THE UNIVERSITY OF ALBERTA

BREEDING OF THE PIKA IN RELATION TO THE ENVIRONMENT

by

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ABSTRACT

Reproductive parameters of the pika, Ochotona princeps (Richardson),
were documented over three years in southwestern Alberta to evaluate
the relationship between reproductive success and environmental
parameters, particularly food supply. This involved the collecting
of large samples of animals throughout the breeding season and the
documentation of reproductive success in populations of marked animals.

The pika has the potential to produce two litters of 2 - 4 young
each breeding season. All animals mature as yearlings, and females
breeding for the first time are as successful as older females.
Breeding commences in late April and early May, prior to the emergence
of new vegetation, and the last conceptions occur in early July.
Males go out of breeding condition in late June and early July.

Almost all females were successful at producing offspring to
birth, although in May 1970 some terminated pregnancies (59%) may have
been related to adverse weather conditions. Females with terminated
pregnancies bred again and the only apparent adverse effect of these
losses on first litters was a delay in the timing of births. Only 34%
of marked females conceived second litters in 1970; these losses may
have been related to the delay caused by terminated first pregnancies.
Most reproductive losses involved whole litters during lactation; 48%
of all litters were lost at that time. These losses involved most
second litters, some first litters from populations of high density,
and may have been related to behavioral changes in females. Partial
prenatal and post natal losses were greatest in large litters and
females drained their fat reserves during lactation. Litter-size

appeared limited by a uterine capacity of three embryos and a
lactation capacity of two nestlings.

No reproductive losses were attributed to a quantitative or
qualitative shortage of vegetation.

ACKNOWLEDGMENTS

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INTRODUCTION

The breeding pattern of any species is ultimately the result of selection for the system that will contribute the maximum number of new parents to the next generation. Superimposed on this evolved pattern are environmental factors that may cause yearly, seasonal, or regional variations in the production of offspring.

Variations in fecundity have been recorded for many mammals and may be caused by factors in the physical or social environment. One of the most obvious and frequently considered factors that may affect fecundity is food supply. Lack (1954) suggested that litter-size corresponds with the largest number of young for which the parents can, on the average, provide enough food, and that animals with a good source of food are more successful at producing offspring than those with a poor source. In his view, the food supply is the most important proximate, as well as the most important ultimate, factor influencing fecundity.

Although there is little doubt that drastic changes in the quality or quantity of food can influence reproductive processes, normal seasonal or regional variations in availability of food will cause changes in patterns of reproduction only if the species is using its food resources to the fullest extent. Sadleir (1969a), in a review of the role of nutrition in the reproduction of wild mammals, suggested that selection for a particular breeding season alleviates the detrimental effects of poor nutrition on reproductive processes so that reproductive malfunctions can seldom be attributed to nutrition under natural conditions.

This study was undertaken to examine the effect of food supply on fecundity in natural populations of the pika, _Ochotona princeps_ (Richardson). Fecundity was documented through the autopsy of collected animals and observations of marked animals. The relative importance of food resources was evaluated through examination of condition of collected animals and availability of forage on feeding areas. The importance of hay piles as a source of food was evaluated by comparing amounts stored by animals in the wild with the amounts utilized by captive animals. The study was conducted in alpine and subalpine regions of southwestern Alberta from May 1968 to October 1970.

BACKGROUND

Although the taxonomy of species within the family Ochotonidae is unclear, the family appears to be represented by a single genus (Ochotona) and at least 14 species; 12 in Asia and 2 in North America (Ellerman and Morrison-Scott 1951).

The Asian pikas occupy a wide range of habitats, from alpine and arctic tundra to deserts, valley bottoms, and steppe meadows. Some are restricted to boulder fields and piles of loose rock where natural crevices are utilized for runways, while others are similar to ground squirrels in that they live in burrows. Considerable variation is seen in their breeding habits (see Appendix I). Most, if not all Asian pikas are diurnal, highly vocal species that store food and do not hibernate.

The most widespread North American pika, Ochotona princeps, is virtually restricted to piles of broken rock of sufficient size to provide natural runways. Found only in mountainous regions of western North America, it ranges from central British Columbia to northern New Mexico, and from alpine tundra to sea level.

O. princeps is primarily diurnal, although nocturnal activities have been recorded (Krear 1965). Adult males and females appear to possess territories which may be maintained through aggression, vocalization, or odors from cheek glands or fecal piles (Broadbooks 1965, Kilham 1958, Krear 1965, Sharp 1970) Each home range includes a portion of a rock slide and an adjoining feeding area where a wide variety of plants are utilized for food. Vegetation is collected during summer and autumn and stored within the rocks for winter use. Pikas are not known to hibernate, but utilize extensive runway systems

beneath the snow during winter (Krear 1965).

Breeding commences as early as March in some areas (Severaid 1955) but generally occurs from May to July (Johnson 1967). The gestation period is 30 days, weaning occurs at 3 - 4 weeks, and a post partum estrus is possible (Severaid 1950, 1955). Litters are small, usually consisting of 2 - 4 young (see Appendix II).

The collared pika, O. collaris (Nelson), found in northern British Columbia, Yukon and Alaska, is very similar in habits to O. princeps (Broadbooks 1965, Rausch 1961).

The habits of the pika make it a useful subject for many ecological studies. It forms discrete populations, is diurnal, and is easily trapped and handled; hence individuals can be closely examined or observed. The formation of discrete hay piles permits evaluation and manipulation of food resources, and was the main reason the pika was chosen for the present study.

METHODS

Study Areas

Although pikas were found wherever accumulations of broken rock provided suitable habitat, only specific widely separated areas were chosen for study (see Fig. 1). These were chosen mainly on the basis of accessibility. Access roads to Plateau Mountain and The Gap were generally open in early May, and Sheep River was open in late May. Elbow River, Junction Mountain, and Forget-me-not Mountain were not accessible until late June or July.

Elevations of study areas varied from about 4500 to over 8500 feet (1370 to 2590 m), and habitats varied from subalpine forest to alpine tundra. Areas of forest were generally dominated by spruce (_Picea engelmannii_) or fir (_Abies lasiocarpa_) and were generally sparse in grasses and forbs. Open slopes at lower elevations and sheltered slopes at higher elevations supported a lush growth of grasses and forbs while rocky or exposed slopes supported only scattered patches of grasses, forbs, and cushion plants.

Analysis of vegetation and hay piles was done only on the Sheep River, Elbow River, Junction Mountain and Forget-me-not Mountain areas. All of the mark-recapture program was conducted on Gibralter Mountain, Sheep River. Animals were collected from all areas except Forget-me-not Mountain and the marked populations. No significant differences were detected in reproductive parameters of collected animals from different study areas, and data from all areas were combined for all other comparisons.

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Figure 1. Map of general study area showing relative locations of The Gap, Plateau Mountain, Junction Mountain, Sheep River, Elbow River, and Forget-me-not Mountain. Specific study areas shaded black.

115°

Elbow R.

Forget-me-not
Mt.

Sheep R.

Gibralter
Mt. Junction
Mt.

Highwood R.

BOW
FOREST

8 miles
14.8 km

N

Plateau Mt.

CROWSNEST
FOREST

ALBERTA

50°

The Gap
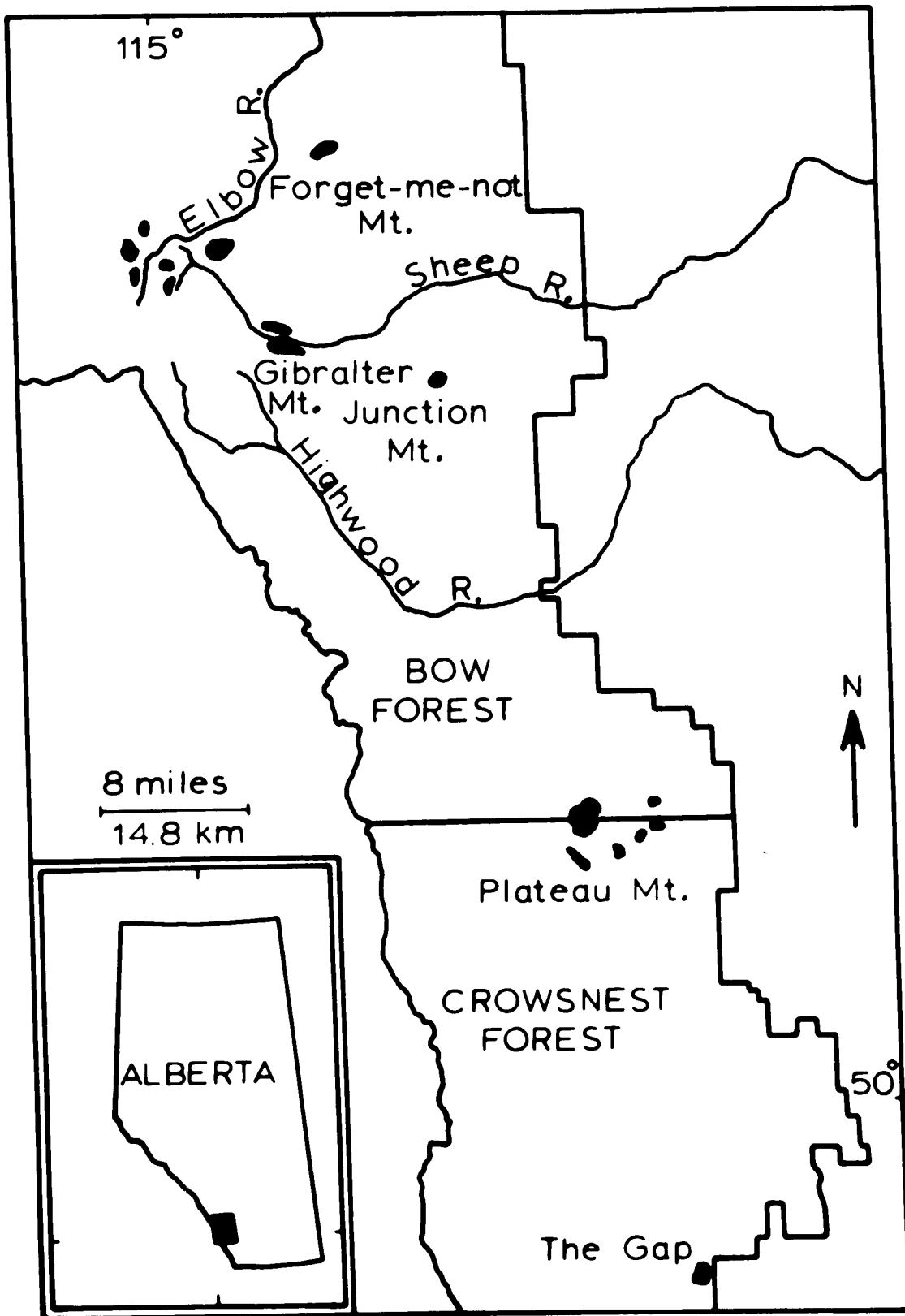
Capture and Marking

Populations of marked animals on Gibralter Mountain were followed throughout the study. Pikas were captured in 10 x 10 x 36 cm Sherman traps baited with willow leaves (Salix spp.) or other green vegetation and placed in sheltered spots within rock slides. The bait tended to attract pikas and individuals could readily be recaptured every few days. Few trap deaths occurred as traps were checked every 2 - 4 hours. Each animal was placed in a plastic bag, grasped around the neck and handled without anesthesia. Sexing was possible in all animals greater than about two months of age by everting the cloaca (Duke 1951) and examining for a penis or clitoris. A numbered mouse tag and a color combination of plastic ear discs (Krear 1965) served to identify individuals.

Rock slides separated by forest and meadows provided 10 distinct populations linearly arranged along a one mile (1.8 km) section of north facing slope. The surface area of four slides was determined and two of these were staked off in 50 x 100 foot (15.2 x 30.4 m) grids to facilitate plotting of home ranges. All animals on these four slides, as well as some animals on others were individually marked; hence some data on population densities were obtained.

Food Resources

Comparisons of forage availability among all study areas were made by classifying feeding areas as one of three arbitrary types: lush meadow, stunted meadow, or sparse meadow. Vegetative characteristics of these types were determined by analysing available vegetation on them. A total of 50 quarter square meter plots were located subjectively

on lush meadow, stunted meadow and sparse meadow habitats on several study areas. These plots were clipped in August 1970, air dried, weighed, and 1 - 4 homogenized samples from each habitat type were analysed for protein, calcium, and phosphorus by the Alberta Department of Agriculture Soil and Feed Testing Laboratory. Similar bimonthly samples of 5 - 10 plots from one meadow (lush meadow) provided an estimate of seasonal change in the quantity and quality of forage.

Winter food resources were estimated from hay piles from several areas. Hay piles were located by intensive search throughout the summer and weighed at the end of September when most haying had ceased. Location, number of sub-piles, distance to vegetation, previous use of the site, and the dominant plant in each hay pile was also recorded. Examination of hay piles of marked animals provided comparisons among age and sex groups. Homogenized samples of hay pile material from different habitat types were also analysed for protein, calcium, and phosphorus. The relative importance of hay piles as a source of food during winter was estimated by comparing the amount of material stored by animals in the wild with the amount consumed by captive animals.

The relative importance of different plant species as a source of food was estimated by comparing the composition of available forage on one feeding meadow (sparse meadow) with the composition of hay piles from the same area.

An indirect evaluation of food resources involved the determination of body weight and fat content of collected animals. No animals had large deposits of fat, but three fairly discrete fat bodies were located in the interscapular, cardiac, and splenic regions. These were removed

from all animals collected, stored in 70% alcohol, blotted to remove

excess moisture, and weighed to the nearest mg. Mg fat per 100 gm

body weight was calculated for each animal.

Absolute age of collected animals was determined by examining

incremental rings in the bone of the lower jaw, after Bernstein and

Klevezal (1965). Details of the technique are presented in Appendix

III. Age of young of the year was based on body weights (Appendix V).

Age classes were grouped as follows: juvenile - young of the year;

yearling - born the previous year; adults - all older animals; mature -

yearlings and adults combined.

Reproduction

Reproductive parameters were obtained from collected and marked

animals. Collecting by shooting throughout the breeding season yielded

667 animals, each of which was weighed and reproductive status and

location noted. Whole carcasses were fixed in A.F.A. for future

laboratory analysis. Testes and epididymides of 65 males and ovaries

of 234 mature females were embedded in paraffin, sectioned at 7 - 10μ

and stained with Delafield's haematoxylin and eosin. Corpora lutea

and corpora albicantia were counted in serial sections of ovaries.

Embryos were counted, and crown-rump length, weight, and sex recorded

when possible. Age of embryos was determined from an embryonic

growth curve, adapted from Huggett and Widdas (1951), and used to

determine conception and birth dates. Details of the technique are

presented in Appendix IV. Post partum reproductive tracts were cleared

in benzyl-benzoate (Orsini 1962) to provide accurate counts of

implantation sites.

Reproductive success from birth to weaning was determined on the marked populations. All females on slides of known area, as well as a few from other slides, were recaptured as often as possible (usually 2 - 3 times per week), weighed, and the presence of pregnancy or lactation noted. Examination of nipples of collected post partum females indicated that swollen nipples (1 - 2 mm in diameter; 1.5 - 4 mm long) and matted or worn hair around the nipples denoted lactation. Intensive trapping within the female's home range 3 - 4 weeks after the initiation of lactation ensured that all juveniles were marked, or at least observed, at weaning.

Captive Animals

Pikas were held in cages in the field and laboratory to monitor utilization of food and obtain breeding data. All animals were provided with 15 x 15 cm nest boxes, and fed natural foods (fresh vegetation in the field and dried pile material in the laboratory) and commercial rabbit pellets.

