while moving the head forward and backward), and stripping leaves (removing leaves by running branches through the mouth). The prehension behavior of each lamb was recorded for randomly selected bites until 30 prehension events were completed (Scheaffer et al., 1979). The success or failure of each prehension attempt was also recorded. Successful attempts were those that resulted in the harvest of one or more leaves or twigs. Discriminant analysis (Afifi and Clark, 1984)

was used to determine whether or not there were differences in prehension skills, bite rate, and intake per bite between control and treatment lambs.

Results

Trial 1: Feeding Response to Harvesting Difficulty

A lamb's ability to ingest pelleted or chopped A. alnifolia was not affected by prior experience with whole plants (Table 1). Experienced lambs were more ($P<.05$) efficient at foraging from entire plants than inexperienced lambs. This result is in general agreement with our first prediction that experienced lambs harvest forage more efficiently than inexperienced lambs as forage becomes more difficult to harvest.

Table 1. Intake rate (g/min) by lambs of serviceberry shrubs in pelleted, chopped, or entire form.

Lambs	Pellet	Chopped	Entire
Inexperienced	37.5[a]	6.7[a]	4.1[a]
Experienced	35.9[a]	7.4[a]	4.7[b]

[ab]Means for inexperienced and experienced lambs followed by a different letter are different ($P<.05$).

Trial 2: Ingestive Behavior on Pasture

Experienced lambs consumed more ($P<.05$) forage per unit time than inexperienced lambs and maintained a more rapid rate of biting

than inexperienced lambs (Table 2). Inexperienced lambs increased bite size ($P<.05$), but this increase did not compensate for less prehension skill. Leaf:stem ratios were not affected by prior experience ($P>.05$). These findings agree with our second prediction that experienced lambs ingest more forage per unit time than inexperienced lambs.

Table 2. Bite rate, bite size, leaf:stem ratio, and intake rate for lambs with differing amounts of experience browsing the shrub serviceberry.

Lambs	Bite Rate (bites/min)	Bite Size (g)	Leaf:Stem	Intake Rate (g/min)
Inexperienced	24[a]	0.20[a]	14.3[a]	4.3[a]
Experienced	33[b]	0.16[b]	14.6[a]	5.0[b]

[ab]Means for inexperienced and experienced lambs followed by a different letter are different ($P<.05$).

Experienced and inexperienced lambs used similar prehension strategies (Fig. 1). Plucking individual leaves was the primary feeding mode, followed by breaking twigs and stripping leaves. Lambs in both groups experienced higher probability of failure when they attempted to break twigs and strip leaves than when they plucked individual leaves. However, inexperienced lambs were less ($P<0.05$) successful than experienced lambs at breaking twigs (56 vs. 77% success), stripping leaves (65 vs. 77% success), and plucking individual leaves (81 vs. 89% success). These data are consistent

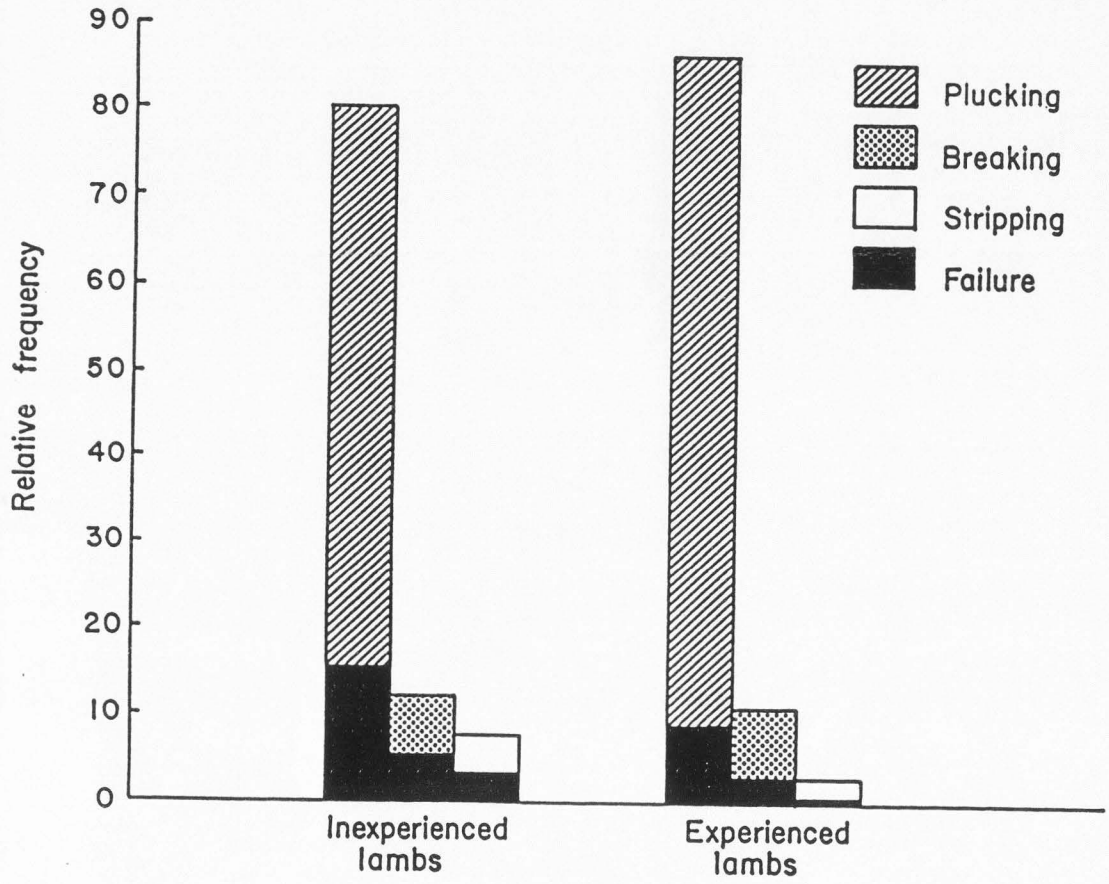

Figure 1. Prehension patterns of lambs with differing amounts of experience browsing the shrub serviceberry.

with the third prediction that experienced lambs have better developed prehension skills.

