FOOD HABITS IN RELATION TO THE ECOLOGY AND POPULATION DYNAMICS OF BLUE GROUSE

by

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ABSTRACT

The late spring and summer diet of blue grouse on lowland breeding ranges on Vancouver Island was determined by examination of the contents of 875 crops taken from birds collected on 3 study areas in the years 1950 through 1952 and 1957 through 1966.

The spring and early summer diet of males was mostly conifer needles, while adult females ate mainly leaf material and flowers during the same period. The food of chicks was mainly invertebrates until the birds reached the age of approximately three weeks, at which time plant material formed the greater portion of the diet. In late summer the diet of both adult and juvenile grouse was primarily fruits and seeds of trailing blackberry, salal, huckleberry, and other plants.

Selection of plant foods occurred at the time of ovulation and moult. As a result, the protein and mineral content of the diet was highest during periods of greatest need.

No apparent differences in the spring diet of females were found which could be related to poor early survival of chicks, or to a delayed hatch in 1962.

The various food types were eaten in similar relative proportions by adult and yearling grouse, and differences in reproductive performance of these two age classes could not be related to the diet of the grouse.

The altitudinal migration of blue grouse in late summer and autumn does not appear to be related to the availability or condition of the food supply at the time of departure of the birds.

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INTRODUCTION

The objectives of this study are to add to what is known of the late spring and summer food habits of blue grouse, *Dendragapus obscurus fuliginosus* (Ridgway) on Vancouver Island, and to determine their relevance to the biology and population dynamics of grouse.

The blue grouse has been studied on Vancouver Island from 1942 through 1944 by Fowle (1960) and by Bendell and his co-workers from 1950 through 1953 and from 1957 to the present. During this period there have been important changes in the ecology of the region under study and marked changes in the populations of blue grouse (Zwickel and Bendell, 1967).

This study was undertaken to determine the food habits of grouse on the different study areas, to relate these to the general ecology of the birds, and to examine them for possible correlation with known changes in the density and reproductive success of the populations. Food habits were studied by examination of crop contents. Other data on the behaviour and population ecology of the populations of blue grouse used in this study are mostly from Bendell (1954, 1955a and b), Zwickel (1965), Bendell and Elliott (1966, 1967) and Zwickel and Bendell (1967). The data obtained from analysis of crops permitted a relatively intensive study of summer food habits and a comparison of food habits between grouse from different populations. Most crops were collected in the years 1957 through 1966; 118 came from Lower Quinsam Lake and 543 from Middle Quinsam Lake.

Additional samples were those of 148 birds from Lower Quinsam Lake from 1950 through 1952, and 66 from Comox Burn in the years 1962 through 1966.

The migratory behaviour of blue grouse on Vancouver Island limits their presence on the summer breeding ranges to a period of approximately four months for males, six months for females, and three to four months for chicks. During the remainder of the year, they inhabit the conifer forests of the surrounding mountains (Hoffman, 1956; Bendell and Elliott, 1967). The adequacy of their food during the winter period may influence the performance of the birds during the subsequent breeding season (Koskimies, 1955; Boag, 1963; Jenkins _et al._, 1967), but this was outside the limits of the present study.

The population of blue grouse at Lower Quinsam Lake from 1950 through 1952 was extremely dense, and was stable (Bendell, 1954). By 1957, structural changes in the habitat had occurred and the population of grouse had greatly decreased (Zwickel, 1965; Bendell and Elliott, 1967). The populations at Middle Quinsam Lake and Comox Burn were relatively stable when studied (Zwickel and Bendell, 1967), with densities considerably lower than that found at Lower Quinsam Lake in the early 1950's. There were no apparent differences in annual mortality rates of adults among the populations studied (Zwickel and Bendell, 1967). No significant differences in brood sizes were found between areas, but such differences did occur between years on the study areas (Zwickel and Bendell, 1967; and unpublished data).

The study areas are near Campbell River on the east coast of Vancouver Island, and are described elsewhere (Bendell, 1954; Bendell and Elliott, 1967; Zwickel and Bendell, 1967). All areas had been climax forest which was logged and burned. Middle Quinsam Lake and Comox Burn were in relatively early stages of plant succession (Zwickel, 1965) during the period when grouse were collected, as was Lower Quinsam Lake from 1950 through 1952 (Bendell, 1954). Artificial replanting of conifers at Lower and Middle Quinsam Lakes increased the importance of conifers in the plant cover and hastened plant successional stages. By 1957, the vegetation at Lower Quinsam Lake had become very dense, due largely to the growth of coniferous trees. During the seral period following logging and burning, the numbers of blue grouse, black-tailed deer (*Odocoileus hemionus columbianus*), and black bear (*Ursus americanus*) on an area increase (Zwickel and Bendell, 1967), while mature forest is unsuitable breeding range for blue grouse (Bendell, 1954).

MATERIALS AND METHODS

Crops were obtained from grouse collected throughout the summer in the course of research on the population dynamics of blue grouse, and from those shot by hunters in autumn. Usually, an entire viscera was removed, wrapped in cheesecloth, and stored in 10 per cent formalin until examination. Contents of some crops were air-dried and stored in individual envelopes. All grouse were identified as to age and sex when the crop was removed; the date, time and place of collection was noted, as was the behaviour of the grouse at the time of collection. A total of 976 crops was collected from the summer ranges at Lower and Middle Quinsam Lakes and Comox Burn (Table 1). Of these, 101 were empty and were discarded.