Animals held in 25 x 90 cm cages did not breed successfully and all died within 7 months. Better reproductive success and survival was obtained with pikas in 75 x 90 cm and 120 x 120 cm cages.

Little information directly applicable to the present study was found in the literature on pikas; hence a considerable amount of basic information had to be documented before the main aims of the study could be fulfilled. Although not all information obtained is presented here, some data not related to the main theme of the study are included as background information.

All statistical analyses involved x^2 or Student's t tests; $P \leq .05$

was considered significant. In all cases, the term "significant" refers to statistical significance. Throughout the text, means are presented as average $\pm$ standard error. On all figures, the term "two standard errors" refers to one standard error each side of the mean.

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RESULTS

Habitat and Food Resources

Environmental conditions in mountainous regions of southwestern Alberta favor growth of vegetation for only a short time each year. In general, slopes were free of snow by mid May, growth of vegetation began in early June and ceased in late July or August. The initiation of growth was closely synchronized; almost all plants on a given area produced new shoots within a one week period. Considerably more variation was evident between study areas.

Some variations in the growing season in the Sheep River area were noted during the years of the study. Weather data are presented in Appendix VI. Slopes were free of snow by mid May in 1968, but cool temperatures prevented new plant growth until the third week of June. Heavy rains during August maintained vegetation in a lush green state until the end of the month. Slopes were again free of snow by mid May in 1969 and with mild temperatures, growth of vegetation was evident during the first week of June. Lush green vegetation persisted only until late July when all slopes became extremely dry. In 1970, a heavy snowfall on all study areas on April 28, left a 35 cm snow cover in mid May in Sheep River. However, with subsequent mild weather, growth of vegetation again commenced during the first week of June. Low rainfall during late summer of that year caused a drying of vegetation in early August.

The seasonal progression in the amount and quality of green forage on one meadow (lush meadow, Sheep River) was determined by clipping quarter square meter plots at bimonthly intervals during

1970 (Fig. 2). These data indicate that the quantity of green
vegetation was highest in mid July. Protein and phosphorus content
of the vegetation decreased throughout the growing season, while
calcium content did not change significantly.

All pikas had access to food resources on feeding meadows, but
there was considerable variation in the amount of vegetation present
on different areas. Vegetative characteristics of lush meadow,
stunted meadow, and sparse meadow habitats are presented in Table 1.
These data indicate that the amount of forage available to pikas
varied considerably between habitat types, but the actual differences
were much greater than the data suggest. Plots were subjectively
placed where vegetation occurred, and while lush and stunted meadows
were usually fairly continuous masses of vegetation, sparse meadows
supported vegetation only in small, scattered patches (see Plate I).
The quality of vegetation on these areas appeared similar. The
quality of forage from sparse meadow areas was probably higher than
the single sample (Table 1) suggests; hay piles were not of poorer
quality than those from other areas.

Pikas had access to growing green vegetation for only a few
weeks each year. However, relatively good feeding conditions were
apparently maintained into the winter through the utilization of
foods stored during summer and fall. A few animals began collecting
vegetation in late June and some hay piling activity was still evident
in October. The most intensive period of hay collecting occurred
in August. Records of the dates of initiation of haying were not
kept, but mature males appeared to begin haying earlier than mature
females, and mature females earlier than juveniles.

Figure 2. Seasonal progression in quantity (gm/quarter square

meter) and quality (per cent protein, calcium, and

phosphorus) of air dried green forage on one meadow

(lush meadow), in Sheep River during 1970. Average

quantity based on 5 - 10 random quarter square meter

plots per bimonthly period. Average quality based on

1 - 4 samples from homogenized bimonthly samples.

Vertical lines denote two standard errors.
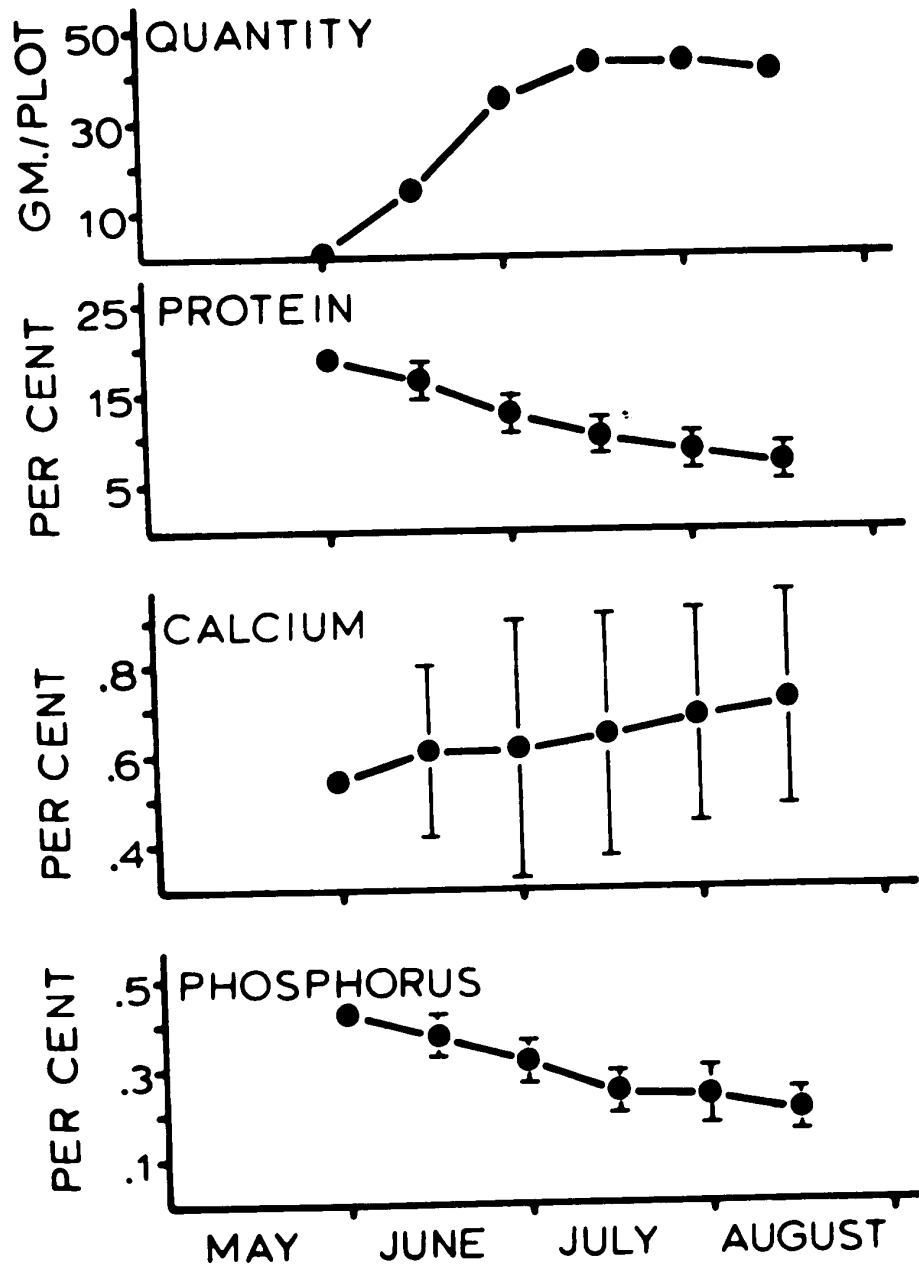
Table 1. Quantitative and qualitative characteristics of habitat types in August, and their associated hay piles in late September. Average quantity of air dried green forage (gm per square meter) based on quarter square meter plots on several study areas. Average size of hay piles (gm ± se) based on hay piles from several study areas. Average quality of forage and hay piles (% protein ± se) based on homogenized samples.

Habitat	Description	Quantity of forage	Quality of forage	Size of hay piles	Quality of hay piles
Lush meadow	Solid sod cover, generally moist sheltered areas, lush grasses predominate, cushion plants scarce.	(20) 179	(4) 10.9 ± .36	(9) 2383 ± 486	(5) 12.5 ± 1.04
Stunted meadow	Solid sod cover, generally dry sheltered slopes, stunted grasses predominate, cushion plants common.	(15) 80	(4) 9.8 ± .45	(34) 2644 ± 260	(5) 13.4 ± 1.08
Sparse meadow	Partial sod cover, generally dry exposed slopes, stunted grasses scattered, cushion plants common.	(15) 22	(1) 5.9	(62) 1881 ± 149	(5) 12.2 ± 1.09

Note: Sample size in brackets. No significant differences except size of hay piles between sparse meadow and stunted meadow (t = 2.69; P <.01), and between quality of forage and quality of hay piles on stunted meadows (t = 2.50; P <.05).

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Plate I.   Feeding meadows available to pikas.

A.   Lush meadow at edge of rock pile, 7000 feet (2100 m).

B.   Stunted meadow in foreground and in valley bottom,
7500 feet (2200 m).

C.   Continuous meadow of stunted vegetation, 7800 feet
(2300 m).

D.   Sparse meadow - note patches of mountain avens -
7500 feet (2200 m).

E.   Sparse meadow - note small scattered patches of
vegetation - 6000 feet (1800 m).

A
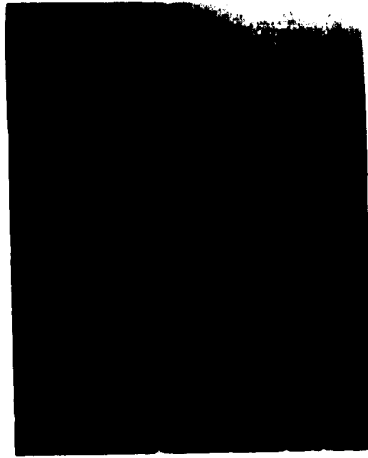
B

C

D

E

A

B   C
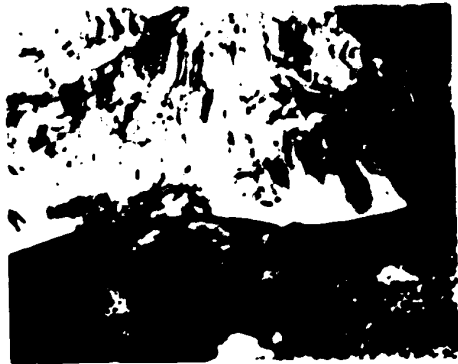
D   E
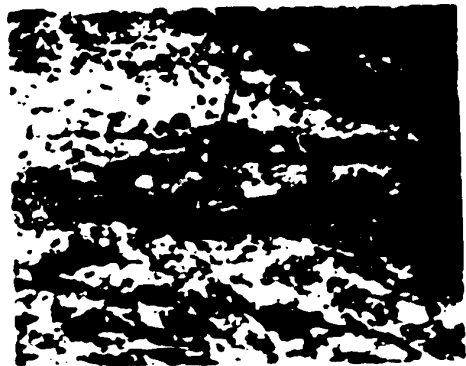
Characteristics of hay piles on several areas were recorded during late August and September. Observations of marked individuals indicated that each hay pile was made by a single individual. Most hay piles were located beneath or beside large rocks near the rock slide - feeding meadow ecotone; 71% of 211 hay piles from all areas were less than 6 m from an adjoining meadow. Many hay piles (82% of 183) were located on sites where hay piles had been constructed in previous years, but observations of marked animals indicated that individuals did not necessarily use the same site every year. Most animals (82% of 219) constructed only one or two large hay piles, but a few, particularly those living on slides consisting of small rocks, made 5 - 6 small piles within a small area.

Observations of plant species eaten by pikas were not recorded, but almost all green plants appeared to be utilized. Comparisons of the species composition of available vegetation and species composition of hay piles provided an index of selection for specific plants. Availability of each species was calculated as the per cent mean cover, after Daubenmire (1959), while utilization of each species was calculated as the per cent composition by weight of hay pile material. Per cent utilization divided by per cent availability provided an arbitrary index of selection for each species (Table 2). These data indicate that a wide variety of plants were utilized but only a few preferred. Grasses (_Elymus_ spp.) and sedges (_Carex_ spp.) were utilized most extensively, although columbine (_Aquilegia flavescens_), hedysarum (_Hedysarum_ spp.), flixweed (_Descuriana sophia_), gooseberry (_Ribes_ spp.), willow (_Salix_ spp.) and buffalo berry (_Shepherdia canadensis_) were also favored. All preferred plants were fairly large

Table 2. Availability, utilization and index of selection of common plants on one feeding area (sparse meadow) in Sheep River. Availability based on per cent mean cover of species up to 15 cm in height in 203 quarter square meter plots (adapted from Daubenmire 1959). Utilization based on per cent species composition by weight of 373 gm of hay pile material. Index of selection based on utilization ÷ availability; preference by pikas arbitrarily set at an index of selection of ≥ 1.3.

Species	Availability	Utilization	Index of Selection
Herbs in clumps			
Grasses, Sedges (Elymus spp., Carex spp.)	11.4	44.9	3.9*
Beard Tongue (Penstemon lyallii)	3.2	1.7	0.5
Columbine (Aquilegia flavescens)	0.8	1.4	1.7*
Saw Wort (Saussurea densa)	0.2	—	0.0
Hedysarum (Hedysarum spp.)	1.0	4.5	4.5*
Flixweed (Descurainia sophia)	0.3	0.6	2.0*
Shrubs and Trees			
Gooseberry (Ribes spp.)	3.5	11.9	3.4*
Willow (Salix spp.)	4.8	6.5	1.3*
Buffalo Berry (Shepherdia canadensis)	1.9	22.1	11.6*
Spruce (Picea engelmannii)	15.2	1.2	0.1
Juniper (Juniperus communis)	7.4	0.2	0.0
Cinquefoil (Potentilla fruticosa)	0.6	0.6	1.0
Honeysuckle (Lonicera involucrata)	0.2	0.1	0.5
Fir (Abies lasiocarpa)	0.4	0.3	0.7

(Continued)

Table 2 (Continued)

Species	Availability	Utilization	Index of Selection
Small Solitary Herbs			
Large Fleabane (Erigeron grandiflorus)	2.6	0.4	0.1
Daisy Fleabane (Erigeron compositus)	1.7	—	0.0
Fireweed (Epilobium augustifolium)	1.3	1.3	1.0
Strawberry (Fragaria glauca)	1.7	—	0.0
Everlasting (Antennaria nitida)	0.6	0.2	0.3
Arnica (Arnica cordifolia)	0.9	0.4	0.4
Anemone (Anemone drummondii)	1.4	—	0.0
Horizontal and Cushion Plants			
Saxifrage (Saxifraga bronchialis)	7.2	0.1	0.0
Twinflower (Linnaea borealis)	18.3	0.8	0.0
Mountain Avens (Dryas hookeriana)	9.9	—	0.0
Moss Campion (Silene acaulis)	0.6	—	0.0
Kinnikinnik (Arctostaphylos uva-ursi)	2.9	0.8	0.3

*Species considered to be preferred by pikas.

and conspicuous and grew in dense clumps or as shrubs. As a group, preferred plants had a significantly higher protein content than non preferred plants, but no differences were evident in calcium or phosphorus content (Table 3).

Small solitary plants and low growing and cushion plants were not utilized extensively for hay pile material, but were eaten during summer, and may have been grazed from snow tunnels during winter; both saxifrage (Saxifraga bronchialis) and moss campion (Silene acaulis) were found to be heavily grazed each spring.