Discriminant analysis classified experienced and inexperienced lambs differently based on bite rate and prehension skills (Fig. 2). The unstandardized discriminant function was: treatment group = 3.66 - .17 (bite rate) + .19 (stripping with success, %) + .30 stripping with failure, %). Values for canonical variables ranged from -2.5 to 0 for experienced lambs and from .5 to 4.0 for inexperienced lambs. The lower the canonical value the more skillful lambs were at prehending and ingesting forage. Two inexperienced lambs (10%) were classified as experienced lambs by the discriminant analysis. However, canonical values for the two inexperienced lambs were only equal to those of the least skillful of the lambs in the experienced treatment group. Thus, the results of the discriminant analysis support predictions two and three concerning the effect of prior foraging experience on bite rate and prehension skills.

Discussion

The results generally support the three predictions. The only exception was that it was assumed the difficulty encountered eating chopped shrub would correspond to differences in harvesting performance between experienced and inexperienced lambs. Hodgson (1971) found calves that had ingested chopped hay before weaning subsequently ingested chopped hay more rapidly than those that had not eaten hay. This difference in the performance of sheep and cattle may reflect morphological differences in prehension ability.

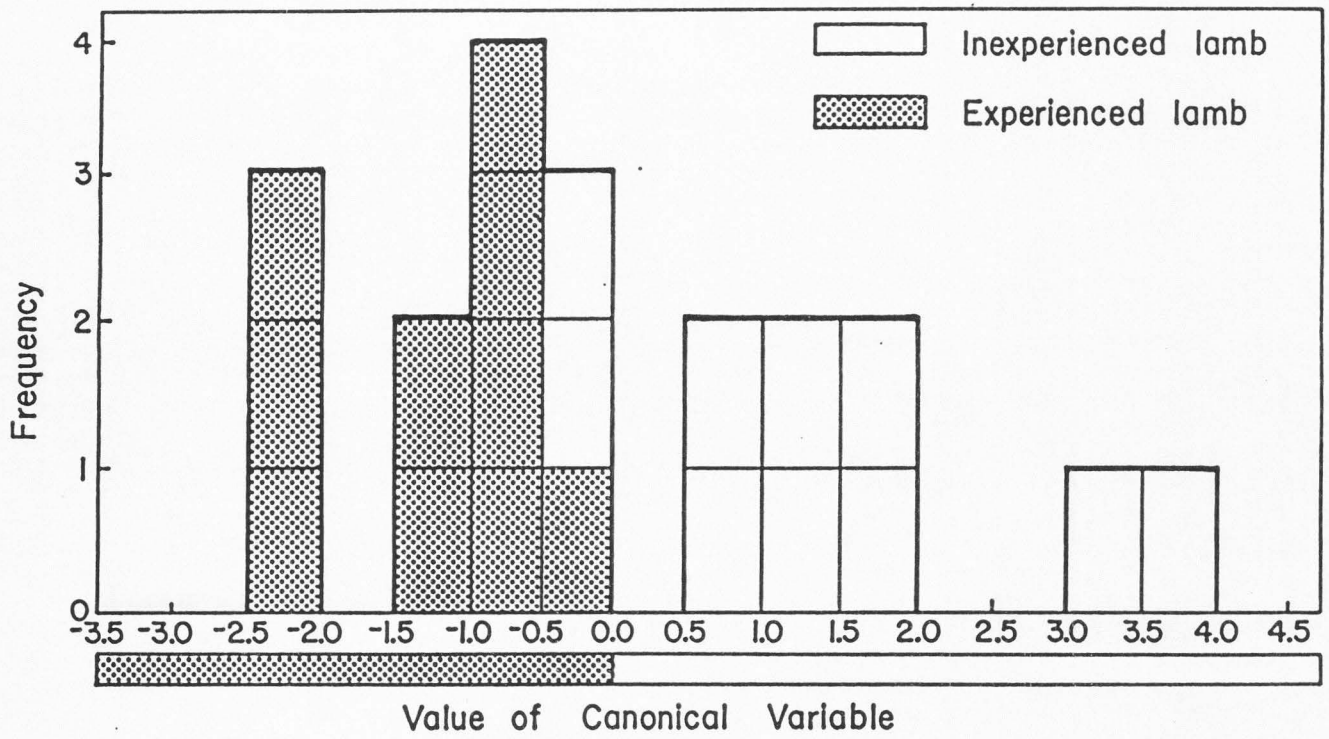

Figure 2. Classification of lambs as experienced or inexperienced by discriminant analysis on the basis of bite rate and prehension skills when foraging on the shrub serviceberry.

Large tongue size and lack of tongue mobility may decrease the ability of cattle to prehend (Leight, 1972) and ingest chopped forage, whereas even unskilled lambs experienced no difficulty prehending chopped material.

Experience improves the precision and timing required to perform tasks involving motor skills (Singer, 1980). Lambs with experience were more successful at prehending forage than inexperienced lambs (Fig. 1). Failure to prehend forage reduces the amount harvested per unit feeding time unless animals can adjust feeding behavior. Increasing bite size and biting rate are among the main behavioral mechanisms grazing animals use to adjust to changes in availability and structure of forage (Arnold and Dudzinski, 1978; Hodgson, 1982). Inexperienced lambs increased bite size (Table 2), but this did not prevent a significant reduction in ingestion rate.