The contents of each crop were separated into items and identified. Where possible, plants in the crops were identified to species and by part eaten, and animals to family. Plant names are from Peck (1941) and Preston (1961), those of invertebrates from Borror and DeLong (1954) and Borradaille _et al_. (1961). Unidentifiable plant material and grit were recorded separately. Foods were damp-dried and their volumes determined to the nearest 0.1 cc by water displacement in a graduated cylinder. Volumes less than 0.1 cc were recorded as "Trace". The dry weight of each food item in crops collected from 1957 through 1966 was also taken. To determine this weight, the materials were oven-dried (80°C) to constant weight, and weighed to the nearest milligram. Dry-weights are much more precise than volumetric

Table 1. Number of crops of blue grouse used in this study, by month of collection.

Month		March	April	May	June	July	Aug	Sept	Total
1957 through 1966 Lower and Middle Quinsam Lakes, and Comox Burn	males*	4	22	80	37	22	4		169
	females		10	45	33	32	45	50	215
	chicks				22	91	118	112	343
1950 through 1952 Lower Quinsam Lake	males*		1	15	9	4			29
	females		1	11	8	14	2		36
	chicks				17	44	22		83
							Grand total		875

* males and females include all birds of approximately one year of age and older, chicks are all birds less than 4 months old (both sexes)

measurements (Watson, 1964). This is important when considering the food of chicks, which often consume small quantities of a number of food items. Dry weights were not obtained for contents of crops collected from 1950 through 1952. All items were classified into one of five food types for general analysis, as follows; conifer needles, broad-leaf material, flowers, fruits and seeds, and animal matter. Broad-leaf material included all leaves except those of conifers.

All data were recorded on individual crop analysis forms. The aggregate percentage method of Martin et al. (1946) was used in tabulation of per cent volume and per cent weight. Frequency of occurrence was also determined, as it often presents a more accurate measure of what is eaten than volumetric data (Gilfillan and Bezdek, 1944).

The relative abundance of food species was measured in the field to determine the relationship between what was available and what was eaten. Data on plant abundance were obtained from Lower Quinsam Lake in 1952 and 1957, and from Middle Quinsam Lake in 1960 and 1966. The amount of ground covered by plant species and their frequency of occurrence on the summer range were determined from line intercepts and quadrats (Bendell, 1954; Elliott, 1966; and unpublished data).

The relative abundance of common invertebrates was determined by two sampling methods. Between May 25 and July 5, 1958, invertebrates were sampled at Middle Quinsam Lake. All invertebrates observed within a strip of ground and on the

vegetation to a height of one foot above the ground were collected (Stiven, 1961). During 1962, invertebrates were sampled in late July at Middle Quinsam Lake and Comox Burn with an insect sweep net at sites at which broods of grouse had been observed. Sweeps were made close to the surface of the ground for a distance of approximately 100 feet in each of the four cardinal directions from the approximate center of the brood location (F.C.Zwickel, personal communication). The frequency of occurrence of the groups of invertebrates was calculated as a percentage of the total number of samples taken.

RESULTS

Types of food eaten on the summer range

Crop contents of grouse collected on all areas from 1957 through 1966 were combined to determine the general food habits of blue grouse on their lowland breeding ranges on Vancouver Island.

Adult males

The food of males from the time of their arrival on the summer range to about the middle of June was predominantly conifer needles (Fig. 1). There was a rapid shift in diet from needles to fruits in the month of June. The amount of leaf material apparently increased in early April, and together with needles formed the bulk of the diet during the breeding season. After June, fruits rapidly became the main food and remained so for the rest of the summer. Flowers were eaten in greatest quantity during June, July and early August. Animal food was taken infrequently and in very small amounts.

Adult females

A striking difference between males and females was the preference shown by hens for early spring leaves (Fig. 2). Leaf material formed 55 per cent of the diet of females during April, May and early June, compared with 24.5 per cent of the food of males during the same period. A gradual transition from needles to other materials occurred in the diet of females from April to about the end of June (Fig. 2). The amount of fruits and seeds in the diet of the hens increased rapidly

FIGURE 1

Diet of adult males, March through August, 1957 through 1966.