Some relatively low protein plants such as spruce (Picea engelmannii), mountain avens (Dryas hookeriana) and kinnikinnik (Arctostaphylos uva-ursi) were dominant plants in hay piles in some areas, generally where little else was available. In most areas, grasses and sedges, hedysarum, or gooseberry were both available and heavily utilized. Further evidence indicating that plants containing high protein are selected is seen in Table 1. The quality of stored food was generally higher (significantly higher on stunted meadows) than the quality of random forage samples, indicating that pikas select plants high in protein content for hay pile material.

The extent of winter food stores was determined by weighing hay piles in late September when most storage had ceased. Many hay piles were inaccessible beneath rocks and total weights were determined for only 105 of 219 located. The amount of material stored by individual animals varied from about 400 gm to over 6000 gm. At least some of the variation could be attributed to the sex and age of the animal involved. Differences in dry weight of hay piles of individually marked mature males, mature females and juveniles were found. Hay

Table 3. Per cent protein, calcium and phosphorus in green parts of preferred and non preferred plants from Sheep River during August. Preference based on Table 2.

	% Protein	% Calcium	% Phosphorus
Preferred Species			
Grasses, Sedges (Elymus spp., Carex spp.)	14.1	0.69	0.18
Hedysarum (Hedysarum spp.)	20.9	0.94	0.21
Flixweed (Descurainia sophia)	10.3	2.32	2.13
Gooseberry (Ribes spp.)	13.6	1.23	0.19
Willow (Salix spp.)	10.3	2.32	0.13
Buffalo Berry (Shepherdia canadensis)	16.9	0.85	0.16
Mean ± se	14.3 ± 1.51	1.39 ± .26	0.16 ± 0.1
Non Preferred Species			
Spruce (Picea engelmannii)	5.2	0.70	0.08
Juniper (Juniperus communis)	4.0	1.56	0.09
Cinquefoil (Potentilla fruticosa)	12.0	0.86	0.28
Saxifrage (Saxifraga bronchialis)	5.4	1.91	0.15
Twinflower (Linnaea borealis)	6.0	1.72	0.09
Mountain Avens (Dryas hookeriana)	9.1	1.28	0.16
Moss Campion (Silene acaulis)	10.2	5.50	0.16
Mean ± se	7.4 ± 1.04	1.93 ± .30	0.14 ± .02

Note: Per cent protein significantly different (t = 3.52; P < .01).

piles of mature males (n = 26) averaged 2911 ± 284 gm, significantly

larger (t = 2.02; p = .05) than 1973 ± 291 gm stored by mature females

(n = 13). Juveniles (n = 14) stored 1107 ± 187 gm, significantly less

(t = 2.69; P < .02) than mature females. Another possible source

of variation was found in the distance material had to be transported.

A regression of size of hay piles of mature males against distance

from hay piles to feeding meadow (Fig. 3) indicates that the further

material had to be transported, the less was stored.

The size of stores of food also varied with the type of habitat

available. Hay piles located adjacent to lush meadows were too few

for valid comparisons, but those adjacent to sparse meadows were

significantly smaller than those adjacent to stunted meadows (Table 1).

Therefore, animals living near sparse meadows probably had to forage

more during winter than animals living near better meadows.

An estimate of the value of stored material as a winter food

source was made by comparing the amount of material stored with the

amount of material consumed by captive animals. Six pikas were held

in 25 x 90 cm cages at room temperature (approximately 20 degrees C),

given a known excess amount of hay pile material over 382 animal days,

and the residue subtracted. Hay piles contain a certain proportion of

inedible material such as stems and twigs, hence inedible material

left by captive animals was considered to be utilized. The figures

cited here are of hay pile material used, and not the actual amount

eaten. The six captive animals utilized 26 - 31 gm of material per

animal per day. Two animals held at a temperature of 10 degrees C

utilized about the same amount as animals held at room temperature

(20 degrees C), using 28 and 34 gm of material per animal per day over

Figure 3. Regression of size of hay piles (gm) of mature males

in late September against distance from hay piles to

feeding meadow, on one habitat type (sparse meadow)

in Sheep River. Y = 3760 - 155X. A significant

portion (F = 62.15; P < .001) of the variance of Y is

explained by regression on X (Sokal and Rohlf 1969,

p. 423).

Y = hay pile wt. (kg)

X = distance to vegetation (m.)
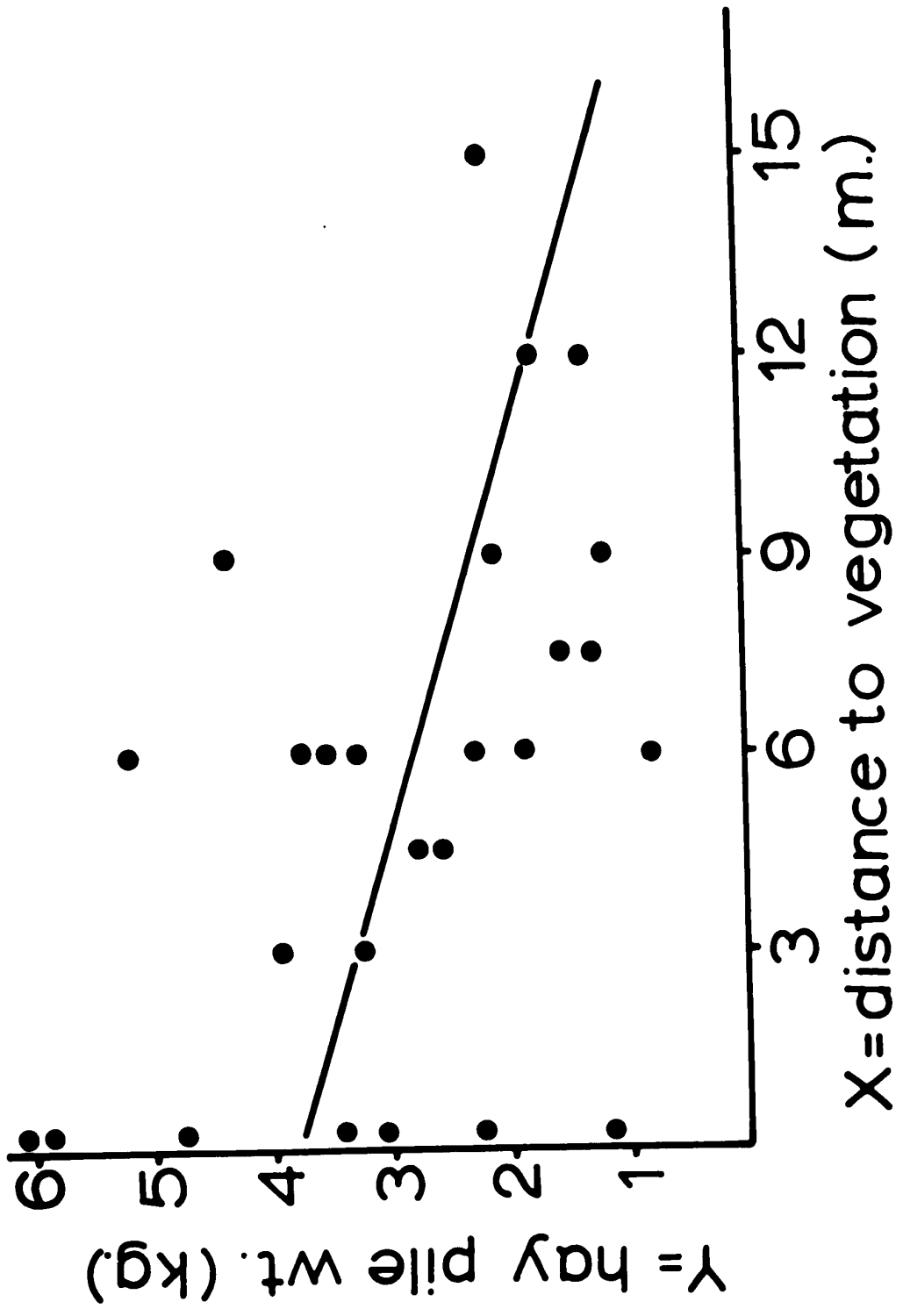
72 animal days. These figures may not be representative when applied to wild animals, but if they are even close, then few pikas stored sufficient material to allow them to feed exclusively on stored material throughout the winter. Each animal would require approximately 6000 gm of material to last 6 months, and only 3 of 105 hay piles contained that much. Since size of hay piles was extremely variable and appeared to be a poor indication of availability of forage, comparison of habitat types is considered the best means of estimating food resources.

Condition

Condition of adult pikas was estimated from body weight and relative fat content of collected animals. Although heavy or fat animals are not necessarily healthy animals, heavy and fat pikas must be obtaining, or at least storing, more energy in relation to their requirements than thin animals. Mature males were considered the most reliable index of condition in relation to environmental parameters because weight and fat content of mature females varies considerably with breeding condition.

Males were lightest in late May, after the slopes were free of snow and before new vegetative growth occurred (Fig. 4). Mean body weights increased slightly over summer. Females were also lightest in late May, and heaviest during pregnancy in June and July. No yearly differences were evident (Table 4), but yearling females were significantly lighter than adult females at the beginning of the breeding season.

Relative fat content (index of fat = mg of interscapular, cardiac,

25

Figure 4. Mean body weights for bimonthly samples of mature
male (open circle, broken line) and female (closed
circle, solid line) pikas collected on all study
areas, all years combined. Vertical lines denote
two standard errors.
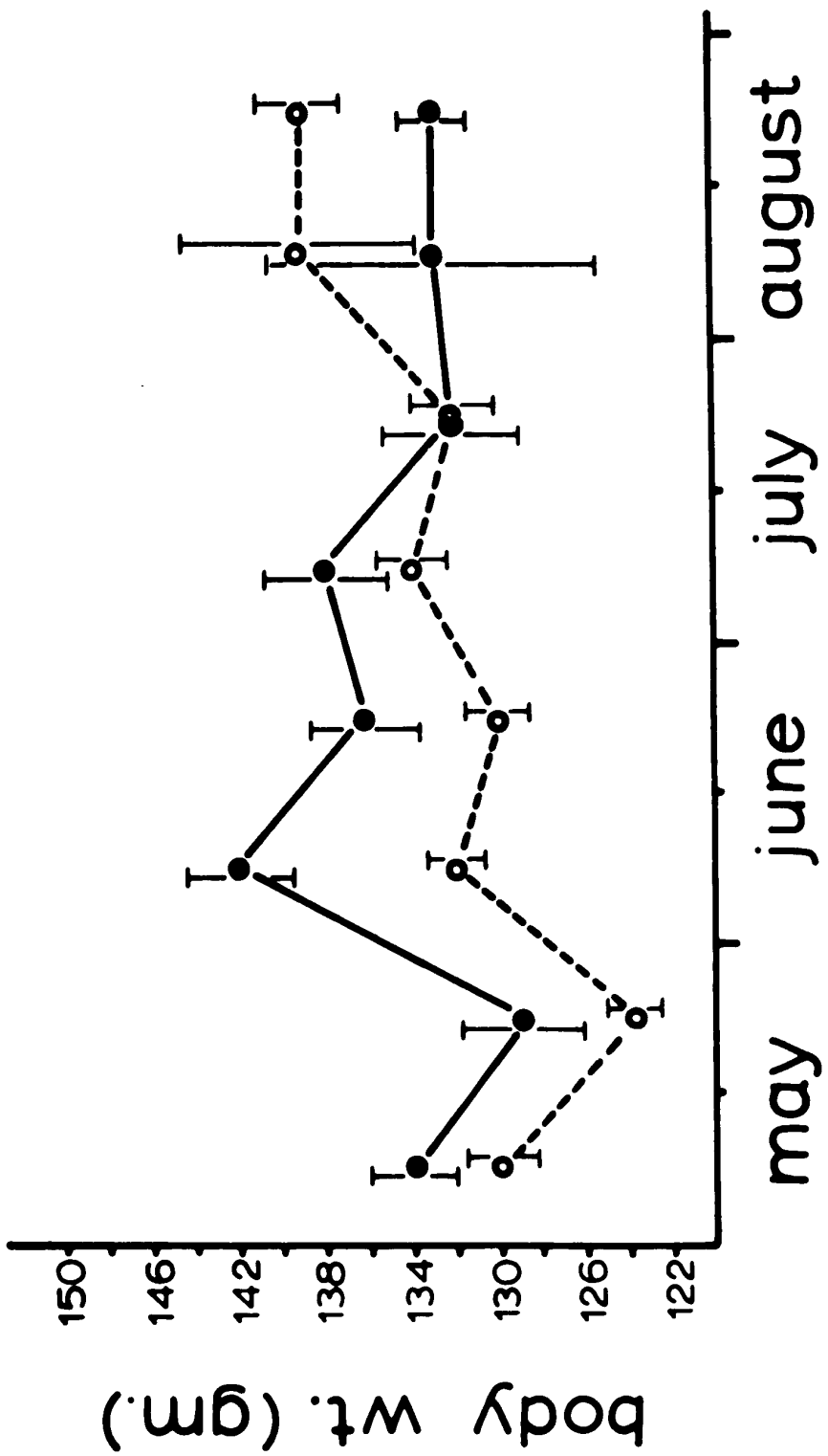
Table 4. Mean body weights (gm $\pm$ se) of pikas
collected during May, in relation to sex,
year and age. All study areas combined.

Sample	Sex	
	Female	Male
1968	(2) 134 $\pm$ 7.43	(1) 128
1969	(27) 133 $\pm$ 2.30	(47) 127 $\pm$ 1.48
1970	(17) 128 $\pm$ 2.84	(43) 124 $\pm$ 1.52
Yearlings	(15) 125 $\pm$ 3.35	(39) 124 $\pm$ 1.74
Adults	(22) 134 $\pm$ 2.38	(42) 128 $\pm$ 1.55

Note: Only yearling and adult females significantly
different (t = 2.18; P < .05).

and splenic fat bodies per 100 gm body wt) was much greater in mature females than mature males during the breeding season (Fig. 5). Fat content of mature males was lowest during late May and increased over summer. The fat content of mature females was lowest during early July, when many were both pregnant and lactating, but increased rapidly following the breeding season. Mature males appeared to be in better condition in May 1970 than in May 1969 (Table 5), and yearling males appeared in better condition than adults.

The relative fat content of females in relation to stage of pregnancy (Fig. 6) indicated that fat stores increased during pregnancy and decreased during lactation. The relative fat content of lactating mature females averaged 197 $\pm$ 20.36 on lush meadow habitat (n = 9); 185 $\pm$ 17.44 on stunted meadow habitat (n = 33); 200 $\pm$ 19.30 on sparse meadow habitat (n = 19), with no significant differences.

Using fat and body weight as indices, pikas were in poorest condition in late May, but even then none were devoid of fat or appeared unhealthy. No consistent differences were noted between years or age groups.

Reproduction

The Breeding Season

Pikas in southwestern Alberta had a 2 - 3 month breeding season during which most females produced two litters. Birth dates, extrapolated from age of healthy embryos in collected females (see Appendix IV) and from age of collected juveniles and marked litters (see Appendix V) are presented in Tables 6 and 7, respectively. These data indicate that most females bred in early May and gave birth

Figure 5. Mean index of fat (mg of interscapular, cardiac, and

splenic fat bodies per 100 gm body weight) in bimonthly

samples of mature male (open circles) and female

(closed circles) pikas collected on all study areas.