Inexperienced and experienced lambs selected diets that contained similar proportions of leaf and stem (Table 2). Plucking leaves was the primary mode of feeding for inexperienced and experienced lambs. Breaking twigs, which increased the amount of stem harvested per bite, was a prehension pattern used infrequently by lambs (Fig. 1).

The physical characteristics of A. alnifolia allowed lambs to exercise all prehension modes. This may not be the case with other shrubs. Goats foraging on Coleogyne ramosissima consumed the leaves with the twigs, probably because leaves were small, about 10 mm long and 2 mm wide (Provenza and Malechek, 1986). This suggests that the

prehension behavior of lambs is also influenced by the physical characteristics of the forage.

In conclusion, I believe the results are consistent with the hypothesis that experienced lambs are more skilled at harvesting forage than inexperienced lambs. Experienced lambs, therefore, should expend less time and energy to meet intake requirements (Arnold, 1970; Arnold and Maller, 1977).

CHAPTER III

ON FORAGING SKILLS OF LAMBS EXPERIENCED WITH GRASS OR SHRUB

Summary

Livestock that are moved from one area to another often are required to forage on plants with different life forms. The degree to which experience foraging on one plant form affects foraging performance on another plant form is unknown. The foraging skills of grass- vs. shrub-experienced lambs was compared on monocultures of mature crested wheatgrass (Agropyron cristatum x Agropyron desertorum) and the shrub serviceberry (Amelanchier alnifolia). Grass-experienced lambs were more successful ($P<.05$) at prehending (99% vs. 85% success) and ingesting (4.6 vs. 3.7 g/min) grass than shrub-experienced lambs. Grass bite rate (16 vs. 14 bites/min) and bite size (.30 vs. .28) were also greater but insignificantly so ($P<.05$). Conversely, shrub-experienced were numerically, but not statistically ($P>.05$) more successful than prehending (93% vs. 86% success) and ingesting (5.0 vs. 4.5 g/min) shrub. Shrub-experienced lambs had a higher ($P<.05$) bite rate (26 vs. 20 bites/min) than grass-experienced lambs when ingesting shrub, but bite size (.20 vs. .23 g/bite) was similar ($P<.05$). I conclude that the skills acquired by foraging on one plant form are to an important extent specific to that plant form. However, grass-experienced lambs foraging on shrubs

were aided more than shrub-experienced lambs foraging on grass by their respective experiences.

Introduction

Livestock often forage on rangelands dominated by either grasses or shrubs. Animals with experience foraging on shrubs (Flores et al., 1988a) or grass (Hodgson, 1971) develop better prehension skills for the plants they eat, and as a result ingest more forage per unit time than do naive animals. Unknown, however, is how the experience of foraging on one plant form affects foraging performance on another plant form. I explored this question by comparing the harvesting behavior of animals that differed in experience with different plant forms. The objective was to determine if harvesting ability acquired during foraging on either grass or shrub is to a significant extent specific to that plant form. My approach was first to familiarize lambs with both grass and shrubs and then to give the animals more extensive experience foraging on either grass or shrub. I then compared the grass- and shrub-experienced lambs skills' at prehending and ingesting both grass and shrub.

Material and Methods

Twin lambs from each of 10 range-experienced ewes were tagged and randomly assigned to either a grass (Hycrest crested wheatgrass, Agropyron cristatum x A. desertorum) or shrub (serviceberry, Amelanchier alnifolia) treatment at 7 wk of age. During the first 7 wk of life, lambs were restricted to mother's milk, concentrate

pellets and alfalfa pellets. When lambs were 8 wk old, all were exposed for 10 min on four occasions with their mothers to grass and shrub to familiarize them with both plant forms. Lambs were subsequently exposed either to grass or shrub monocultures for 2 hr/d for 15 d in small pastures. Exposures occurred in the mornings after an overnight fast to insure that the animals would forage actively.

One week after the lambs finished the exposures, trials were conducted on monocultures of shrub and grass. Trials lasted 5 min/d and were conducted twice during the summer of 1987. The experimental area was prepared daily during testing by placing four potted plants in holes at regular intervals in a 2.5 x 2.5 m plot. Plants of similar architecture were offered to both experimental groups (Fig. 3). Shrubs were considered similar if they had the same volume, height and number of leaves. Grasses were similar if they had the same basal area, height and number of tillers. This procedure allowed me to control for bulk density, height and forage availability during testing. Except during trials, all animals remained in pens and were fed a maintenance ration of alfalfa pellets.

Ingestive Behavior During
Trials on Grass

Hycrest crested wheatgrass plants had an average 50 tillers, of which 25% were flowering. The remaining vegetative tillers were 30 cm tall and their internodes had elongated. Available forage before grazing was estimated by multiplying the number of tillers and the average weight per tiller. Fifteen percent of the tillers from each

Figure 3. Flowering hycrest creasted wheatgrass (left) and the shrub serviceberry (right) drawn to a scale of 1/4.

plant were selected at random, clipped and weighed to assess average weight per tiller. Dead tillers were removed. The amount of forage remaining after each trial was determined by clipping plants to a height of 5 cm and weighing the forage that was removed. The difference in forage weight before and after grazing was used to estimate grass ingestion. Two observers recorded the ingestive behavior of the experimental lambs. One recorded the total number of bites, the other recorded prehension patterns. Bite rate was then calculated from records of the total number of bites that occurred during a test. Intake per bite was calculated as intake rate (g/min) divided by bite rate (bites/min).

Two prehension modes were observed: jerking (gripping tillers with the teeth while jerking the head forward or backward) and chewing (removing the tillers by biting with the teeth). The prehension behavior of each lamb was recorded for randomly selected bites until 15 prehension events were completed (Scheaffer et al. 1979). The success or failure of each prehension attempt was also recorded. Successful attempts were those that resulted in the harvest of one or more tillers.