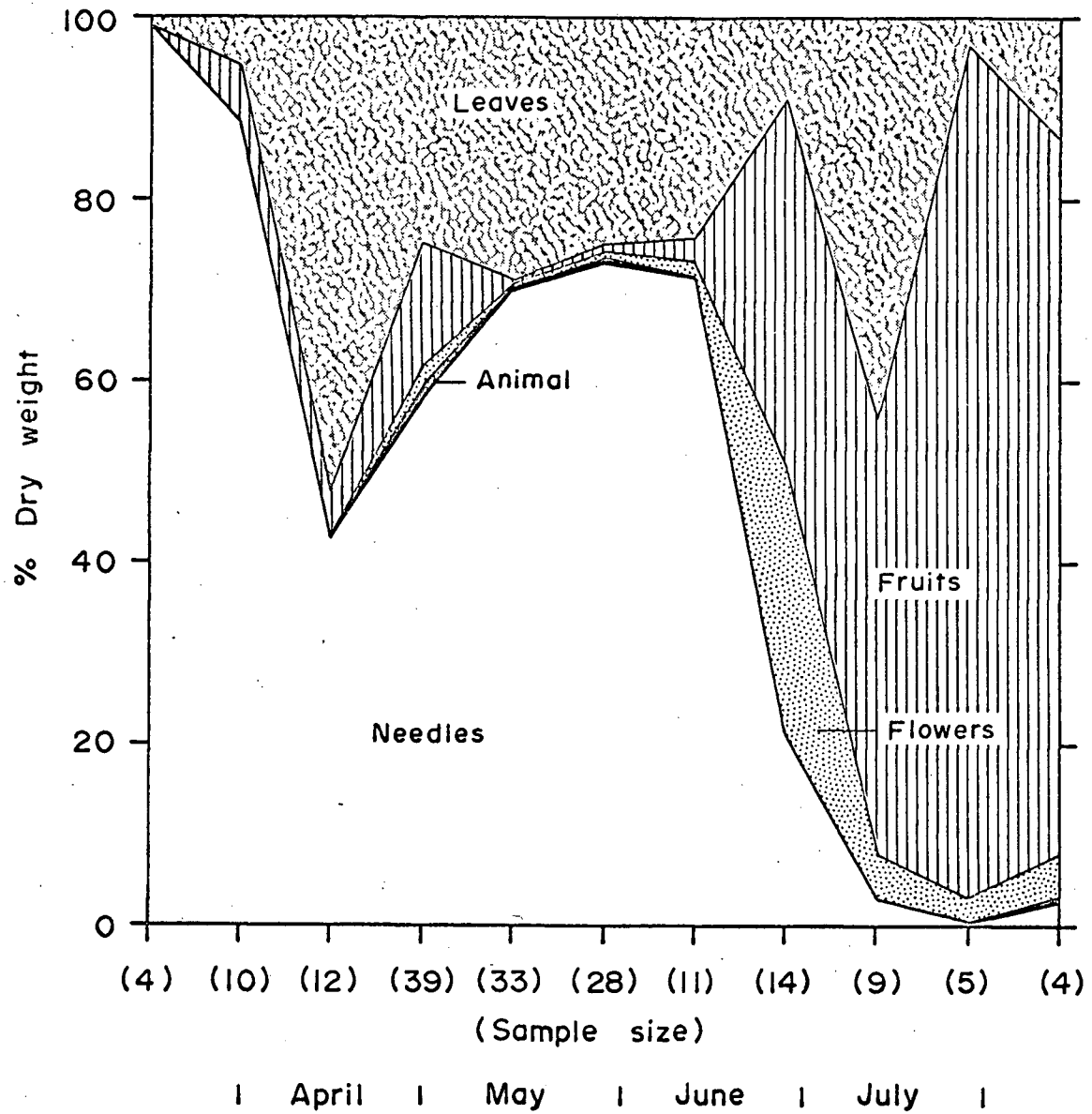
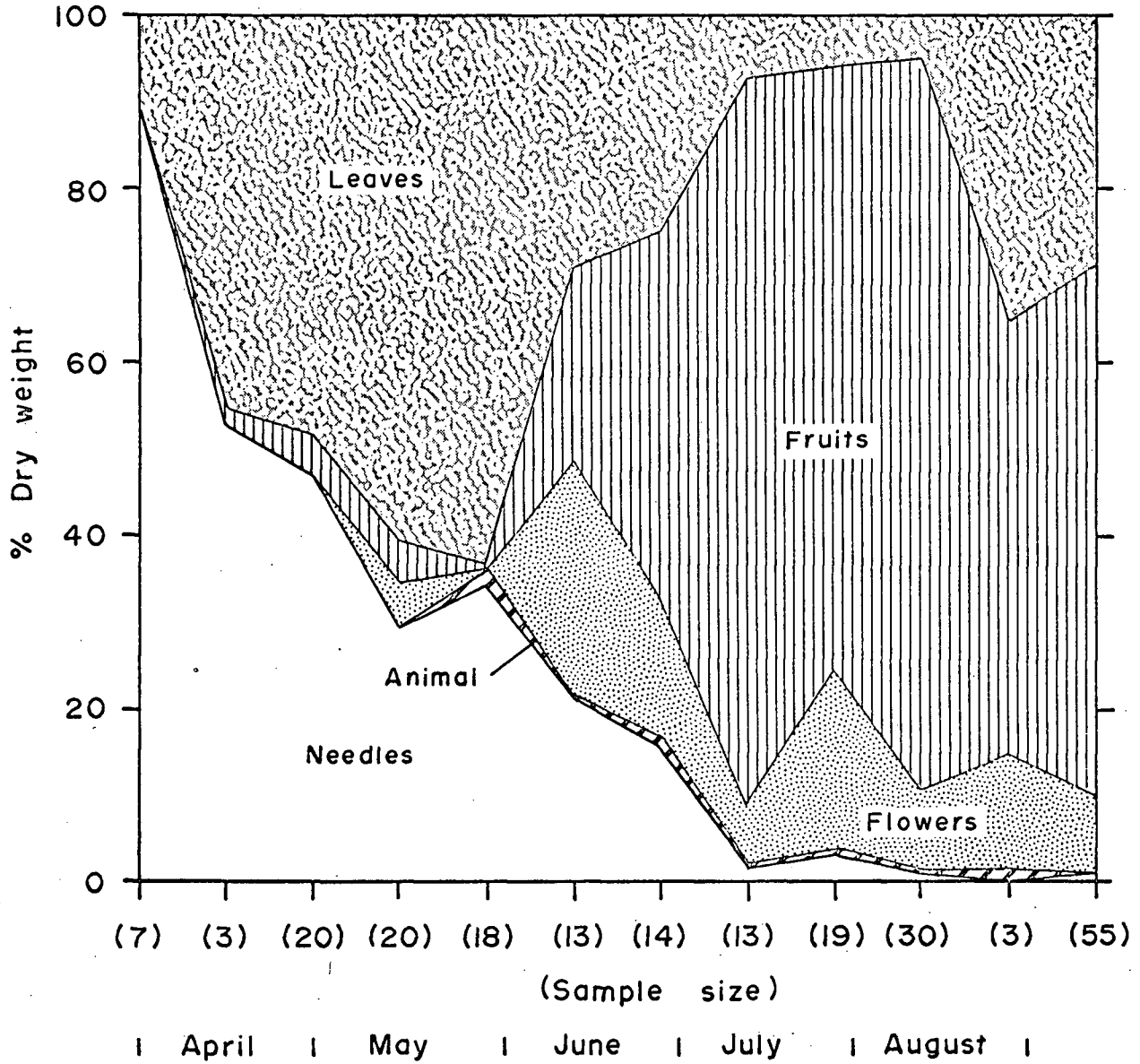