All years combined. Vertical lines denote two standard

errors.
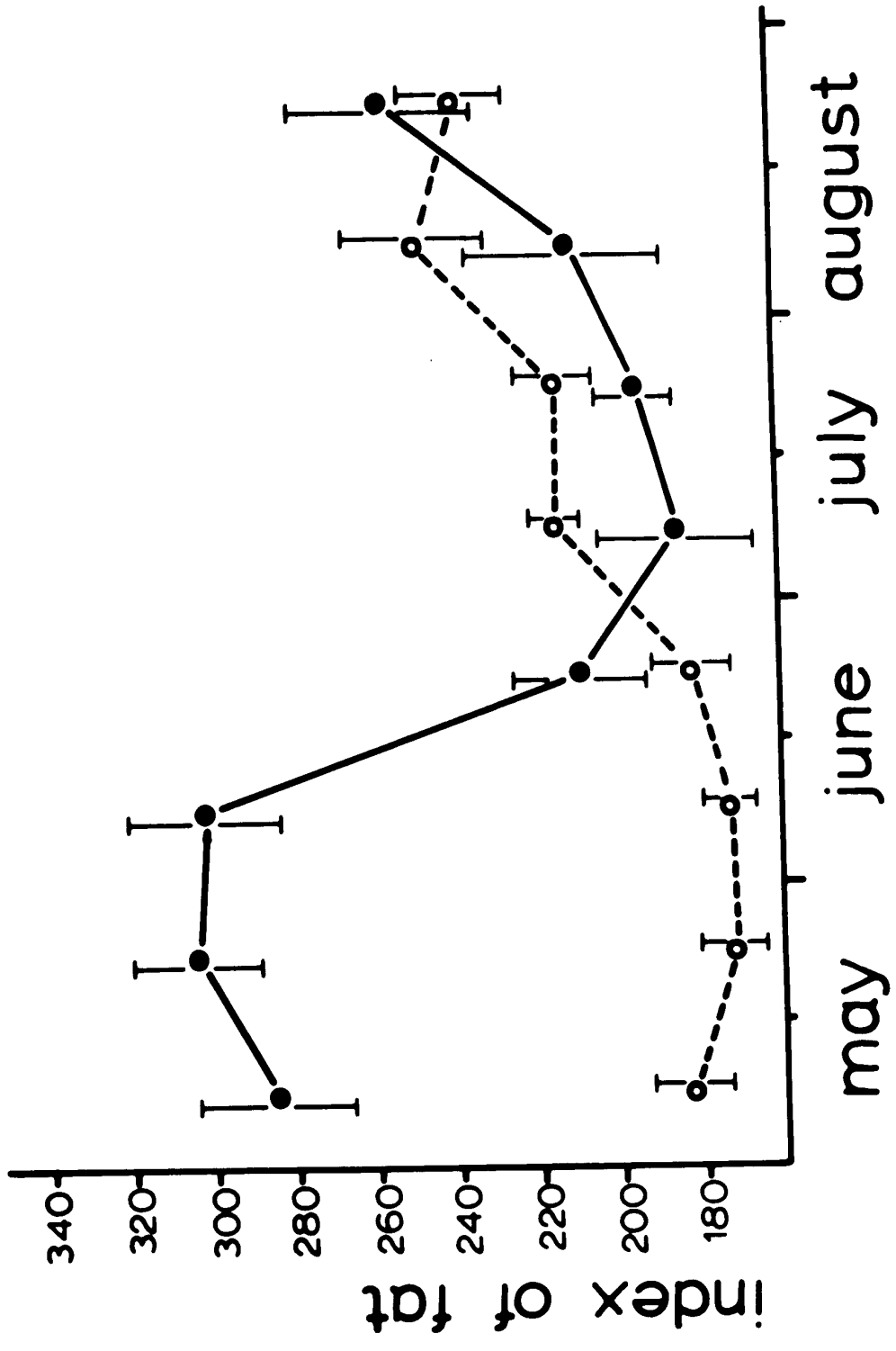
Table 5. Mean index of fat (mg of interscapular, cardiac, and splenic fat per 100 gm body weight) ± se of pikas collected during May in relation to sex, year, and age. All study areas combined.

Sample	Sex	
	Female	Male
1968	(2)* 380 ± 79.62	(1) 214
1969	(27) 281 ± 18.31	(46) 136 ± 9.52
1970	(17) 310 ± 21.82	(42) 210 ± 9.82
Yearlings	(15) 266 ± 17.56	(38) 203 ± 12.61
Adults	(22) 307 ± 23.31	(41) 155 ± 8.87

* Sample size

Note: Males significantly higher in 1970 than 1969 (t = 5.34; P < .001). Yearling males significantly higher than adult males (t = 3.10; P < .01).

Figure 6. Mean body weights (gm) and mean index of fat (mg

interscapular, cardiac, and splenic fat per 100 gm

body wt) of mature females in relation to stages

of pregnancy and lactation. Vertical lines denote

two standard errors.

Note: Fat index during lactation not significantly

different between first and second litters (t = .832;

P > .40).
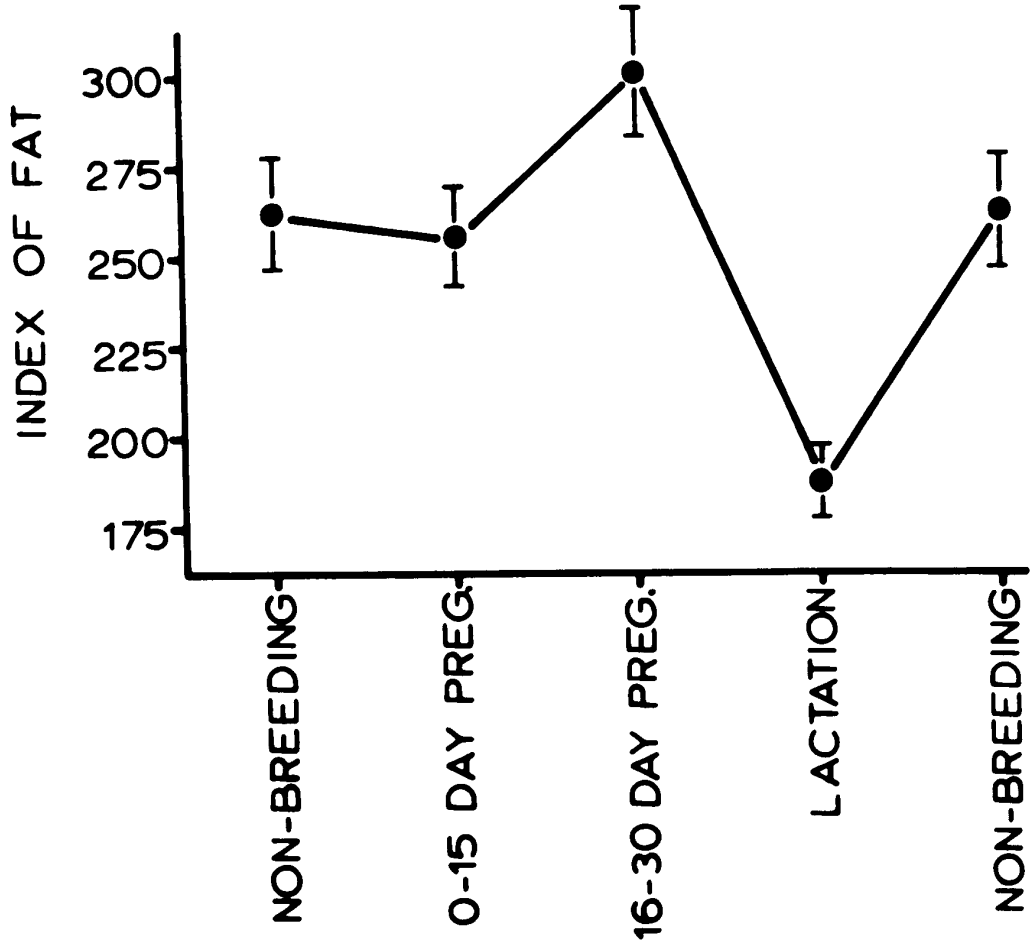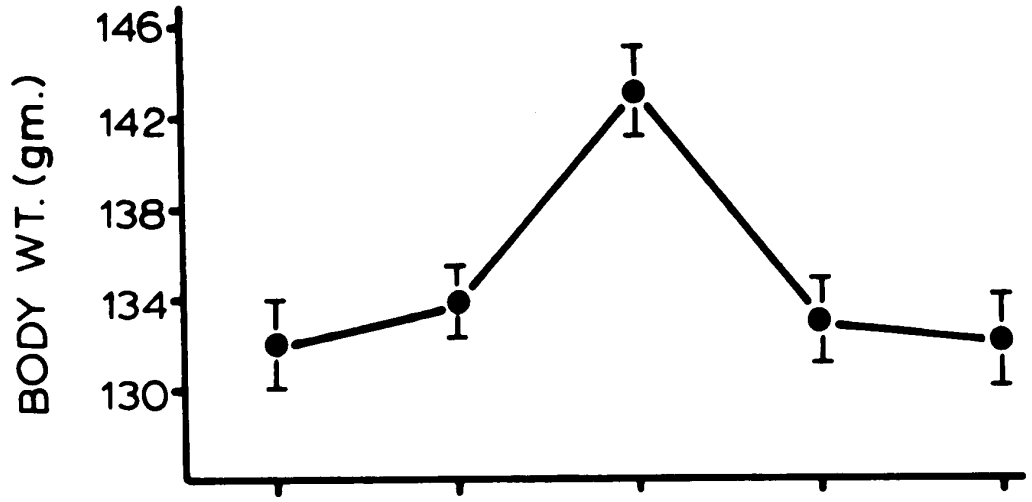
Table 6. Timing of births by bimonthly periods, calculated as a percentage of births in each littering period. Birth dates predicted from age of healthy embryos. First and second litters distinguished by presence of lactation and corpora albicantia in females carrying second litters.

Littering Period	Sample	Percentage of Births							
		May		June		July		August	
		A*	B	A	B	A	B	A	B
1968 First Litter	3			100					
Second Litter	7					29	57	14	
1969 First Litter	37		24	57	19				
Second Litter	30				20	60	17	3	
1970 First Litter	27			37		43			
Second Litter	21				63		57		

A* = first to 15th of month; B = 16th to end of month.

Table 7. Timing of births by bimonthly periods, calculated as a percentage of births in each littering period. Birth dates predicted from age of collected juveniles and marked litters. First and second litters not distinguished.

Year	Sample	May		June		July		August	
		A*	B	A	B	A	B	A	B
1968	17		41	53	—	6			
1969	32	12	16	63	9				
1970	50			52	14	9	1		

A* = first to 15th of month; B = 16th to end of month.

to their first litter in June. These young were weaned during early July at an age of 3 - 4 weeks (see Appendix IV). Second litters were conceived soon after birth of the first litter, born in July, and weaned in early August.

Although samples taken in 1968 were too small to be considered reliable, those taken in 1969 and 1970, although not significantly different, indicate a slight delay in births during 1970. There was a significant difference in the proportion of mature females pregnant or lactating during May, between 1969 and 1970 (Table 8).

The functional period of mature males was determined by plotting the proportion of males in breeding condition by bimonthly periods. Microscopic examination of 65 testes and epididymides revealed sperm in both structures of males with testes greater than 11 mm in length. On the basis of testes length, all mature males were capable of breeding when collecting began in May of each year (Table 9). Some mature males were out of breeding condition by early June and most were incapable of breeding by early July. No yearly differences in the timing of the functional period of mature males were detected.

Participation in Breeding

The potential reproductive output of a population may be reduced through the failure of some females to participate in breeding. The prevalence of pregnant or lactating mature females in monthly samples of collected females was used to estimate participation in breeding (Table 8). No juveniles matured during the summer of their birth, but all bred in the same time period as adults the following summer. Most,

Table 8. Percentage of collected females pregnant or lactating in monthly periods. First and second litters distinguished by presence of lactation and corpora lutea in females carrying second litters. Sample sizes in parentheses.

Littering Period	Per Cent Pregnant or Lactating			
	May	June	July	August
1968 First Litter	(2) 100	(5) 80	(15) 20	(5) 0
Second Litter	(2) 0	(5) 40	(15) 70	(5) 0
1969 First Litter	(27) 96	(34) 97	(27) 15	(5) 0
Second Litter	(27) 0	(34) 50	(27) 81	(5) 20
1970 First Litter	(17) 41	(28) 100	(26) 38	(17) 0
Second Litter	(17) 0	(28) 21	(26) 54	(17) 29

Note: First litter May 1970 significantly lower than in 1969 ($x^2 = 4.22$; $P < .05$). Peak in second littering period 1970 (July) significantly lower than peak in first litter 1970 (June) ($x^2 = 4.01$; $P < .05$). Some females were pregnant with second litters as well as nursing first litters, hence total frequencies for monthly samples frequently exceeded 100 per cent.

Table 9. Percentage of functional males in bimonthly samples. Males with testes 11 mm long or greater considered capable of breeding. Sample sizes in parentheses.

Year	May		June		July		August	
	A*	B	A	B	A	B	A	B
1968	(1) 100	—	(1) 100	(9) 44	(4) 0	(13) 0	(7) 0	(3) 0
1969	(16) 100	(30) 100	(41) 78	(21) 62	(31) 13	(21) 5	(8) 0	(6) 0
1970	(17) 100	(26) 100	(29) 86	(9) 56	(21) 5	(23) 4	(5) 0	(19) 0
Total	(34) 100	(56) 100	(71) 83	(39) 56	(56) 9	(57) 3	(20) 0	(28) 0

A* = first to 15th of month; B = 16th to end of month.

if not all mature females produced a first litter in all three years.
Most mature females also conceived a second litter except in 1970
when less than half bred a second time. Both yearling and adult
females were included in the nonbreeding group. The same trend was
also evident in the marked population (Table 10). Although the exact
reasons remain unknown, the reduction in the prevalence of second
litters during 1970 may have been related to the delay in birth of
first litters that year.

Potential Litter-Size and Prenatal Losses

Although the reproductive output of a population is strongly
influenced by the length of the breeding season and the number of
females participating in the breeding effort, variations in the
number of ova shed or losses during pregnancy may influence the number
of offspring produced.

Counts of corpora lutea are frequently considered to represent
the number of ova shed and hence the potential litter-size, but
are valid only if each corpus luteum represents the ovulation site
of only one ovum. Several factors, including polyovulation, twinning
of ova, and the formation of accessory corpora lutea may bias these
estimates. None of these factors appeared important in the present
study. Polyovulation and twinning of ova would result in females
having more embryos than corpora lutea, but this situation was not
observed. Twinning of ova would result in some embryos sharing a
chorion with another, but again, none were found. The formation of
accessory corpora lutea would result in counts of corpora lutea
being much higher than counts of embryos. In the pika, counts of

Table 10. Percentage of females pregnant in populations of marked
animals. Pregnancy determined by increases in body
weights, swollen abdomens and subsequent presence of
lactation. Sample sizes in parentheses.

Year	First Littering Period	Second Littering Period
1968	(2) 100	(2) 100
1969	(12) 100	(12) 100
1970	(29) 100	(29) 34

Note: Second littering period 1970 significantly lower than first
littering period 1970 (x^2 = 9.25; $P < .005$) and second
littering period 1969 (x^2 = 6.78; $P < .01$).

corpora lutea were very similar to counts of embryos, and rarely differed by more than one, hence the assumption was made that accessory corpora lutea were not formed. In all cases, counts of corpora lutea are considered to represent the number of ova shed.

Little variation in counts of ovulation sites was found among animals. Most females shed two or three ova, a few shed four, and none produced only one. No significant differences were evident between littering periods or years (Table 11). Females breeding for the first time (yearlings in their first littering period) shed an average of 2.67 ± .08 ova (n = 43), while females producing subsequent litters shed an average of 2.65 ± .06 ova (n = 113); hence breeding experience did not appear to affect ovulation rate. Despite the small variation found, the number of ova shed by one female was not rigidly fixed. In cases where the presence of active corpora lutea and corpora albicantia in the same animal provided two counts for one female, it was apparent that individual females did not produce a fixed number of ova. No trends were evident and all variations in ovulation rates were considered to be by chance.