Ingestive Behavior During Trials on Shrub

Sampling procedures to characterize the lamb's ability to prehend and ingest serviceberry were similar to those used when lambs were on crested wheatgrass. Shrubs were 60 cm tall and had an average of 200 leaves. The difference between leaf and stem weight before and after browsing was used to estimate the amount ingested.

The weight of leaf material ingested was determined by multiplying the number of leaves harvested by the average weight per leaf. A regression model (log W = -2.07 + 3.72 log D; r^2 = .98; where W = twig weight and D = diameter at the browsing point) was developed to estimate twig consumption. Three prehension patterns were observed: plucking individual leaves, breaking twigs and stripping leaves of branches (Flores et al. 1988a).

Statistical Analysis

Bite rate, bite size and intake rate were subject to least square analysis of variance utilizing a split block design (ewe with two lambs) to test for the main effect of treatment (grass-experienced lambs vs. shrub-experienced lambs) and the subplot effect of day (Montgomery, 1983). Discriminant analysis was used to determine the degree of similarity between the prehension skills of both experimental groups (Afifi and Clark, 1984).

Results

Grass-experienced lambs when tested on grass had higher bite rates and larger bite sizes than shrub-experienced lambs, but the differences were not statistically significant (Table 3). However, grass-experienced lambs ingested grass faster ($P<.05$) than shrub-experienced lambs. Grass-experienced lambs were also more successful ($P<.05$) at jerking tillers than shrub-experienced lambs (99% vs. 85% success: Fig. 4). Chewing tillers, a feeding mode that was seldom successful, was more common ($P<.05$) among shrub- than grass-experienced animals. The discriminant analysis indicated that the

similarity between lamb's ability to jerk tillers successfully was 24%.

Table 3. Bite rate, bite size and intake rate of grass- and shrub-experienced lambs foraging on hycrest crested wheatgrass and the serviceberry shrub.

Lambs	Bite Rate (bites/min)	Bite Size (g)	Intake Rate (g/min)
Test on Grass			
Grass experienced	16[a]	.30[a]	4.6[a]
Shrub experienced	14[a]	.28[a]	3.7[b]
Test on Shrub			
Grass experienced	20[a]	.23[a]	4.5[a]
Shrub experienced	26[b]	.20[a]	5.0[a]

[a,b]Means for grass and shrub-experienced lambs followed by a different letter are different ($P<.05$).

Shrub-experienced lambs foraging on shrubs had higher bite rates ($P<.05$), but numerically smaller bite sizes ($P<.05$), than grass-experienced lambs (Table 3). Intake rate was numerically, but not statistically ($P>.05$), greater for shrub- than for grass-experienced lambs. Likewise, shrub- and grass-experienced lambs were equally successful ($P>.05$) at prehending shrub material, although the mean for shrub-experienced lambs was numerically higher than that for grass-experienced lambs (93% vs. 86% success; Fig. 4). The similarity between the prehension success of both groups of lambs when foraging on shrub was 36%.

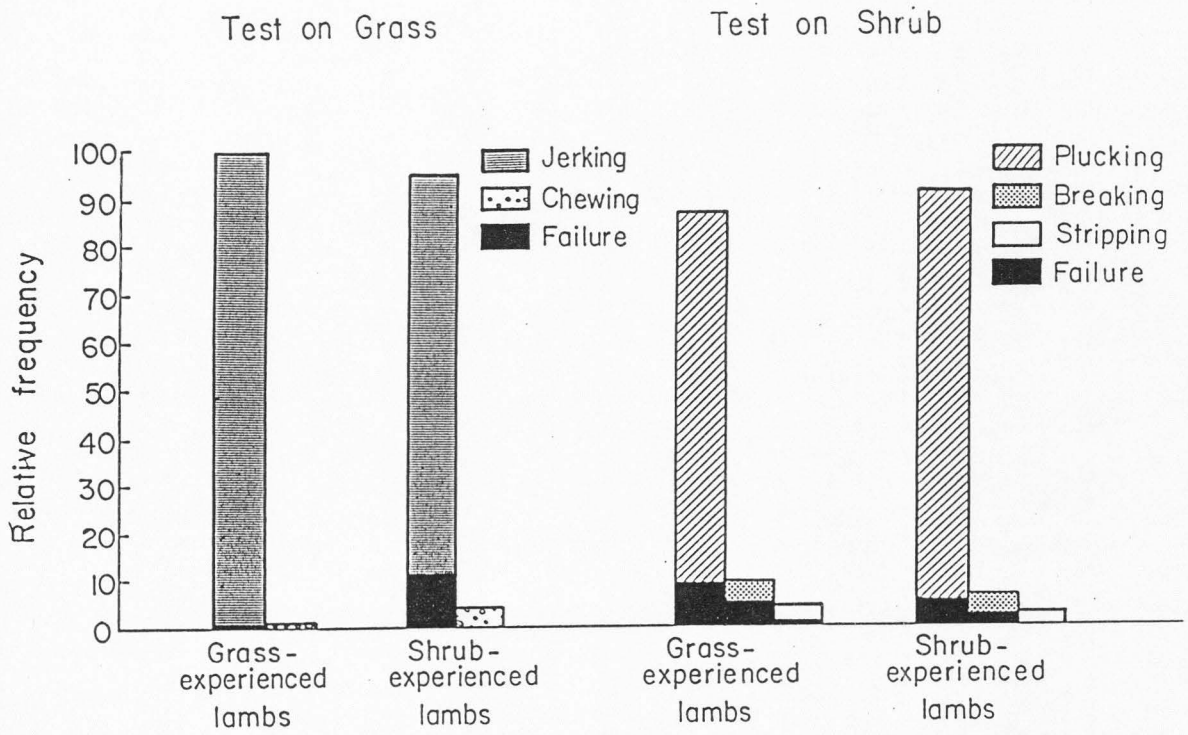

Figure 4. Prehension patterns and failures of lambs with differing amounts of grass and shrub experience foraging on hycrest crested wheatgrass or serviceberry shrub. Grass-experienced lambs were more ($P<.05$) successful at prehending grass than shrub-experienced lambs. Shrub- and grass-experienced lambs were equally ($P>.05$) successful at prehending shrub.