100
80
60
40
20
0
% Dry weight
Leaves
Animal
Needles
Fruits
Flowers
(4) (10) (12) (39) (33) (28) (11) (14) (9) (5) (4)
(Sample size)
April
May
June
July

FIGURE 2

Diet of adult females, April through September, 1957 through 1966.


100
80
60
40
20
0
% Dry weight
Leaves
Fruits
Animal
Needles
Flowers
(7) (3) (20) (20) (18) (13) (14) (13) (19) (30) (3) (55)
(Sample size)
April
May
June
July
August

during June and July, replaced leaves, and formed the bulk of their food from then until September when they left the summer range. Hens appeared to eat more flowers and fruits than males, but like them, consumed only a small amount of animal material.

Chicks

Blue grouse chicks, like the young of most tetraonids, feed largely on invertebrates during their early life (Fig. 3). Zwickel (1965) gives the peak of hatch for blue grouse on Vancouver Island as occurring between June 11 and July 1. In their first two weeks after hatching, the diet of chicks contained over 75 per cent animal food (Fig. 4). Some plant food was taken by chicks in June, and by July (Fig. 3) or when the chicks were approximately 20 days of age (Fig. 4), vegetation made up more than half their diet. By late July, chicks ate virtually the same kinds and relative amounts of food as the adults, with perhaps a larger amount of leaf material. This agrees with the findings of Beer (1943). Only small amounts of conifer needles were consumed by chicks, and these were eaten during the late summer.

Main foods eaten by adults and young

The main kinds of food consumed by grouse on the summer range are shown in Table 2. These species made up more than 80 per cent of the food eaten by all grouse. The remainder of the food came from a minimum of 38 species of plants. Unidentifiable material constituted less than 1.5 per cent of the total crop contents, and was largely leaf fragments. Thus

FIGURE 3

Diet of chicks, June through September, 1957 through 1966.