Potential litter-size may be reduced through termination of pregnancy or through the loss of part of a litter. Pregnancy may be terminated at any time; through a failure of all embryos to implant, through resorption of all embryos, or through abortion of all embryos. The frequency of terminated pregnancies is difficult to quantify because the reproductive tracts of affected females rapidly revert to the anoestrous state, but some were evaluated indirectly.

Table 11. Counts of corpora lutea and corpora albicantia (mean ± standard error) in relation to littering periods and years. Sample sizes in parentheses.

Year	First Littering Period	Second Littering Period	Total
1968	(9) 2.77 ± .14	(13) 2.54 ± .18	(22) 2.64 ± .12
1969	(45) 2.75 ± .09	(36) 2.66 ± .10	(81) 2.72 ± .07
1970	(52) 2.54 ± .07	(20) 2.60 ± .13	(72) 2.55 ± .06
Total	(106) 2.65 ± .06	(69) 2.62 ± .08	(175) 2.64 ± .04

Note: No significant differences between any samples.

Failure of litters to implant was not estimated; all females possessing active corpora lutea but no embryonic swellings were considered to be in early stages of pregnancy.

Abortion appeared to cause few reproductive losses. Abortions could not be recorded directly, but the examination of 46 collected females with recent post partum reproductive tracts indicated that only two were not lactating. These may have aborted their litters or may have been taken immediately after successfully giving birth, before lactation could be detected. Abortions were also not apparent in the marked population, and all pregnant females (n = 86) were later found lactating.

Some total litter resorptions were recorded. Ten of 17 females (59%) taken in May 1970 had all embryos resorbing, but no females taken subsequently or in previous years showed similar losses. The losses in May 1970 occurred on both collecting areas visited at that time, indicating the losses were not simply a local phenomenon. The high frequency of pregnant females in subsequent samples in 1970 (100% of 28 females in June) indicated that they soon recovered and later bred successfully. Litter resorptions may have been related to the unusually heavy snow cover in May, 1970.

Partial loss of litters during pregnancy was estimated by comparing numbers of corpora lutea to numbers of embryos and implantation sites (Table 12). Some embryos failed to implant while others were resorbed after implantation. Visible resorbing embryos were found only between days 12 and 18 of pregnancy. Assuming all resorbing embryos to be distinguishable by day 13, counts of corpora lutea and healthy embryos in pregnancies greater than 13 days provided

Table 12. Losses between ovulation and birth in successful pregnancies, based on differences between counts of ovulation sites and healthy embryos after day 13 of gestation. Tabulated as a percentage of females that have losses and a percentage of ova that are lost, and compared among years and between littering periods and age groups. Sample sizes in parentheses.

Group	Losses	
	% of Females	% of Ova
1968	(8) 12.5	(20) 5.0
1969	(39) 28.2	(107) 11.2
1970	(33) 39.4	(78) 19.2
First Littering Period	(51) 35.3	(127) 15.7
Second Littering Period	(29) 24.1	(78) 10.2
First Breeding	(19) 47.3	(51) 21.5
Subsequent Breeding	(45) 31.1	(123) 12.2
Total Sample	(80) 31.2	(205) 13.0

Note: No significant differences (x^2).

an estimate of losses between ovulation and birth. Swollen placental
sites in recent post partum reproductive tracts were counted as
healthy embryo sites. Comparisons of losses between age groups,
littering periods and years indicated no significant differences.
Partial litter losses almost always involved only one embryo per
female; they were found in 31% of all females, and accounted for 13%
of all ova shed.

Assuming no resorptions prior to day 12 of pregnancy and all
implantation sites to be visible until day 18, counts of corpora
lutea and implantation sites in pregnancies less than 18 days provided
an estimate of losses between ovulation and implantation. Comparisons
among age groups, littering periods, and years (Table 13) indicated
no significant differences. Preimplantation losses were found in
25% of all females examined and accounted for 10% of all ova shed.

The difference in losses between ovulation and birth, and losses
prior to implantation provide an estimate of losses after implantation.
These losses were found to be small, being found in only 31% - 25% = 6%
of all females, and accounting for only 13% - 10% = 3% of all ova shed.

Post Natal Losses

Losses of young between birth and weaning are seldom determined
for natural populations of small mammals. However, such estimates
can be made in the pika because young can be counted at weaning and
associated with particular females, and frequency of litter-sizes
at weaning compared to counts of embryos.

Post natal losses, like prenatal losses, may involve complete
litters or only part of a litter. Total litter losses in the pika

Table 13. Losses between ovulation and implantation
in successful pregnancies, based on
differences between counts of ovulation
sites and implantation sites prior to day
18 of pregnancy. Tabulated as a percentage
of females that have losses and a percentage
of ova that are lost, and compared among
years and between littering periods and age
groups. Sample sizes in parentheses.

Group	% of Females	% of Ova
1968	(5) 40.0	(14) 14.3
1969	(28) 21.4	(76) 9.2
1970	(28) 25.0	(75) 10.6
First Litters	(37) 21.6	(99) 9.1
Second Litters	(24) 29.2	(66) 12.1
First Breeding	(15) 13.3	(36) 5.5
Subsequent Breeding	(42) 28.6	(115) 12.2
Total Sample	(61) 24.6	(165) 10.3

Note: No significant differences (x^2).

were determined directly in the marked populations by calculating
the proportion of females known to be pregnant that produced young to
weaning (Table 14). Most females (77%) successfully raised a first
litter, but very few (8%) successfully raised a second litter. No
significant differences were detected among years. Samples were too
small to compare age groups statistically, but yearlings and adults
appeared to be equally successful.

Partial losses of litters between birth and weaning could only
be determined indirectly since counts of embryos through palpation
of pregnant females could not be made accurately. A comparison of
average litter-size at birth, based on counts of late gestation
embryos in collected females, (2.33 $\pm$ .07; n = 80) with average
litter-size at weaning from the marked population (1.83 $\pm$ .08; n = 35)
indicates a partial litter loss of 21% of all young during lactation.

Partial Litter Losses in Relation to Initial Litter-Size

Partial litter losses were tabulated in relation to potential
litter-sizes (number of ova shed) to determine whether or not large
litters were as successful as small litters. When prenatal losses
between ovulation and birth were examined in this way, there were no
significant differences in losses between females ovulating two ova
and those producing three ova, but those producing four ova suffered
significantly greater losses (Table 15). The same pattern was evident
when losses prior to implantation were examined. Thus there appeared
to be a limit to the number of embryos that females could carry
successfully.

Partial litter losses between birth and weaning can be estimated

Table 14. Percentage of pregnant females successful to weaning, based on observations and recaptures of marked females. Compared among years and between littering periods. Sample sizes in parentheses.

Year	Littering Period		Total
	First	Second	
1968	(2) 100	(2) 0	(4) 50.0
1969	(12) 100	(12) 8.3	(24) 54.2
1970	(29) 65.5	(10) 10.0	(39) 51.3
Total	(43) 76.7	(24) 8.3	(67) 52.2

Note: First and second litters significantly different in 1969 $(x^2 = 9.31; P < .005)$. No significant differences among years.

Table 15. Losses in successful pregnancies in relation to initial litter-
sizes. Total prenatal losses based on differences between
counts of ovulation sites and healthy embryos after day 13
of gestation. Preimplantation losses based on differences
between counts of ovulation sites and visible implantation
sites prior to day 18 of gestation. Tabulated as a percentage
of females that have losses and a percentage of ova that are
lost. Sample sizes in parentheses.

Initial Litter Size	Total Prenatal Losses		Preimplantation Losses	
	% Females	% Ova	% Females	% Ova
2	(33) 21.2	(66) 10.6	(24) 20.8	(48) 10.4
3	(39) 28.2	(117) 10.2	(31) 19.3	(93) 6.4
4	(8) 87.5*	(32) 28.1*	(6) 66.6*	(24) 25.0*

* Significantly higher than in females shedding 3 ova ($x^2 > 4.50$; $P < .05$).

by comparing litter frequencies at birth and at weaning (Table 16).
These data indicate that the frequency of litters of three decreased
significantly between birth and weaning, while the frequency of
litters of two increased; hence, females giving birth to three young
appear to lose one during lactation. No significant increase in the
frequency of litters of one was evident, hence those females giving
birth to two young appear to raise two. Thus there appeared to be
a limit of two young that most females could nurse.

Reproduction in Relation to Food Supply

A seasonal survey of food resources, condition of animals, and
reproduction can only provide a very general indication of the
relationship among these factors. An attempt was made to obtain more
meaningful data by comparing reproductive performance of females
living in three habitat types of known characteristics and by
experimentally manipulating food resources of some marked animals.

A comparison of reproductive performance in relation to habitat
type (Table 17) indicates no significant differences among types
with respect to ovulation rates or prenatal losses. Post natal
reproductive success could not be compared between habitat types
because all marked animals were living in one type (sparse meadow).

The importance of winter food supply to subsequent reproductive
performance was determined by manipulating the amount of material
stored in hay piles. Hay pile material was removed from Elbow River,
Junction Mountain, and Forget-me-not study areas during August and
September of 1969, and 1000 gm of material was added to the hay piles
of 75 marked animals in four discrete populations on the Sheep River

Table 16. Frequency of litter-sizes at birth and at weaning. Litter-sizes at birth based on counts of healthy embryos after day 13 of gestation from collected females. Litter-sizes at weaning based on counts of young weaned by marked females. Tabulated as a percentage of the totals for each group. Sample sizes in parentheses.

| Litter-Size | Frequencies | |
	Birth	Weaning
1	(8) 10.0	(8) 22.8*
2	(38) 47.5	(25) 71.5**
3	(33) 41.2	(2) 5.7***
4	(1) 1.3	(0)

* Not significantly different between birth and weaning.
** Significantly higher at weaning than at birth ($x^2 = 7.01$; p <.01).
*** Significantly lower at weaning than at birth ($x^2 = 10.09$; P <.005).
Note: Litter-size (average ± standard error) at birth = 2.33 ± .07 and at weaning = 1.83 ± .08; difference = 21.0 per cent.

Table 17. Initial litter-size, preimplantation losses and total prenatal losses between ovulation and birth in relation to habitat types. Losses tabulated as a percentage of females with losses and a percentage of ova lost. Sample sizes in parentheses.

Habitat	Ovulation rate	Preimplantation Losses		Total Prenatal Losses	
		% Females	% Ova	% Females	% Ova
Lush meadow	(29) 2.77 ± .11	(12) 25.0	(35) 14.3	(18) 44.4	(49) 20.4
Stunted meadow	(71) 2.66 ± .06	(23) 26.1	(61) 9.8	(35) 20.0	(93) 7.5
Sparse meadow	(75) 2.57 ± .07	(26) 23.1	(69) 8.7	(27) 37.0	(73) 15.0

*See p. 15 for habitat characteristics.

study area during late September of that year. Total populations, rather than individuals, were used in case individuals did not restrict their feeding activities to their own hay piles during winter. The control area included one isolated population of marked animals where no manipulations were made. All hay piles of experimental and control animals were depleted during winter. During 1970, the reproductive performance of 15 experimental females, 6 control females, and 8 newly established females that had moved onto the experimental areas during winter was documented (Table 18). These data indicate that the experimental addition of 1000 gm of hay pile material to the food resources of females did not improve their reproductive performance the following summer.

Reproduction in Relation to Social Environment

Although the social behavior of the pika was not investigated, some data from the marked populations was applicable as long as the assumption was made that social pressure increased with population density. Data from collected animals could not be utilized because densities of populations from which animals were collected were not determined.

Density of the marked populations varied from .6 to 3.7 mature animals per hectare of rock slide, but consistent trends in density were not evident. For example, between 1969 and 1970, two marked populations increased, while two decreased. The reproductive success of females in relation to population density is presented in Table 19. Only the success of first litters was considered because second litters were generally unsuccessful. Although samples were too small

Table 18. Reproductive performance of marked females in relation to food reserves in hay piles.

	N	First Litter			Second Litter		
		Z Pregnant	Z Success to Weaning	Mean Litter-size Successful	Z Pregnant	Z Success to Weaning	Mean Litter-size Successful
Experimental*	15	100	53.3	1.62 ± .17	33.3	0.0	—
Control	6	100	100	2.00 ± .22	33.3	50.0	2.00
Other	8	100	62.5	1.80 ± .17	37.5	0.0	—
Total	29	100	65.5	1.79 ± .12	34.5	10.0	2.00

* Experimental - 1000 gm natural food added to hay pile in late September.
Control - normal hay pile
Other - unmarked animals that moved into experimental areas over winter.
Note: Increased food resulted in no significant increase in fecundity.

Table 19. Success of first litters to weaning in relation to population density. Includes only populations with all individuals marked and containing 5 or more mature females. Density based on mature animals per hectare of rock -- feeding meadow area excluded.

Density	No. Females Pregnant	% Females Successful	Mean Litter-Size of Successful Females ± se
0.6	5	100.0	1.80 ± .33
0.7	6	100.0	2.00 ± .23
1.0	6	100.0	2.00
1.8	12	58.3	1.85 ± .13
3.7	6	16.6	2.00

Note: No significant differences.

to be significantly different, these data indicate a decrease in reproductive success with high density, hence losses of first litters during lactation may have been related to density, and perhaps social pressure. No similar trend in the size of successful litters was evident.

Losses of second litters were not necessarily related to population density since second litters were uniformly unsuccessful, but social factors may be involved. Two explanations are possible. Losses of second litters may have been related to a conflict in the interests of the females between caring for young and collecting hay, or may be related to interference by first litter young. The first hypothesis could not be tested, but an attempt to test the second hypothesis was made in 1970 by removing all first litter young at the time of emergence from one population. The experiment was conducted on an area of low population density (0.7 mature animals/ hectare of rock) that included six mature females. Unfortunately, many females did not conceive a second litter during 1970, and only two of the six experimental females became pregnant. One of these females successfully raised a second litter. The experiment was unsuccessful because of small sample size, but the results suggest that the experiment is worth repeating.

Population Parameters

Several parameters were recorded that were of no direct relevance to the study, but which may be relevant to future studies of population dynamics of the species.

Although sex ratios determined from collected samples indicate

a very high proportion of males, ratios based on populations of marked animals and embryos from collected females in late stages of gestation were not significantly different from 1:1. Sex ratio at birth, based on late gestation embryos was 91 males per 100 females (n = 44) and was not significantly different from 103 males per 100 females (n = 172) in marked populations of mature animals.

Productivity was considered to be the number of young produced to weaning and was based on 1) 76.9% (n = 86) pregnancy rate; 2) 52.2% (n = 67) pregnant females producing young to weaning; 3) two litters per year; 4) 1.83 (n = 35) young produced per successful litter. On this basis, each female produced an average of 1.49 offspring to weaning each year.

Mortality of juveniles and adults was recorded. Juvenile animals generally disappeared immediately after weaning (20%; n = 49) when they were less than 65 gm; or a few weeks after weaning at a weight of about 100 gm, when 33% (n = 27) of the surviving juveniles disappeared. The early losses were apparently due to death since no immigrants or transients were that small. The later losses were apparently primarily due to dispersal, since immigrants and transients were 100 - 120 gm and some of the missing juveniles were later found established in other areas. Juveniles were considered to be established in a population if they were making a hay pile. Over winter mortality of established juveniles (n = 34) amounted to 38%, which was slightly lower, but not significantly different than the 54% (n = 55) mortality rate for established mature animals. Data on mortality rates of mature animals was also obtained from age structure of collected

animals (see Appendix III). Assuming populations to be stable, the proportion of yearlings in the population is equal to the loss of mature animals during the previous winter. On this basis, mature pikas had a 45% (n = 448) mortality rate which was not significantly different than the 54% mortality rate in the marked population. There was no significant difference in mortality between mature males and mature females.