Discussion

There are a variety of prehension patterns and head orientations associated with harvesting forage. Different plant forms necessitate, to varying degrees, different motor patterns in their harvest (Fig. 1). I hypothesize that animals learn the head movements and orientations appropriate for efficiently prehending forage from a particular plant form. This hypothesis is supported by the fact that grass-experienced lambs were more successful ($P<.05$) at prehending grass tillers than shrub-experienced lambs (99% vs. 85%; Fig. 4), and the fact that shrub-experienced lambs maintained higher bite rates ($P<.05$) while plucking shrub leaves than grass-experienced lambs (26 vs. 20 bites/min; Table 3). Moreover, shrub-experienced lambs were more successful than grass-experienced lambs at plucking shrub leaves (96% vs. 91%), though insignificantly ($P>.05$) so.

Some prehension patterns may require more experience than others because they involve more complex motor patterns and greater neck and jaw strength. I hypothesize that breaking and jerking require more experience than plucking. This hypothesis is based on several lines of evidence. Breaking was a prehension pattern used infrequently by lambs (Fig. 4, Flores et al. 1988a), suggesting breaking requires more skills than plucking. Moreover, a greater probability of failure was associated with breaking twigs than plucking leaves for shrub-experienced (47% vs. 4% failure) and grass experienced (54% vs. 9% failure) lambs (Fig. 4; Flores et al. 1988a). Likewise, jerking may require more experience than plucking. Grass-experienced lambs were relatively more ($P<.05$) successful at jerking grass tillers than

shrub-experienced lambs (99% vs. 85% success), while shrub- and grass-experienced lambs were equally ($P>.05$) successful at plucking shrub leaves (96% vs. 91% success).

The ingestion rates of 5.0 g/min for the shrub-experienced lambs eating shrub is similar to that of 4.6 g/min for grass-experienced lambs eating grass (Table 3). However generalizations concerning potential intake rates of shrubs and grasses are difficult to make because factors such as plant form, prehension pattern and prior experience interact to determine intake rate (Flores et al. 1988a). Moreover, potential intake rates vary within plant species as a result of phenology (Dougherty et al. 1988).

I believe a relationship exists between plant form, prehension pattern and foraging experience. The less (more) similar plant species are in form the less (more) prehension skill is transferable, and the more (less) difference there will be in the performance of experienced and inexperienced animals. I believe the relationship between plant form and experience provides at least a partial explanation for the fact that grass-experienced lambs were relatively more successful at plucking shrub leaves than were shrub-experienced lambs at jerking grass tillers.

Finally, an important constraint on foraging is the extent to which animal morphology is matched to feeding on a particular plant form. An animal with a small mouth may have less difficulty plucking leaves from a shrub than jerking tillers from a mature grass because of the size, shape and movement potential of its mouth. I suggest mouth size and movement potential also helps explain the fact that

grass-experienced lambs were more skilled at foraging on shrub than those experienced with shrub were at foraging on grass.

CHAPTER IV

RELATIONSHIP BETWEEN PLANT PHENOLOGY AND FORAGING EXPERIENCE OF LAMBS GRAZING HYCREST CRESTED WHEATGRASS

Summary

I compared the ingestive behavior of shrub- and grass experienced lambs on monocultures of vegetative and flowering grass (Agropyron cristatum x Agropyron desertorum) to test the prediction that lambs experienced with different plant forms should vary in their ability to harvest different phenological stages of the same plant species. A split block design was used to test for the main effects of phenology and experience and their interaction. The results support the prediction. (1) Phenology: bite size (.29 vs. .10 g/bite) and intake rate (4.2 vs. 3.3 g/min) were higher ($P<.01$) while bite rate (15 vs. 33 bites/min) was lower ($P<.01$) for lambs grazing flowering compared with vegetative grass. (2) Experience: Grass-experienced lambs ingested grass faster ($P<.05$) than shrub-experienced lambs (4.1 vs. 3.4 g/min). Grass-experienced lambs had numerically higher bite rates (25 vs. 24 bites/min) and took larger bites (.21 vs. 18 g/bite) but differences were not statistically significant ($P>.05$). (3) The interaction between plant phenology and experience was not significant ($P>.05$). Grass-experienced lambs were more efficient ($P<.05$) at ingesting both vegetative (3.6 vs. 3.0 g/min) and flowering (4.6 vs. 3.7 g/min) grass than shrub-experienced

lambs. Shrub-experienced lambs failed more ($P<.05$) at prehending flowering vs. vegetative grass (16% vs. 5%) while grass-experienced did not (1.2% vs. 1.4%). I conclude that flowering grass was more difficult for lambs to harvest than vegetative grass but these differences were offset by prior experience foraging on grass.

Introduction

Growing evidence suggests that experience is important in the development of foraging skills of lambs. For example, lambs experienced at foraging on shrubs harvest shrubs more efficiently than those without such experience (Flores et al. 1988a). In addition, harvesting skills acquired while foraging on shrubs or grass are relatively specific to the particular shrubs or grass (Flores et al. 1988b). This led me to predict that lambs experienced with different plant forms should vary in their ability to harvest different phenological stages of the same plant species if the stages differ in form. This paper presents results of a study that compared the ingestion rate and prehension success of shrub- and grass-experienced lambs foraging on vegetative and flowering stages of hycrest crested wheatgrass.