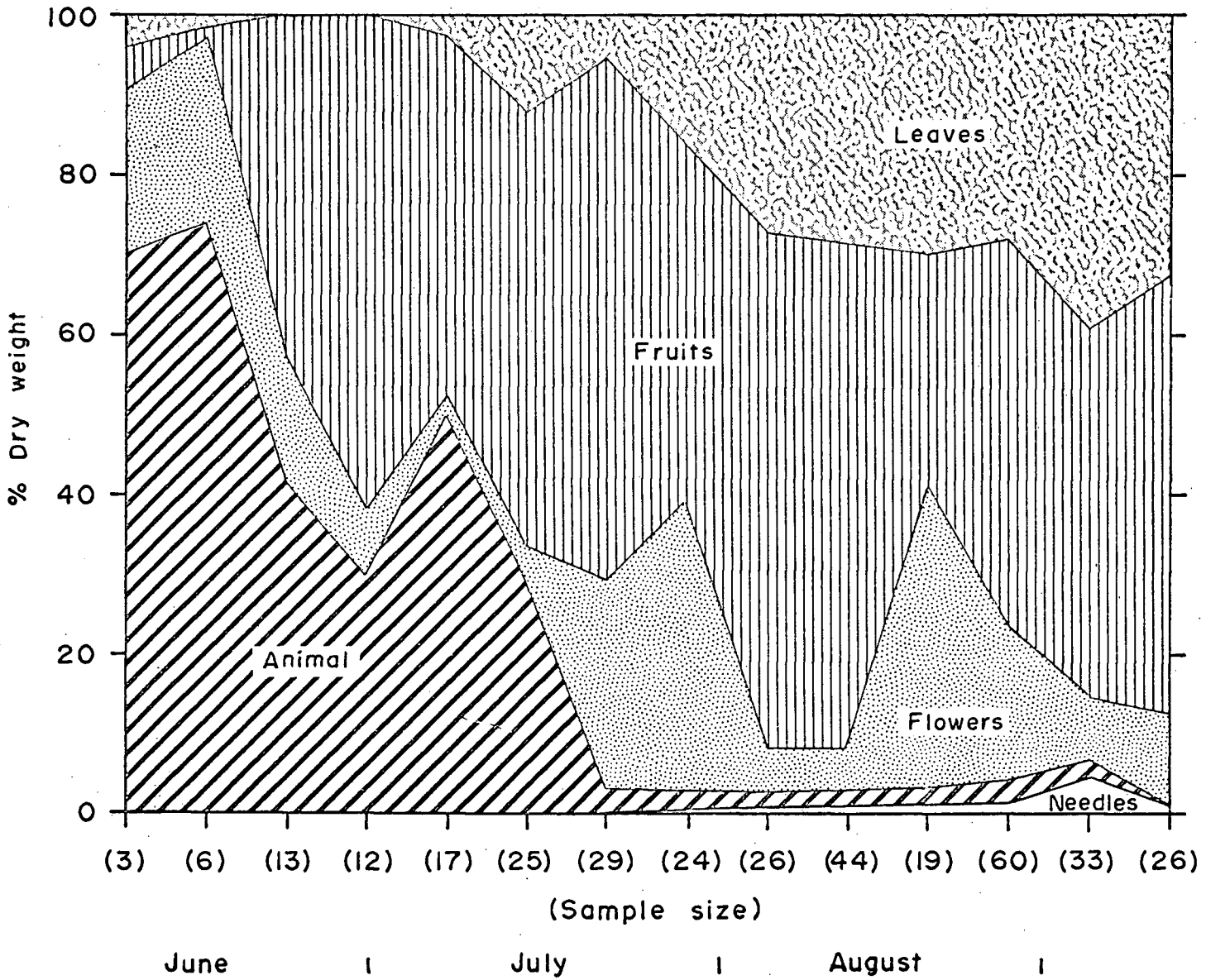

100
80
60
40
20
0
% Dry weight
Leaves
Fruits
Animal
Flowers
Needles
(3) (6) (13) (12) (17) (25) (29) (24) (26) (44) (19) (60) (33) (26)
(Sample size)
June
July
August

FIGURE 4

Amount of animal material in the diet of chicks.

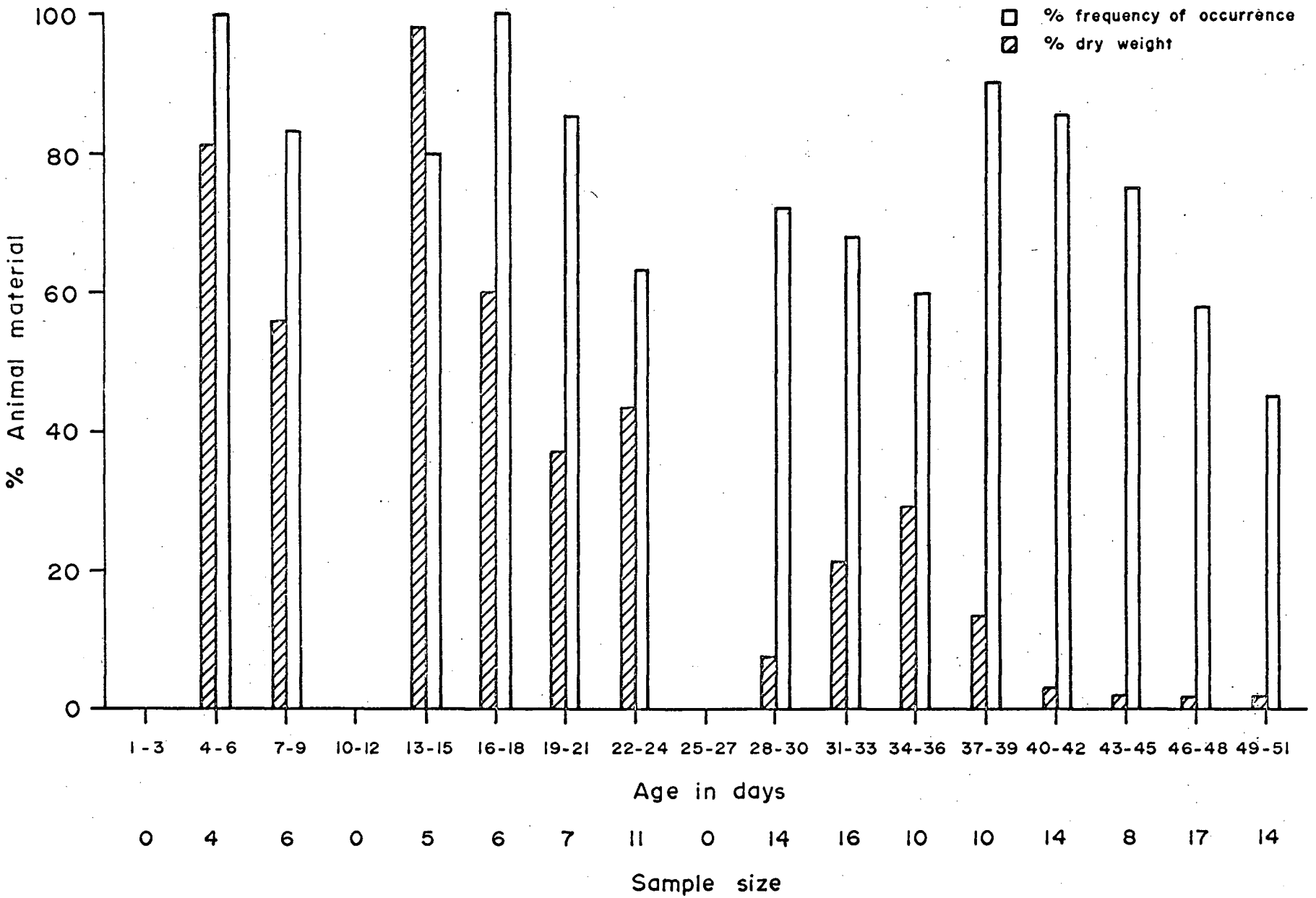

% frequency of occurrence
% dry weight
% Animal material
100
80
60
40
20
0
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
37-39
40-42
43-45
46-48
49-51
Age in days
0 4 6 0 5 6 7 11 0 14 16 10 10 14 8 17 14
Sample size

Table 2. Main kinds of foods in the summer diet of blue grouse, 1957 through 1966*.