Data on dispersal was also obtained. Half of all juveniles surviving to 100 gm did not move but established hay piles beside or within the home range of the female. Sex, point of origin, and post dispersal location was known for 17 juveniles; 67% (n = 6) of the juvenile females and 9% (n = 11) of the juvenile males settled more than 100 meters from their point of origin. Significantly more females than males moved (x^2 = 4.48; $P < .05$). Unknown immigrants and transients were most frequently found to be females; only 9% (n = 11) were males (significantly different from 1:1; x^2 = 7.36; $P < .01$). Hence movements away from home populations appear to be made primarily by juvenile females.

DISCUSSION

Many reproductive parameters (eg. ovulation rate) showed little variation. These parameters appeared related to an evolved reproductive potential, and appeared not to be affected by short term changes in environmental conditions. Therefore the evolutionary aspects of reproduction in the pika are considered first to form a basis on which the influence of the proximate environment can be considered. Although evolved patterns are frequently difficult to separate from factors within the immediate environment, reproductive parameters exhibiting little or no variation are considered to be evolved.

Evolution of Reproductive Rates

Reproductive rates may be considered to have evolved through natural selection, natural selection being the favoring of those individuals that contribute the most new parents to the next generation. In a hypothetical system containing animals of unlimited physiological potential and an environment providing unlimited food, space, and shelter, those animals producing the most offspring would leave the most descendants and reproductive rates would increase through evolution. However, animals do not have an unlimited physiological potential, environments do not provide unlimited resources, and reproductive rates do not necessarily increase through evolution. Many factors may affect fecundity by influencing the number of litters possible during the breeding season, the period of time to reproductive maturity, and the number of offspring produced at each littering period.

Reproduction is undoubtedly restricted to that time of year when

conditions are favorable for raising offspring. The numbers of litters raised during that period depends not only on the length of the favorable period, but also on the period of time required to produce each litter. In any stable environment, major changes in the time needed to produce one litter may be required to increase the numbers of litters produced each season.

Pikas in southwestern Alberta are able to produce two litters per season, apparently because they have a short gestation period (30 days), a short weaning period (3 - 4 weeks) and a post partum estrus. Throughout most of their range, pikas are probably able to produce at least two litters per year. Studies indicating more than one litter per breeding season have been conducted in Colorado and Utah (Johnson 1967; Hayward 1952) and Alaska (Rausch 1961). More than two litters per year are produced in California (Severaid 1955) and by some Asian species of pika (see Appendix I).

The production of more than one litter each breeding season in subalpine and alpine habitats puts the pika in a rather unique position in relation to other mammals of similar size. Least chipmunks (Eutamias minimus) produce only one litter per year in subalpine habitat in Colorado (Vaughan 1969) and E. minimus and yellow-pine chipmunks (E. amoenus) produce only one litter per year in mountainous regions of southwestern Alberta (Sheppard 1969). Columbian ground squirrels (Spermophilus columbianus) produce one litter per year (Moore 1937) and small samples of golden mantled ground squirrels (Spermophilus lateralis) (present study) indicated but one litter per year.

The proximate stimulus to breeding in the pika remains unknown,

but did not appear related to green forage as it is in rabbits
(Oryctolagus cuniculus) (Poole 1960), since breeding always commenced
prior to the appearance of new foliage. Breeding may be in response
to photoperiod as reported for hares (Lepus europaeus) (Flux 1965).
With a "fixed optimal breeding season" (Sadleir 1969b), breeding in
response to photoperiod would always result in litters being produced
at the most favorable time.

Age at reproductive maturity ultimately depends upon the size and
physiological condition that must be attained before breeding can
be successful. This may depend upon the size of the young at birth
or weaning and the potential rate of growth as well as the availability
of food and social position of the animal. Even if a mature size is
attained at an early age, breeding may not occur, as appears true
with the pika. Juvenile pikas grow rapidly during the summer of
their birth and some reach mature size by the end of August. Despite
this rapid growth rate, reproductive maturity is not attained until
the spring following their birth (see Appendix IV). At least one
species of Asian pika, Ochotona pusilla, breeds at 4 - 5 weeks of age
(Shubin 1965) and several others breed during the summer of their
birth (see Appendix I). The evolutionary precursors of the North
American pika, at some time in the past, may also have reached
reproductive maturity during the summer of their birth, but under
present conditions in southwestern Alberta, early maturation is not
feasible. Juvenile females breeding at about 6 weeks of age (75 gm)
would conceive in early August and wean litters in late September
when environmental conditions would likely prevent the survival of
young. Hence, juveniles must wait until the following year before

breeding successfully.

Even then the pika has a reproductive advantage over other subalpine and alpine mammals of similar size. Eutamias minimus and E. amoenus do not always breed as yearlings in southwestern Alberta (Sheppard 1969), and many E. minimus do not breed as yearlings in Colorado (Vaughan 1969). Females of Spermophilus columbianus do not breed as yearlings at higher elevations (Moore 1937), and unpublished data on Spermophilus lateralis (present study) indicate that they do not always breed as yearlings. All of the above species except pikas are hibernators, and the earlier maturity evident in pikas may result from their relatively large size in autumn and their ability to continue development over winter.

Many mammals appear to have smaller litter-sizes during their first breeding experience than subsequently, and this may be brought about through a reduction in the number of ova shed (Conaway and Wight 1962; Flux 1967; McIlwaine 1962) or through greater prenatal losses suffered by that age group (Millar 1970, Sheppard 1969). At least one species of Asian pika (Ochotona pusilla) produces smaller litters during their first breeding experience than during subsequent breeding (Shubin 1965). No such differences were found in Ochotona princeps. Yearling females, although significantly lighter than older females at the beginning of the breeding season, shed just as many ova and suffered no greater prenatal losses than females with previous breeding experience.

The evolution of litter-size has probably received more attention than any other reproductive parameter, so will be dealt with in detail. Lack (1948) suggested that the number of young produced per litter

is limited by the numbers of young that the parents can successfully raise, and that there is the evolutionary alternative between producing many small, weak offspring or fewer, but larger and better nourished offspring. A comparison between pikas in California (Severaid 1955) and Alberta (present study) indicates that the same alternative is not always attained. In California, females (average non pregnant weight = 137 gm) produced young weighing an average of 8.3 gm at birth (from litter-sizes of 2 - 5), while in Alberta, females (average non pregnant weight = 133 gm) produced young weighing an average of 10.1 gm at birth (from litter-sizes of 2). Large birth weights may be advantageous with the shorter growing season in Alberta, and may be influential in causing smaller litter-sizes.

There appears to be an upper limit to the number of offspring that can be successfully nourished in Alberta. Many females gave birth to three young, but only two were usually weaned. Although the limit of two young at weaning may be considered a local phenomenon, data from Colorado and Utah indicate that the same limit may exist there. Embryo counts from that area (see Appendix II) indicate that many females (16 of 26) give birth to three or four young, while Krear (1965) noted that the number weaned was usually two.

No other studies were found where survival in relation to litter-size during lactation was documented for a natural mammalian population. However, Hamilton (1962) found a limit to lactation in captive tree mice (Phenacomys longicaudus) fed an abundance of natural foods, and attributed the limit to the low quality of the food consumed by females. Myers and Poole (1963) found faster growth rates in smaller litters of Oryctolagus cuniculus, but did not relate this to food

supply of the female. Although female pikas had low fat reserves during lactation and appeared to be under some sort of nutritional strain at that time, the strain is not likely the result of low quality or quantity of available forage. Forage in the areas studied is nutritious (Johnson et al. 1968) and abundant during the breeding season. Nutritional strain during lactation may be related to the large size and rapid growth of nestlings. Perhaps lactating females do not have sufficient time to forage enough or perhaps the milk supply is limited by the rate at which the females can convert ingested food into milk. Nestlings that die are not likely runts that perish at birth; smallest embryos in litters of three during late gestation averaged only 14% lighter than heaviest embryos. The only dead nestling found in this study was about 14 days of age.

Evolutionary reductions in litter-size to ensure that optimum numbers of young are nursed may be brought about through a reduction in the ovulation rate or capacity of the uterus to support embryos. A uterine capacity may limit the number of embryos implanted as in elephant shrews (Elephantulus myurus) (Horst and Gillman 1941) or through a limit to the numbers of embryos carried to term as in the alpaca (Lama pacos) (Fernandez-Baca et al. 1970). Uterine capacity may be more of a limiting factor to litter-size in wild mammals than previously thought. Greater prenatal losses in larger litters indicates some sort of restriction placed on litter-size by the uterus. Larger losses in large litters have been noted in white-tailed deer (Odocoileus virginianus) (Ransom 1967) and Oryctolagus cuniculus (Poole 1960), and the trend is evident in other data presented for Oryctolagus cuniculus (Brambell 1942), Lloyd 1963, McIlvaine 1962), Lepus europaeus

(Flux 1967) and snowshoe hares (Lepus americanus) (Newson 1964).

The pika appears to have a uterine capacity of three embryos, showing high losses (generally prior to implantation) in litters of four. A uterine capacity of three in conjunction with a lactation capacity of two could be maintained over evolutionary time. A reduction in the ovulation rate or the capacity of the uterus to match the number of young that can be nursed would only be selected for if the wastage of ova contributed in some way to the death of the parent or surviving offspring. Perhaps, in the pika, there is no selective disadvantage to the loss of one "extra" nestling available in case one is lost for some other reason.

Lord (1960) suggested a relationship between latitude, the severity of winter weather, mortality, carrying capacity of the environment, and litter-size. In his view, species with heavy mortality are below the carrying capacity of the environment when breeding commences and are free to raise large litters. Such a system would require those populations with high mortality to have larger litters than populations with low mortality -- a combination that is frequently noted, probably because populations with high mortality and low fecundity tend to become extinct. Litter-size in relation to mortality of mature pikas (Table 20) indicate that the two species with highest mortality rates (Ochotona macrotis and Ochotona rutila) do have the largest litters, but any relationship between mortality and fecundity may be explained by high mortality being necessary to maintain stability in populations with high fecundity. The real issue with Lord's hypothesis is whether or not there is a causal relationship between carrying capacity of the environment and litter-

Table 20. Litter-size in relation to mortality of mature animals in populations of pikas.

Population	Mortality (per cent)**	Mean Litter-Size (embryo counts)	Source
O. princeps (Colorado and Utah).	(85) 43.4	(26)* 2.9	present study Johnson 1968, Hayward 1952
O. princeps (Alberta)	(448) 45.0	(80) 2.3	present study
O. macrotis	(43) 58.2	(?) 6.0	Bernstein 1964
O. rutila	(37) 64.8	(75) 4.2	Bernstein 1964

* Sample size
** Based on % yearlings in mature population. See Appendix III.

size. In the pika, size of successful litters appears limited by the physiological capacity of the female rather than environmental factors.

Spencer and Steinhoff (1968) assumed that parental mortality will vary with the size of the litter produced and suggested that animals producing many litters during a breeding season will have smaller litters than animals having few litters in order to maximize the number of offspring produced during the female's lifespan. A comparison of litter-sizes of pikas in relation to the number of litters produced by mature females each breeding season (Table 21) indicates no trend towards smaller litters with longer breeding seasons. In addition, animals producing litters (females) did not suffer significantly higher mortality than animals not producing litters (males), and the assumption behind their argument may not be valid.

In general, the hypotheses proposed by Lord (1960) and Spencer and Steinhoff (1968) are not supported by data from studies of pikas. The pika appears to be producing as many offspring as can be successfully raised, supporting Lack's hypothesis, at least in part. His view that "...food supplies determine, through natural selection, the reproductive rates of all higher animals..." (Lack 1970) may not be entirely true, since food was superabundant during the breeding season. Sadleir (1969a) suggested that the presence of a breeding season alleviates the detrimental effects of nutrition on reproduction, and this appears to be true for the pika. A combination of factors (size at birth, growth rate of young during dependence, lactation capacity of females) probably limits the number of young successfully

Table 21. Litter-size in relation to numbers of litters per
season in pikas.

Species	Litters per Season	Average Litter-size (embryo counts)	Source
O. hyperborea	1	4.8	Kapitonov 1961
O. princeps (Alberta)	2	2.3	present study
O. princeps (Colorado and Utah)	2	2.9	see Appendix II
O. alpina	2	2.2	Revin 1968
O. daurica	2	7.0	Nekypolov 1954*
O. rutila	2-3	4.2	Bernstein 1964
O. pallasi	2-3	8.0	Shubin 1956*
O. pallasi	3	6.0	Tarasov 1950*
O. macrotis	2-4	6.0	Bernstein 1964
O. princeps (California)	3-4	2.8	Severaid 1955
O. pusilla	3-5	9.0	Shubin 1965

* Not seen; cited by Bernstein 1964.

raised.

Timing of Reproductive Losses

The pika exhibited surprisingly little variation in reproductive parameters, significant differences occurring only in 1970. A schematic summary of reproductive events is presented in Fig. 7.

No losses were attributable to a decrease in the number of ova shed by females contributing to the breeding effort. An overall average of 2.64 $\pm$ .04 ova were shed by all females. Similarly, no variation in partial preimplantation losses (10% of all ova) or partial post implantation losses (3% of all ova) were recorded. Most of the partial prenatal losses were probably caused by failure of ova to be fertilized or subsequent embryonic abnormalities, although 9 of 30 losses (30%) were from females producing four ova and may have been lost because of a limited capacity of the uteri. Partial post implantation losses were not very different from the 4% resorption loss recorded for Ochotona pusilla (Shubin 1965).

Loss of total litters prior to implantation could not be estimated, but losses of whole litters after implantation were recorded only for 10 of 17 females (59%) taken during the first littering period of 1970. Other Lagomorphs, notably Oryctolagus cuniculus, may suffer heavy losses of entire litters during pregnancy (Brambell 1942). In the pika such losses appeared to have little adverse effect upon the total numbers of young produced since all females appeared to breed again. The only consequence of the loss of whole litters during pregnancy was delay in the time of birth of the first litter young. Only 34% of marked females conceived a second litter during 1970,

Figure 7. Schematic summary of reproductive losses in a

hypothetical population of 100 mature female

pikas in relation to availability of forage.

A. Seasonal progression of forage (grams protein
per square meter of feeding area).

B. & C. Breeding during 1968 to 1970. The number
of ova shed (open circles) and number surviving
to implantation (triangles), birth (closed
circles) and weaning (squares) for first litters
(solid lines) and second litters (broken lines)
are presented on an approximate seasonal basis.