Materials and Methods

Twin lambs 8 wk age, each from 10 range experienced ewes, were used in the study. Lambs from each ewe were exposed to either flowering grass (hycrest crested wheatgrass, Agropyron desertorum x Agropyron cristatum) or shrub (serviceberry, Amelanchier alnifolia)

for 15 d. Lambs were exposed in monocultures of grass or shrub for 2 hr/d. Exposures occurred in the mornings after an overnight fast to insure animals foraged actively. One week after lambs finished exposures, tests were conducted on monocultures of vegetative and flowering grass. Lambs from the shrub group were exposed to both grass forms with their mothers for 10 min/d on four occasions one week prior to testing to familiarize them with test plants. Except during trials, all animals remained in pens and were fed a maintenance ration of alfalfa pellets.

Lambs were tested for 5 min/d twice during Spring of 1987. The test area was prepared by locating potted plants in four regularly spaced holes in a 2.5 x 2.5 m plot. Grasses of similar height and bulk density were offered to lambs to control for differences in plant architecture. Vegetative plants had an average 28 tillers. On average tillers were 17 cm tall and had 4.5 leaves (Fig. 5). Flowering plants averaged 50 tillers of which 25% were flowering (Fig. 5). Flowering tillers were 46 cm tall. The remaining vegetative tillers were 32 cm tall.

Two observers recorded the ingestive behavior of the lambs from a distance of less than 1 m. One recorded the total number of bites, the other recorded prehension patterns. Bite rate was calculated from records of the total number of bites that occurred during a test. Grass intake was the difference in forage weight before and after grazing (Flores et al. 1988b). Intake per bite was then calculated as intake rate (g/min) divided by bite rate (bites/min). The success or failure at jerking (gripping tillers with the teeth

Figure 5. Flowering (left) and vegetative (right) hycrest crested wheatgrass plants (scale 1/4).

while jerking the head up and backward) was also recorded for randomly selected bites until 30 prehension events were completed. Successful attempts were those that resulted in the harvest of one or more tillers. Least square analysis of variance utilizing a split block design was used to test for main effects of phenology and experience, and their interaction (Montgomery 1983).

Results

Plant phenology affected ($P<.01$) bite rate, bite size and intake rate (Table 4). Lambs ingested forage faster and took larger bites when grazing flowering grass than when grazing vegetative grass. Bite rate decreased with advancing plant phenology.

Table 4. Bite rate, bite size and intake rate of lambs grazing vegetative and flowering hycrest crested wheatgrass.

Stage of growth	Bite Rate (bites/min)	Bite Size (g)	Intake Rate (g/min)
Vegetative	33[a]	.10[a]	3.3[a]
Flowering	15[b]	.29[b]	4.2[b]

[a,b]Means for vegetative vs. flowering grass followed by a different letter are different ($P<.01$).

The effects of experience are shown in Table 5. Grass-experienced lambs ingested more forage ($P<.05$) than shrub-experienced lambs. Bite rates and bite sizes were numerically, but not

statistically (P>.05), higher for grass- than for shrub-experienced lambs.

Table 5. Bite rate, bite size and intake rate of lambs with differing amounts of grass and shrub experience foraging hycrest crested wheatgrass.

Lambs	Bite Rate (bites/min)	Bite Size (g)	Intake Rate (g/min)
Shrub-experienced	24[a]	.18[a]	3.4[a]
Grass-experienced	25[a]	.21[a]	4.1[b]

[a,b]Means for grass- and shrub-experienced lambs followed by a different letter are different (P<.05).

The interaction between plant phenology and experience was not significant (P>.05, Fig. 6). Grass-experienced lambs were more (P<.05) efficient than shrub-experienced lambs at ingesting both vegetative and flowering grass. Grass-experienced lambs were equally (P>.05) successful at prehending vegetative and flowering grass whereas shrub-experienced lambs experienced a greater (P<.05) probability of failure at prehending flowering grass (Fig. 6).

Discussion

Bite size and intake rate were higher while bite rate was lower for lambs grazing flowering compared to vegetative hycrest crested wheatgrass (Table 4). Similar results were obtained for cattle grazing alfalfa (Dougherty et al. 1988). Height (32 vs. 17 cm) and