Food	males (169)**		females (215)		chicks (343)	
	%wt.	%f.o.***	%wt.	%f.o.	%wt.	%f.o.
Pseudotsuga needles	44.0	55	17.0	28	-	-
Salix leaves	7.1	23	11.3	29	1.0	7
Pteridium fronds	6.6	19	6.5	28	8.0	27
Gaultheria leaves	1.3	9	2.6	13	-	-
Trifolium leaves	0.5	6	2.6	10	3.0	8
Hypochaeris flowers	5.3	25	8.5	41	18.5	44
Rubus fruits	11.6	11	10.7	24	15.5	29
Gaultheria fruits	10.0	22	13.3	31	15.5	36
Vaccinium fruits	0.8	8	5.3	17	5.0	24
Animal matter	0.2	7	0.5	13	22.5	59

* calculated as the averages from weekly values

** sample size

*** frequency of occurrence

a small number of food species can be considered the staple of the summer diet of blue grouse on Vancouver Island. This is similar to the findings of Korschgen (1966) on the food of ruffed grouse (Bonasa umbellus).

Conifer needles

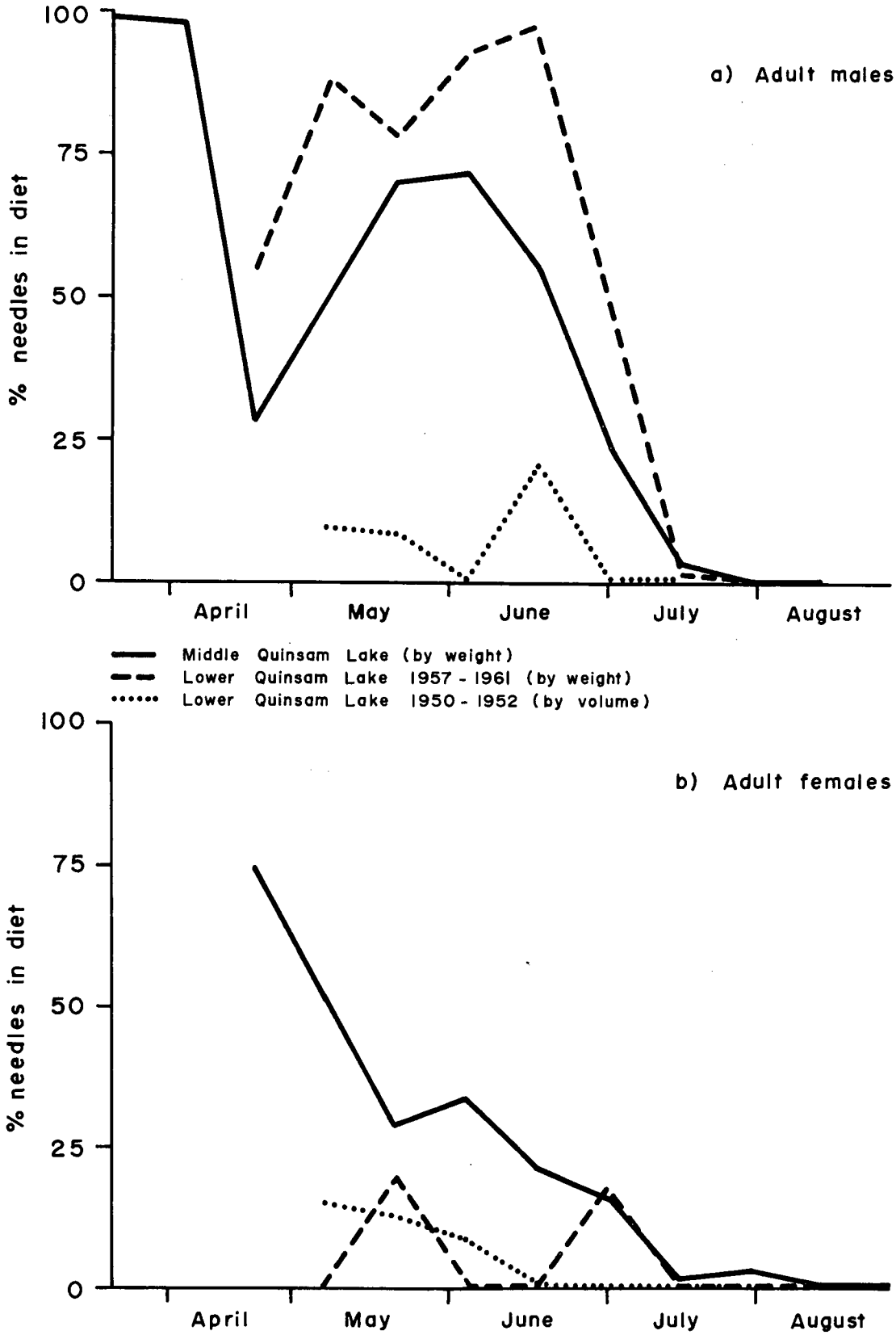
Needles of Douglas fir (Pseudotsuga menziesii) comprised approximately 80 per cent (by weight) of the conifer material eaten by adult males and females. In order of importance, the remainder was: needles of Western hemlock (Tsuga heterophylla), Sitka spruce (Picea sitchensis), and pine (Pinus contorta and P. monticola), and a few seeds of Douglas fir and pine. Other authors have reported the importance of Douglas fir as food of blue grouse (Beer, 1943; Stewart, 1944). Needles of mountain hemlock (Tsuga mertensiana) were the most important food of grouse on the winter range on Vancouver Island (King, in preparation). These birds probably were from the summer ranges at Lower and Middle Quinsam Lakes, so in the spring grouse which had descended to the summer range must have changed their diet from hemlock needles to those of Douglas fir.