A. FORAGE

B. BREEDING 1968 & 1969

C. BREEDING 1970

MAY   JUNE   JULY   AUGUST
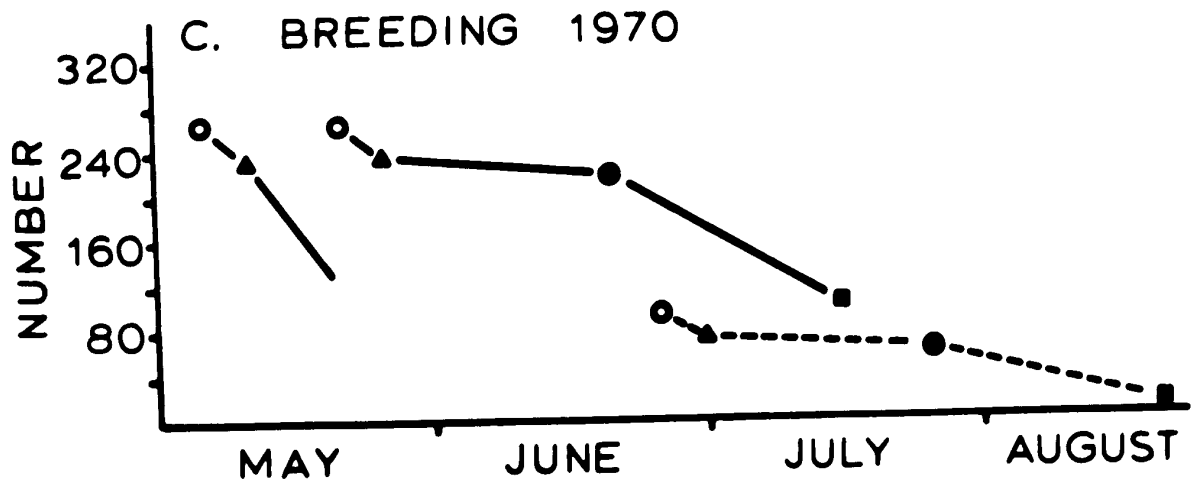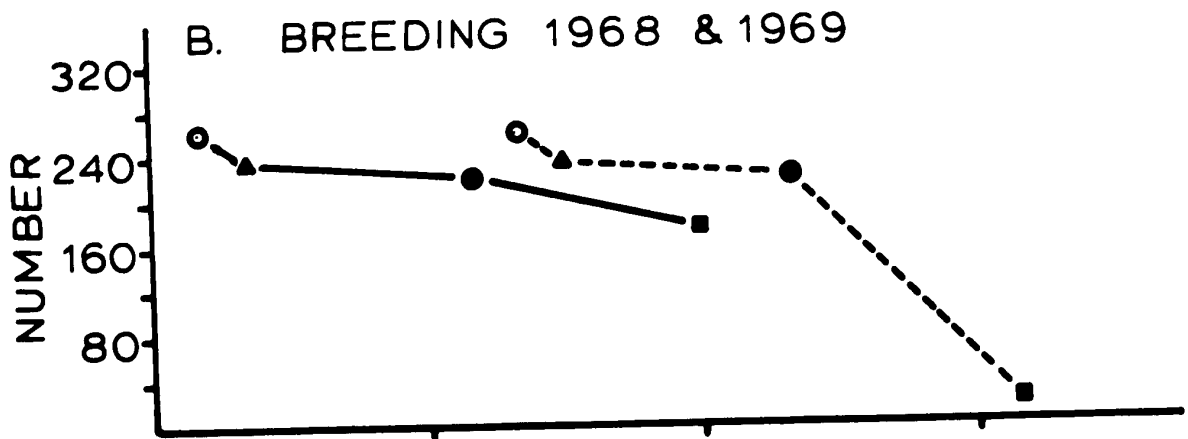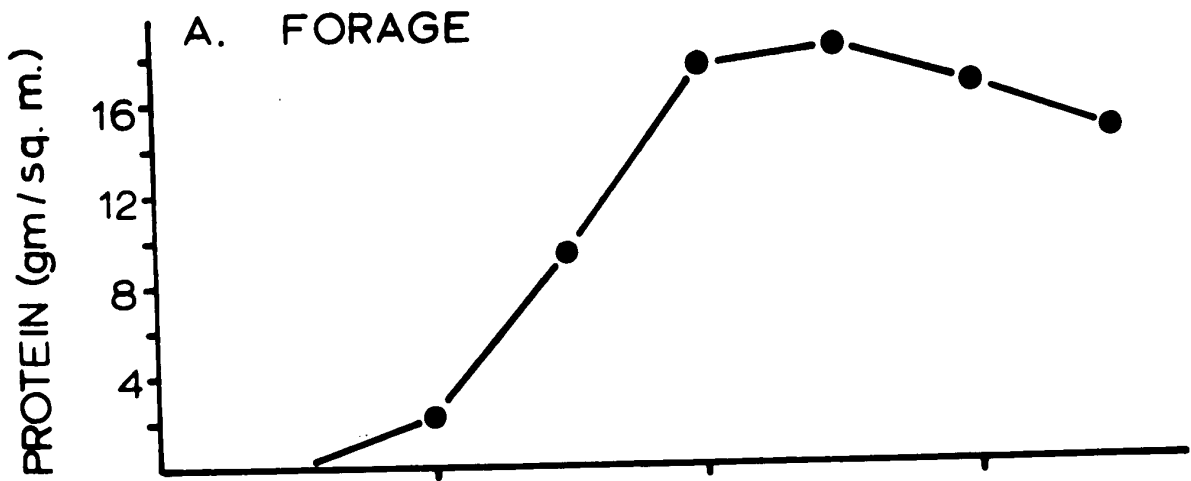
but this had little effect on total productivity since second litter young were generally lost anyway.

By far the greatest reproductive losses occurred between birth and weaning and resulted from both partial and total litter losses. Losses to successful litters accounted for approximately 21% of all live births and were apparently greater in litters of three than in those of two. Loss of whole litters affected 48% of all litters born in the marked population. Different losses were found between the first and second littering periods. Loss of all nestlings during the first littering period was found only in 1970 when 35% of the first litters were lost. Losses of second litters in the nest were heavy during all three years when 92% of all litters were lost.

There appear to be few studies of natural populations where losses during lactation were recorded, but the period of lactation may prove to be the time when greatest reproductive losses occur. Heavy losses during lactation, at least under some conditions, have been estimated for rodents (Hoffman 1958, Krebs 1964, Sadleir 1965), ungulates (Pruitt 1961, Le Resche 1968, Cook et al. 1971) and lagomorphs (Myers and Poole 1963, Conaway et al. 1963).

Reproduction in Relation to the Proximate Environment

Although animals have an evolved limit on the number of offspring produced, the reproductive potential is rarely achieved. Changes in environmental conditions affect the female's ability to produce offspring so that seasonal, regional, or yearly variations in fecundity may be evident. The ability to respond to environmental conditions if presumably subject to natural selection, and hence adaptive.

Reproduction in Relation to Meteorological Conditions

Seasonal changes in meteorological conditions appeared to have little effect on breeding in the pika, possibly because subalpine and alpine conditions, although severe, are fairly stable from year to year, and the pika has adapted to them. However, adverse weather may have been the cause of resorption of total litters during May of 1970, when a late storm left a heavy snow cover. Neither body weights nor relative fat content of carcasses were significantly lower during that period than in previous years and losses did not appear related to starvation or poor nutrition. Similar losses through resorption have been associated with blizzard conditions in black-tailed jack rabbits (Lepus californicus) (Tiemeier 1965) and flooding in swamp rabbits (Sylvilagus aquaticus) (Conaway, Baskett and Toll 1960), but not during flooding in Oryctolagus cuniculus (Meyers and Poole 1962), or following fire in Lepus americanus (Keith and Surrendi 1971). During the present study no changes in breeding were recorded in relation to cool weather in May 1968, heavy rains in June 1969, or extremely dry conditions in August 1969.

The reduction in the number of females carrying a second litter in 1970 may have been a consequence of interrupted breeding during that year. Males went out of breeding condition in late June 1970, as they did in 1968 and 1969, and females giving birth to first litters later than usual may have been too late to conceive again.

Reproduction in Relation to Food Supply

Quantity or quality of food has been suggested as the cause of changes in reproductive parameters in a number of mammals (reviewed

by Sadleir 1969a), but appears to have little effect on pikas living
under natural conditions. No data were obtained that indicated that
availability of food had any effect upon pregnancy or lactation.
Comparisons of ovulation rates and prenatal losses between first and
second littering periods, when quantity and quality of forage, as
well as condition of the animals, differed, indicated no changes in
losses during pregnancy. Similar comparisons between animals from
lush, stunted, and sparse meadow habitats, where the quantity of
available forage and the size of hay piles differed, indicated no
differences in the condition of collected animals or in reproductive
parameters. Juvenile pikas stored significantly less material in
hay piles than older females, but bred as successfully the following
year, and the addition of one month's food supply (1000 gm) to winter
food stores did not cause an increase in the number of young weaned
the following year.

Losses of young during lactation were heavy but did not appear
attributable to the availability of food to the females. Mortality
of nestlings was highest during the second littering period, when
forage was more abundant than during the first littering period (see
Fig. 7). Relative fat content of females was lowest during July when
second litters were being nursed and the strain of producing a first
litter may have affected the females' ability to produce a subsequent
litter, as has been suggested for Odocoileus virginianus (Verme 1967).
However, two second litters were raised by females that also raised
first litters and three females that lost their first litters bred
again but failed to raise a second litter.

Losses during lactation have been attributed to a drying of

pastures in <u>Oryctolagus</u> <u>cuniculus</u> (Myers and Poole 1962, Stodart and
Myers 1966), and to drought in the red kangaroo (<u>Megeleia</u> <u>rufa</u>)
(Newsome 1965). In the present study, losses were heaviest during
August when pastures were generally dry, but nutritious forage was still
available. Water was not in short supply on the areas studied since
it flowed from beneath many rock slides all summer, presumably from
melting ice.

Changes in quality of available forage are difficult to relate
to reproductive losses because the nutritional requirements of the
pika are unknown. Protein, calcium, and phosphorus are considered
important to lactation in domestic animals (Maynard and Loosli 1962,
Moustgaard 1959), but none of these were in obviously short supply
on the areas studied. Protein content of forage decreased throughout
the summer but forage was abundant and plants of high protein content
could be eaten selectively. The same argument applies to calcium
and phosphorus requirements.

Reproduction in Relation to Social Environment

Although the main aim of the present study was to investigate
reproduction in relation to factors of the physical environment,
some data were obtained which indicated that social factors may be
the most important cause of losses of whole litters during the nesting
period. Emotional disturbances or crowding can affect lactation in
laboratory animals (Cowie and Folley 1961, Christian and Lemunyan 1958)
and similar factors may be important in natural populations of the
pika. All nestlings in first litters were lost only in populations
with relatively high densities, and the trend, although based on

rather scanty data, was towards greatest losses at highest densities. These losses may have been in some way attributable to interference from other females or males. Unpublished data on home ranges indicate that females in populations where whole first litters were lost in the nest shared an average of 33% of their home ranges with other pikas, while females in populations where no first litters were lost shared an average of only 10% of their home ranges. Losses may have occurred through direct interference at the nest or through keeping the females from attending the nest. There were no differences in the size of successful litters, indicating that losses were of an all or none effect.

High loss of litters from the second littering period occurred in populations of high and low density, but may be attributable to social interference or to a conflict of interests of the females between collecting hay for winter food stores and caring for young. Although the latter hypothesis can only be checked by comparing losses with areas where hay piling activity does not coincide with reproduction, the lack of importance of the hay pile to the animals' total winter food resources may indicate that the hay piling interests of the females was relatively unimportant.

Losses of second litters during nesting may be caused by interference from other mature animals or from juveniles. Perhaps behavioral changes during hay piling cause increased friction between animals, or perhaps the presence of first litter juveniles, which have a strong tendency to settle on their home area, interfere with the raising of second litter young. An attempt to determine the effect of the presence of first litter juveniles on the raising of second

litter young was attempted by removing all first litter young from one population at weaning. Unfortunately, the experiment was inconclusive because of a lack of second litter conceptions during that year.

Relatively few studies of natural populations of mammals have related nestling losses to density or behavioral phenomena. Sadleir (1965) related juvenile mortality (post weaning) of deer mice (Peromyscus maniculatus) to aggression of males, but such a mechanism does not seem likely in the pika since losses occur prior to weaning. The behavior of females during lactation appears to be a more likely cause of the losses. Myers and Poole (1963) found no relationship between nestling mortality and population density per se or dominance of females in Oryctolagus cuniculus.

SUMMARY AND CONCLUSION

Breeding of the pika in subalpine and alpine regions of southwestern Alberta was evaluated in relation to environmental parameters, particularly food supply. Pikas matured as yearlings and two litters per season were possible, with a potential of 2 - 4 young per litter. Breeding commenced in late April and early May, prior to the emergence of new vegetation, and the last juveniles were weaned in August.

Many reproductive parameters varied little in relation to environmental conditions and appeared related to an evolved reproductive pattern. Lack's hypothesis that females produce as many offspring as can be successfully raised and that "...food supplies determine, through natural selection, the reproductive rates of all higher animals..." (Lack 1948, 1970) is supported only in part by the data. Females apparently produce as many offspring as can be supported, but not in relation to food resources. Quantity and quality of forage varied considerably but did not appear in short supply at any time. The physiological capacity of the female to produce milk may have been important in limiting litter-size.

Greatest reproductive losses involved total litters during lactation. These losses were not attributed to changes in food supply or meteorological conditions and may have been related to behavioral changes in females.

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Appendix I. Summary of reproductive patterns of some Asian Ochotonidae.

Species	Habitat	Litters per Season	Mean Embryo Counts	First Breeding	Source
O. alpina	mountain talus	2	2.2	—	Revin 1968
		2-3	3**	yearling	Khmelevskaya 1961
		2	2-3***	yearling	Yergenson 1939*
O. daurica	thickets, meadows	2	7.0	summer of birth	Nekypolov 1954*
O. hyperborea	rocks	1	4.8	yearling	Kapitonov 1961
O. macrotis	talus, rocky meadows	2-3	5**	yearling	Zimina 1962
		2-4	6.0	summer of birth	Bernstein 1964
O. pallasi	desert rock	2-3	8.0	summer of birth	Shubin 1956*
		—	5.8	summer of birth	Chergenov 1961*
		3	6.0	summer of birth	Tarasov 1950*
O. pusilla	thickets	3-5	9.0	summer of birth	Shubin 1965
O. rutila	rocky fields	2-3	4.2	yearling	Bernstein 1964

* Not seen; cited by Bernstein 1964.   ** Mode.   *** Range.

Appendix II. Litter-size of North American Ochotonidae, based on counts of embryos.

Region	Litter Size					Source
	1	2	3	4	5	
California	1	6	8	2	1	Severaid 1955
		2	3			Grinnell et al. 1930
Nevada		1	5	2		Hall 1946
Oregon				2		Bailey 1936
			2			Roest 1953
Colorado	1	2	1			Johnson 1967
		1	2			Anderson 1959
			1**		1	Dice 1926, 1927
			3	1		Present study
Colorado & Utah			3	4	5	Hayward 1952
Utah			1			Long 1940
British Columbia			1**			Underhill 1962
Alberta	8	38	33	1		Present study
Alaska*				1		Dixon 1938
			2	1		Rausch 1970

* O. collaris
** Born

Appendix III. Determination of age of mature pikas.

Incremental rings in the bones of the lower jaw of a wide variety of mammals have been used as a method of age determination (Bernstein and Klevezal 1965, Meier 1957, Morris 1970). These lines are evident in dense bone and are apparently the result of seasonal changes in growth rates. Annual incremental lines in the diastema of the lower jaw of Ochotona macrotis and Ochotona rutila have been described by Bernstein and Klevezal (1965). In general, their methods have been applied to Ochotona princeps in the present study.

Lower jaws of collected pikas were fixed in A.F.A. and stored in 70% alcohol until sectioned. They were decalcified in R.D.O. (Du Page Kinetic Laboratories Ltd.) for 8 - 12 hours, embedded in paraffin, and sectioned at 15 - 20μ across the diastema (see Fig. 8). The sections were heavily stained with Delafield's haematoxylin.