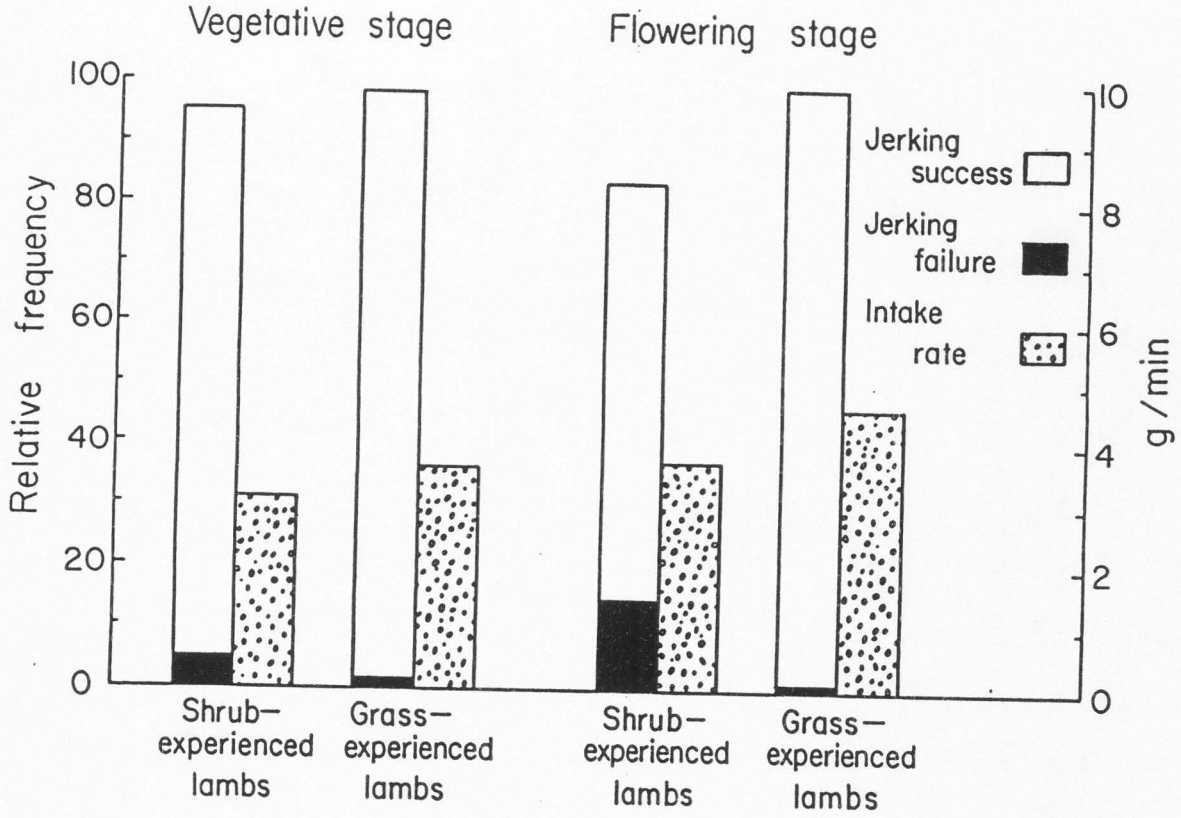

Figure 6. Prehension success (%) and ingestion rate (g/min) of shrub vs. grass-experienced lambs grazing vegetative and flowering hycrest crested wheatgrass.

number (50 vs. 28) of tillers were greater for flowering than for vegetative plants, which probably accounts for the larger bite sizes and higher intake rates of lambs. Sward height (Jamieson and Hodgson 1979, Black and Kenney 1984, Penning 1986) and bulk density (Stobbs 1975) are positively related with bite size and intake rate. Converserly, the lower bite rate on flowering compared to vegetative plants was probaby caused by the large coarse tillers on flowering plants (Scarnecchia et al., 1985, Table 4).

Grass-experienced lambs were more efficient at harvesting flowering and vegetative grass than shrub-experienced lambs (Table 5). We attribute the differences in intake rate to the fact that grass experienced lambs were more successful at prehending grass than shrub-experienced lambs (Fig. 6). Moreover, bite rate and bite size were numerically higher for grass- than for shrub-experienced lambs (Table 5).

Factors other than bite size and bite rate determine intake rate (Hudson and Watkins, 1986). Animals that lack prehension skills may spend more time handling (i.e. prehending and masticating) forage and hence ingest less forage per unit time. I hypothesize that shrub-experienced lambs spent more time handling vegetative and flowering grass than grass-experienced lambs.

I conclude, based on prehension failures that flowering hycrest crested wheatgrass was more difficult for lambs to harvest than vegetative grass, but these differences were offset by prior experience foraging on grass. Thus, the results support our prediction that lambs experienced at foraging on grass are better

able to harvest grass than lambs with experience foraging on shrubs. This outcome also suggests that sheep might better utilize tall, coarse forages if they were exposed to them as lambs (Provenza and Balph 1987, 1988).

CHAPTER V

SYNTHESIS

My analysis of ingestive behavior of lambs on monocultures of shrub and grass revealed that experience influenced forage harvesting skills. Moreover, foraging skills were specific to the plant form with which experience was gained even though considerable changes in form occurred within the same plant species as phenology advanced. Inexperienced lambs failed more at prehending forage and as a result ingested less food per unit time than experienced lambs. The probability of failing at prehending forage depended on harvesting difficulty of the forage.

The extent of improvement in harvesting skills for a given amount of experience was related to the type of prehension pattern. Lambs experience less difficulty plucking leaves than breaking twigs or stripping leaves from the shrub serviceberry. Moreover, lambs emphasize those prehension patterns at which they were most skillful.

The ability of lambs to efficiently harvest a plant form with which they have limited experience is probably determined by the relationship between mouth morphology and plant form. Lambs experience less difficulty plucking leaves from a shrub probably because the size, shape and movement potential of its mouth better matches shrub than grass forms.

Although this study clearly demonstrates that forage harvesting skills are modified by experience, there are several unanswered questions. Future research should determine: (1) the amount of experience required to reach a maximum level of foraging efficiency, (2) how age at which sheep are exposed to forages affects learning efficiency, (3) the persistence of learned responses, (4) the proportion of skills that are transferable between different plant forms, (5) the relative contribution of food neophobia and foraging skills to foraging efficiency of livestock on rangelands, and (6) how experience affects livestock performance under differing levels of forage availability.

LITERATURE CITED

Afifi, A. A., and Clark, V. 1984. Computer-aided multivariate analysis. Lifetime Learning Publications. Belmont, California.

Allden, W. G., and Whitakker, I. A. 1970. The determinants of herbage intake by grazing sheep: The interrelationship of factors influencing herbage intake and availability. Aust. J. Agric. Res. 21:755-766.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behav., 49:227-267.

Arnold, G. W. 1970. Regulation of food intake in grazing ruminants. In A. T. Phillipson (Editor), Physiology of Digestion and Metabolism in the Ruminant. Oriel Press, London, pp. 264-276.