The importance of different species of conifers in the diet of blue grouse varies over the range of the grouse (Bailey, 1927; Beer, 1943; Stewart, 1944; Hoffman, 1956; Boag, 1963). Blue grouse can apparently use needles of Pseudotsuga, Tsuga, Picea, Pinus, Abies, and Larix as staples in their diet.

The quantity of needles eaten by grouse from July to September was small (Fig. 5). In adults, the frequency of

FIGURE 5

Needles in the diet of adult males (a), and adult females (b), by area of collection.


a) Adult males
% needles in diet
100
75
50
25
0
April
May
June
July
August
Middle Quinsam Lake (by weight)
Lower Quinsam Lake 1957 - 1961 (by weight)
Lower Quinsam Lake 1950 - 1952 (by volume)
b) Adult females
% needles in diet
100
75
50
25
0
April
May
June
July
August

occurrence of needles (for two week periods) ranged from 15 to 35 per cent (Figs. 6 and 7) from July until altitudinal migration occurred, but they constituted less than three per cent (by weight) of the total food during that time. Thus, needles were taken infrequently and in small amounts during the latter part of the summer.

A return to the winter diet has been reported by various authors to occur at different dates. No indication of a significant increase in utilization of needles was found in grouse collected on summer range as late as September 17. Less than three per cent of the total amount of food eaten by hens or chicks during the first half of September was conifer needles. No adult males remained on the summer range at this time. The transition to winter diet, at least for hens and chicks, must therefore occur some time after mid-September on Vancouver Island, when the birds are on the winter range. This agrees with the findings of Beer (1943) and Stewart (1944). It is later than the time of change from summer to winter diet reported by Marshall (1946) and Standing (1960).

Leaf material

The relative use of each of the kinds of leaves was similar in both sexes although hens ate more leaves than did cocks. The leaves of willow (*Salix* spp.) were eaten most frequently and in the largest amounts by adults from April to early June, and in a relatively constant but lesser amount for the remainder of the summer (Figs. 6 and 7). Bracken fronds (*Pteridium aquilinum*

FIGURE 6

Seasonal trends in the use of major foods by adult male blue grouse, by two week intervals, March 19 to August 19, over a 10 year period (1957-1966).