Juvenile animals have very porous bone similar to that of the Asian pikas. One line is formed apparently prior to their first winter and is analogous to the "weaning line" observed in the hedgehog (Erinaceus europaeus) (Morris 1970). This line is not always evident, but can generally be distinguished from all other lines by its thinness and somewhat convoluted nature, and is located along the internal edge of the bones (see Plate II).

Mature animals possess incremental lines which are apparently layed down during winter. Ochotona princeps appears to differ from Ochotona macrotis and Ochotona rutila in frequently having more than one line formed during winter, but these lines are clumped and can be separated in all but a few animals.

83

Figure 8. Diagramatic presentation of plane of section of

jaws (A - A) and cross sectional view of diastema

of lower jaw showing area of incremental lines.

BONE

INCREMENTAL
LINES

CARTILAGE

TOOTH

84
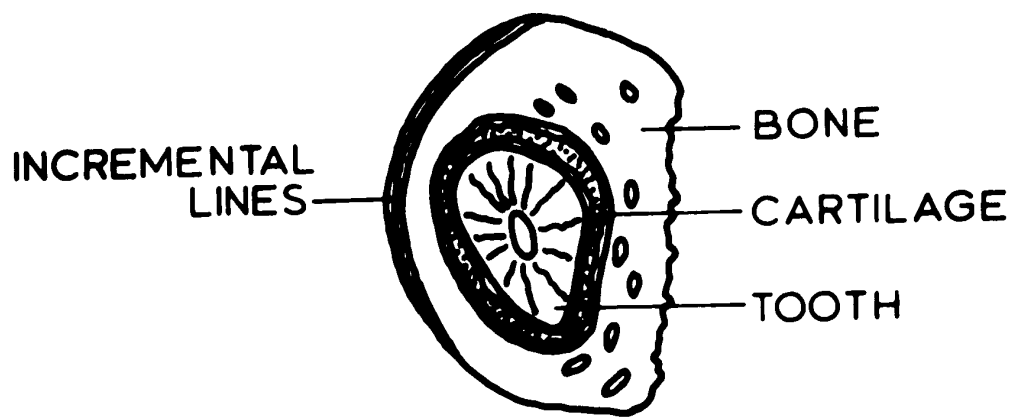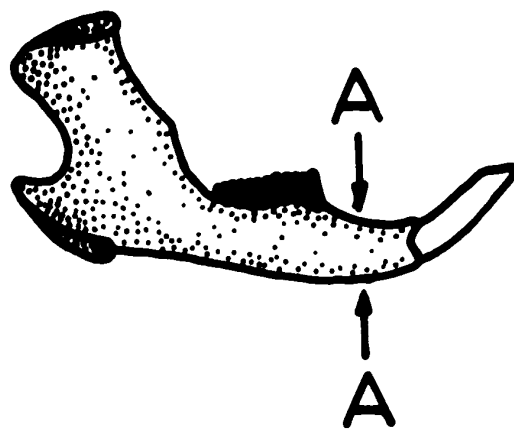
Plate II. Micrographs of jaw sections of pikas. A = juvenile
(August); B = yearling; C = two years; D = four
years. W.L. = weaning line.

A

B

C

D

1

A

B

W.L.

1

C

W.L.

1   2

D

4   3   2   1

The accuracy of the technique was confirmed on 9 known age animals from a marked population in 1970.

Absolute age data for 448 mature pikas from southwestern Alberta and 85 mature animals from Colorado (specimens courtesy Dr. D.G. Cameron) are compared with _Ochotona_ _macrotis_ and _Ochotona_ _rutila_ in Table 22. Assuming a stable population, the proportion of yearlings in the sample indicates the mortality of mature animals. Pika populations in Alberta and Colorado appear to have similar age structures, and tended to live longer than the Asian pikas. Males appeared to live slightly longer (not significantly different) than females.

Table 22. Age structure and mortality rates of pikas. Age structure based on incremental lines in the bone of the lower jaw. Mortality rates based on proportion of yearlings (assumes stable population).

Species	Sex	Age							Per cent Mortality
		1	2	3	4	5	6	7	
O. princeps (Alberta)	female	79	45	19	12	4	2	0	49.06
	male	123	82	40	21	15	5	1	42.85
	Total	202	127	59	33	19	7	1	45.08
O. princeps (Colorado)	female	16	12	3	2	1	0	0	47.05
	male	21	16	6	4	2	1	1	41.17
	Total	37	28	9	6	3	1	1	43.52
O. rutila*	Total	24	10	3	0	0	0	0	64.86
O. macrotis*	Total	25	14	4	0	0	0	0	58.13

* From Bernstein and Klevezal 1965.

Appendix IV. Determination of age of embryos.

During late gestation age of embryos can be determined from
weight of embryos if gestation period and birth weights are known
(Huggett and Widdas 1951). The gestation period of the pika is 30
days (Severaid 1950) and birth weights in Alberta averaged 10.1 gm;
two born in captivity weighed 9.6 and 10.1 gm and the four largest
embryos collected weighed 9.3, 9.9, 10.1 and 11.4 gm.

The formula for determining age (from Hugget and Widdas 1951) is:

$$t = \frac{w^{1/3}}{a} + t'$$

where: t = age of embryo

$w^{1/3}$ = cube root embryo weight

t' = (a constant) .04 x gestation period

a = a specific growth constant (from the formula,

knowing gestation period and birth weight).

In the pika t' = 12 and a = 0.12

Embryo weights at various stages of pregnancy were predicted
from the formula and are presented in Table 23. Corresponding lengths
of embryonic swellings were taken from embryos of known weight.

An attempt was made to check the age scale by breeding animals
in captivity. Eight females were bred and sacrificed at various times
post coitus. Four females sacrificed during early pregnancy had
embryos too small to remove intact, and three sacrificed after mid
pregnancy had resorbing embryos. One female sacrificed on day 14
of pregnancy had 3 embryonic swellings 9 mm in length and a mean embryo
weight of .026 gm.

Age of embryos prior to mid pregnancy was determined from length

Table 23. Weight of embryos and length of embryonic
swellings in relation to stage of gestation.
Weights calculated from the formula (see App.
IV). Length of embryonic swelling based on
known weight of embryos.

Days of Gestation	Mean Weight of Embryos (gm)	Length of Embryonic Swelling (mm)
1	—	—
2	—	—
3	—	—
4	—	—
5	—	0*
6	—	0*
7	—	2*
8	—	3*
9	—	4
10	—	5
11	—	6
12	—	7
13	—	8
14	.02 - .03*	9*
15	.04 - .06	10
16	.07 - .16	11 - 12
17	.17 - .30	13 - 14
18	.31 - .42	15 - 16
19	.43 - .58	17 - 18
20	.59 - .78	19 - 20
21	.79 - 1.02	21 - 22
22	1.03 - 1.98	23 - 24
23	1.99 - 2.64	25 - 27
24	2.65 - 3.39	28 - 30
25	3.40 - 4.21	31 - 34
26	4.22 - 5.29	35 - 38
27	5.30 - 6.45	39 - 42
28	6.46 - 7.78	43 - 48
29	7.79 - 9.30	49 - 55
30	9.31 +	56 +

* Pregnancies of known age.

The accuracy of the technique was confirmed on 9 known age animals from a marked population in 1970.

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	male	123	82	40	21	15	5	1	42.85
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O. princeps (Colorado)	female	16	12	3	2	1	0	0	47.05
	male	21	16	6	4	2	1	1	41.17
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$$t = \frac{w^{1/3}}{a} + t'$$

where: t = age of embryo

$w^{1/3}$ = cube root embryo weight

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IV). Length of embryonic swelling based on
known weight of embryos.

Days of Gestation	Mean Weight of Embryos (gm)	Length of Embryonic Swelling (mm)
1	—	—
2	—	—
3	—	—
4	—	—
5	—	0*
6	—	0*
7	—	2*
8	—	3*
9	—	4
10	—	5
11	—	6
12	—	7
13	—	8
14	.02 - .03*	9*
15	.04 - .06	10
16	.07 - .16	11 - 12
17	.17 - .30	13 - 14
18	.31 - .42	15 - 16
19	.43 - .58	17 - 18
20	.59 - .78	19 - 20
21	.79 - 1.02	21 - 22
22	1.03 - 1.98	23 - 24
23	1.99 - 2.64	25 - 27
24	2.65 - 3.39	28 - 30
25	3.40 - 4.21	31 - 34
26	4.22 - 5.29	35 - 38
27	5.30 - 6.45	39 - 42
28	6.46 - 7.78	43 - 48
29	7.79 - 9.30	49 - 55
30	9.31 +	56 +

* Pregnancies of known age.

of embryonic swellings since embryos were too small to examine.

Judging from variations within litters, embryo weight is probably accurate to within one or two days, while length of embryonic swellings in late gestation is probably accurate to within 3 days.

Appendix V. Determination of age of juveniles.

Age of collected juveniles was determined by relating body weight
to a growth rate scale based on 2 animals born in captivity and 16
independent juveniles in the marked population. Rates were determined
by dividing weight gain by time interval.

Both animals born in captivity (one litter) were fully furred
day 5 (19 gm), had eyes open and were moving around nest day 12 (35 gm),
and were moving about the cage day 13. The female appeared to be
still nursing on day 24 (58 gm).

In the wild, juveniles are probably weaned at about 50 - 60 gm;
the smallest juvenile caught was 45 gm. Juveniles remain near or
within the home range of the female until about 95 gm, the time when
some marked juveniles moved to other areas and stray juveniles (unmarked)
appeared in the marked population.

Mean growth rates of captive and wild juveniles are presented in
Table 24.

Captive juveniles in small cages had depressed growth rates and
are not considered further for that reason. No differences between
live trapped juveniles and those in large cages were evident. Although
the preweaning sample is small, there appears to be no difference in
growth rates between the preweaning and post weaning periods, but
growth slows down in the dispersal period.

These data were used to derive a growth rate curve (Fig. 9).
Growth was considered to be 1.7 gm/day from birth to dispersal, and
1.0 gm/day subsequently. The accuracy of the scale was checked by
plotting the subsequent weights of 16 live trapped juveniles whose

Table 24. Mean growth rates (gm per day) of wild and captive juvenile pikas, determined by dividing weight gain by time interval.

	Premaaning 0 - 50 gm	Post Weaning 51 - 95 gm	Post Dispersal 96 + gm
Live trapped	—	(11) 1.7 ± 0.11	(12) 1.0 ± 0.07
Captive 120 x 120 cm cage	(2) 1.8	(3) 1.6 ± 0.08	—
Captive 25 x 90 cm cage	—	(11) 0.8 ± 0.15	—

Figure 9. Growth rates of juvenile pikas (solid line), based
on a growth rate of 1.7 gm/day until 95 gm and 1.0
gm/ day after 95 gm (see Table 24). Circles
denote subsequent weights of juveniles aged by
weight at initial capture.
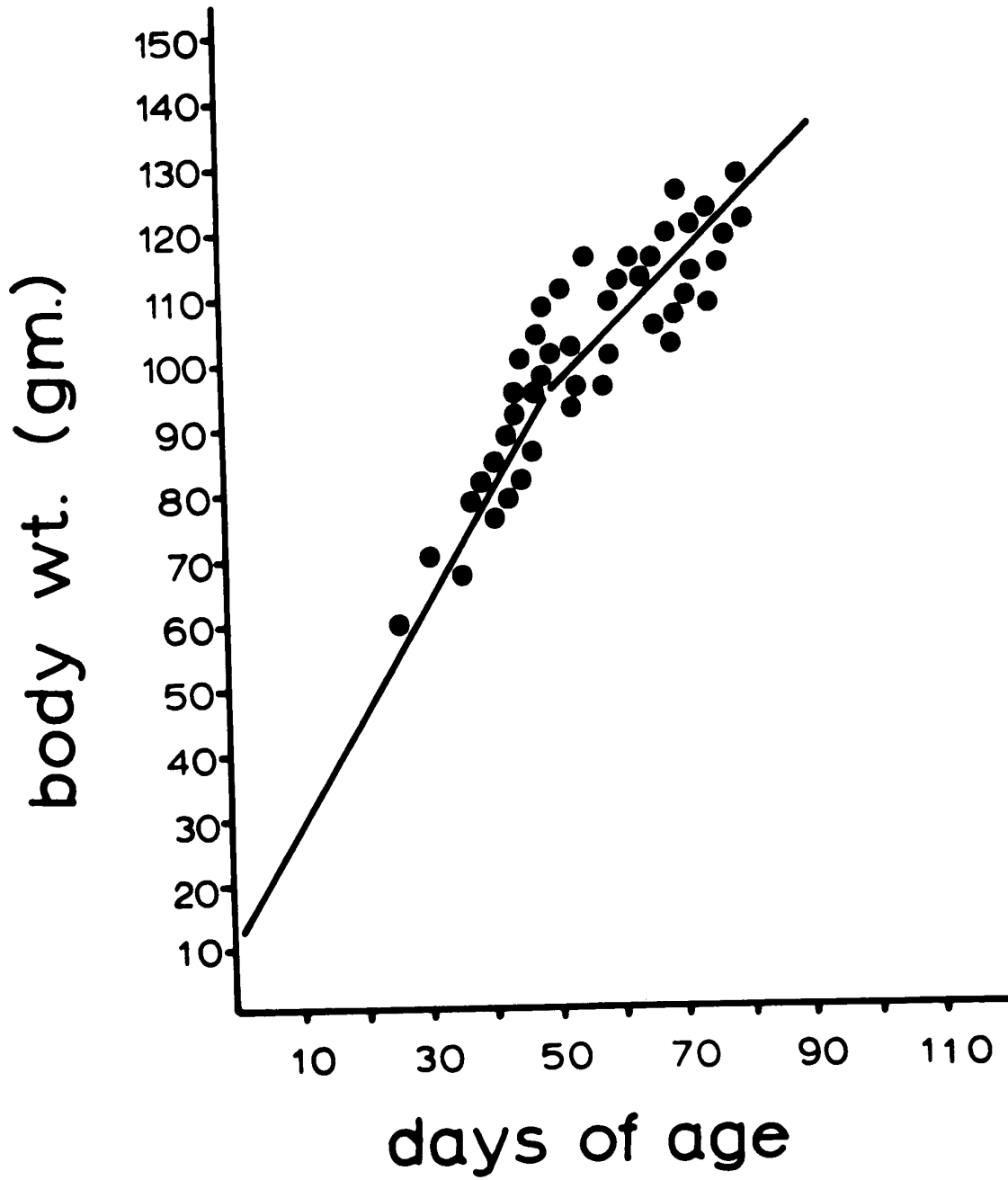
age was determined from weight at initial capture. The scale appears accurate to within 5 days during the post weaning period, and accurate to within about 10 days after dispersal.

Appendix VI. Summary of weather data for Gibralter Mountain, Sheep River, Alberta.

Year		June 1-15	June 16-30	July 1-15	July 16-31	August 1-15	August 16-31
1968	A*	12.5	15.9	23.1	17.1	16.4	13.1
	B	0.1	0.7	3.6	2.1	4.8	1.8
	C	10	8	5	6	7	5
	D	10	9	2	3	1	5
1969	A	14.8	11.0	13.1	19.2	19.4	18.0
	B	2.6	3.8	3.8	4.5	5.7	4.9
	C	3	12	10	1	0	2
	D	2	1	0	0	0	1
1970	A	15.4	17.6	20.8	17.6	20.1	19.5
	B	4.4	6.4	7.5	6.2	6.5	5.3
	C	8	6	3	11	4	3
	D	2	0	0	0	0	1

* A = mean maximum (degrees C)
  B = mean minimum (degrees C)
  C = days precipitation
  D = nights below freezing