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

Arnold, G. W., and Dudzinski, M. L. 1978. Ethology of Free-Ranging Domestic Animals. Elsevier Scientific Publishing Co., Amsterdam. 198 pp.

Black, J. L. and Kenney, P. A. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. Aust. J. Agri. Res. 35:565-578

Chacon, E., and Stobbs, T. J. 1976. Influence of progressive defoliation of a grass sward on the eating behavior of cattle. Austral. J. Agri. Res. 27:709-727.

Chapple, R. S., and Lynch, J. J. 1986. Behavioral factors modifying acceptance of supplementary foods by sheep. Research and Development in Agriculture. 3:113-120.

Dougherty, C. T., Smith, E. M., Bradley, N. W. Forbes, T. D. A., Cornelius, P. L., Lauriault, L. M., and C. D. Arnold. 1988. Ingestive behavior of beef cattle grazing alfalfa (Medicago sativa L.). Grass and Forage Science, 43:121-130.

Dowdy, S., and Wearden, S. 1983. Statistics for Research. John Wiley and Sons, New York. 537 pp.

Flores, E. R., Provenza, F. D., and Balph, D. F. 1988a. Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. Appl. Anim. Behav. Sci., accepted.

Flores, E. R., Provenza, F. D., and Balph, D. F. 1988b. On foraging skills of lambs experienced with grass or shrub. Appl. Anim. Behav. Sci, accepted.

Gluesing, E. A., and Balph, D. F. 1980. An aspect of feeding behavior and its importance to grazing systems. J. Range Manage., 33:426-427.

Hodgson, J. 1971. The development of solid food intake in calves. 1. Effect of previous experience of solid food, and the physical form of the diet, on the development of food intake after weaning. Anim. Prod., 13:15-24.

Hodgson, J. 1982. Influence of sward characteristics on diet selection and herbage intake by the grazing animal. Pages 153-166 in J. B. Hacker, Nutritional Limits to Animal Production from Pastures. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Hodgson, J., and Jamieson, W. S. 1981. Variations in herbage mass and digestibility, and the grazing behavior and herbage intake of adult cattle and weaned calves. Grass and Forage Sci., 36:39-48.

Hudson, R. J., and Watkins, W. J. 1986. Foraging rates of waipiti on green and cured pastures Can. J. Zool. 64:1705-1708.

Jamieson, W. S., and Hodgson, J. 1979. The effects of variation in sward characteristics upon ingestive behavior and herbage intake of calves and lambs under strip grazing management. Grass and Forage Sci. 34:261-271.

Leight, J. H. 1972. Some effects of diet selectivity by vertebrate and invertebrate herbivores on arid- and semi-arid rangelands. Proc. 2nd USA/Australian Rangeland Panel. Australian Rangeland Society, Perth, Western Australia, pp. 125-148.

Montgomery, D. C. 1983. Design and Analysis of Experiments. John Wiley and Sons, New York. 538 pp.

Osuji, P. O. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. J. Range Manage. 27:437-443.

Penning, P. D. 1986. Some effects of sward conditions on grazing behaviors and intake by sheep. In: O. Gudmundsson (Ed.) Grazing Research in Northern Latitudes. NATO ASI Series A. Vol. 1078. Plenum Press. pp. 219-226.

Provenza, F. D., and Malechek, J. C. 1986. A comparison of food selection and foraging behavior in juvenile and adult goats. Appl. Anim. Behav. Sci., 16:49-61.

Provenza, F. D., and Balph, D. F. 1987. Diet learning by domestic ruminants: theory evidence and practical implications. Appl. Anim. Behav. Sci., 18:211-232.

Provenza, F. D., and Balph, D. F. 1988. The development of dietary choice in livestock on rangelands and its implications for management. J. Anim. Sci. 66:2356-2368.

Scarnecchia, D. L., Nastis, A. S., and Malechek, J. C. 1985. Effects of forage availability on grazing behavior of heifers. J. Range Manage. 38:177-180.

Scheaffer, R. L., Mendenhall, W., and Ott, L. 1979. Elementary Survey Sampling. Dexbury Press. Boston, MA. 278 pp.

Singer, R. N. 1980. Motor Learning and Human Performance. McMillan Publishing Co., Inc., New York. 549 pp.

Stobbs, T. J. 1975. The effect of plant structure on the intake of tropical pasture. III. Influence of fertilizer nitrogen on the size of bite harvested by Jersey cows grazing setaria anceps or Kazungula swards. Aust. J. Agric. Res. 26:997-1007.

VITA

Enrique Flores

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Acquisition of harvesting skills by lambs foraging grass or shrub.

Major Field: Range Science

Biographical Information:

Personal Data: Born at Lima, Peru, July 7, 1951, son of Enrique and Piedad Flores.

Education: Graduated from La Salle High School in Lima, Peru, December 1967; received a bachelor in Animal Husbandry with a major in Ruminant Nutrition from the Agricultural State University, December, 1974; received a master in Range Science with a minor in Range Management from Utah State University, June 1983; completed requirements for a Doctor of Philosophy in Range Science with a minor in Range Ecology at Utah State University, August 1988.

Professional Experience. 1988-- Associate Professor, Department of Animal Production, Agriculture State University, La Molina, Peru; 1985-1988 Graduate Fellow, Department of Range Science, Utah State University, Logan, Utah; 1983-1985 Assistant Profesor Range Management, Agricultural State University, La Molina. 1980-1983, Graduate Fellow, Utah State University, Logan. 1975-1980 Research Assistant Professor Agricultural State University, La Molina, 1974-1975 Sheep Nutrition Researcher at the Beef Research Program at La Molina, Peru.