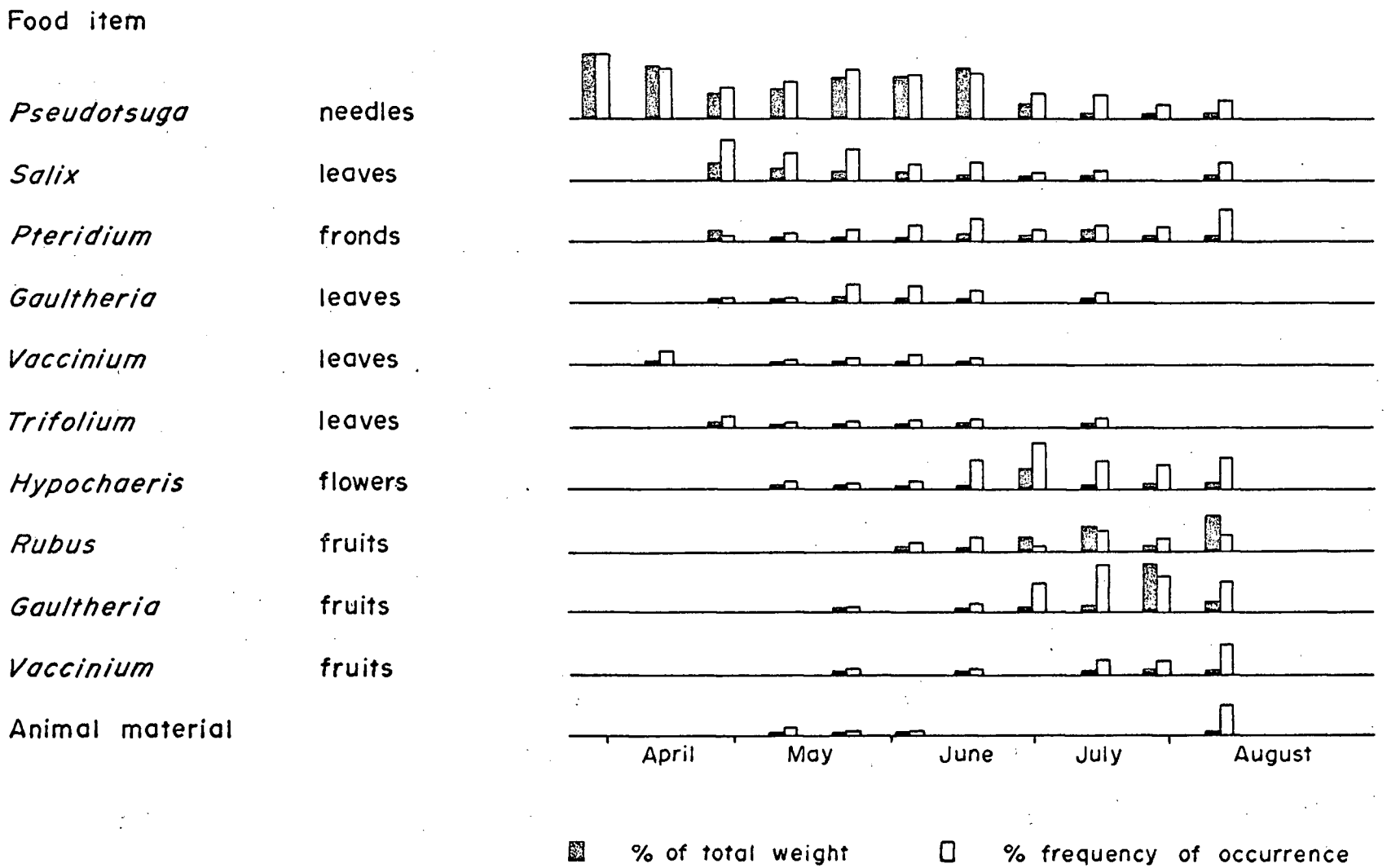
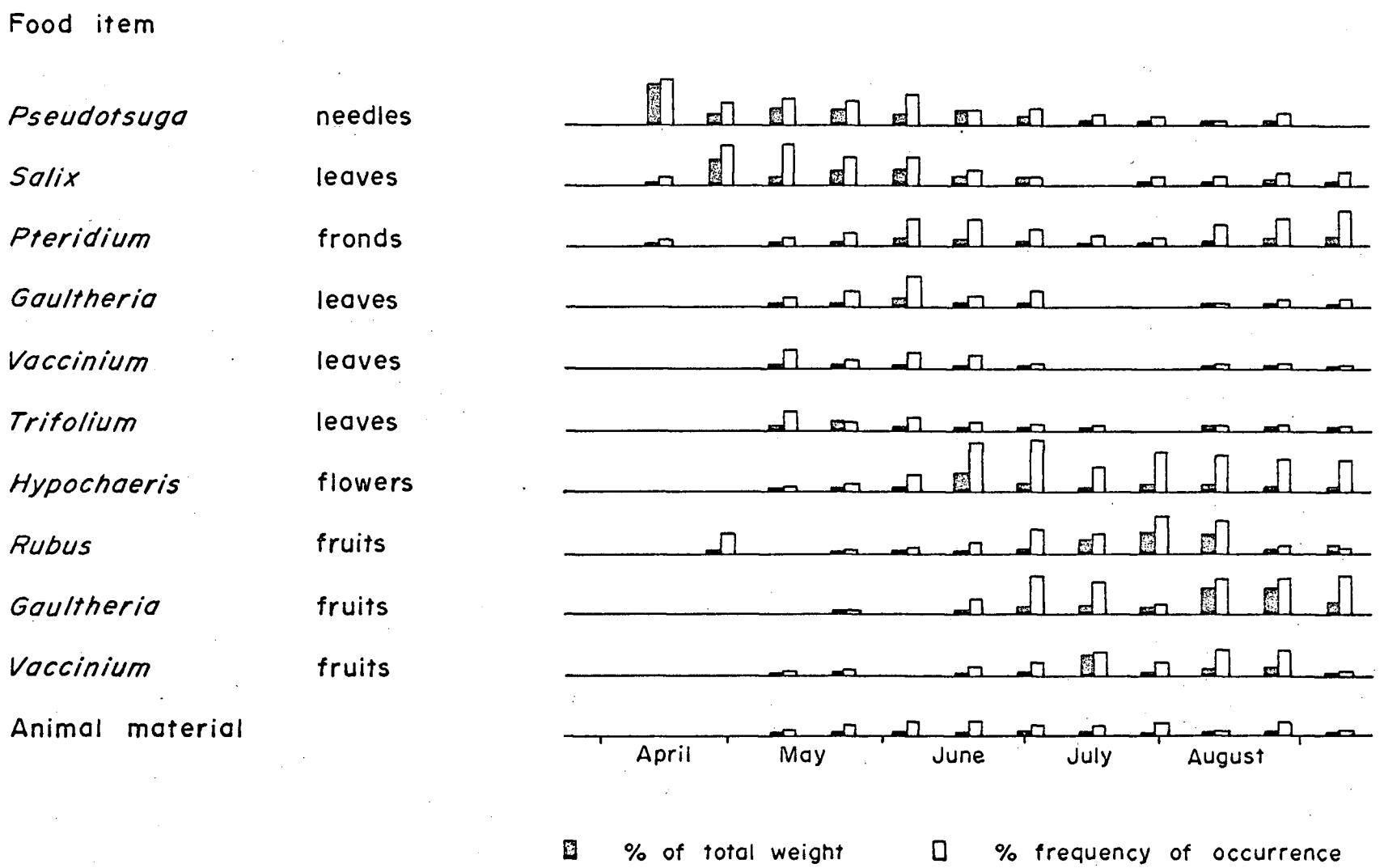

Food item
Pseudotsuga needles
Salix leaves
Pteridium fronds
Gaultheria leaves
Vaccinium leaves
Trifolium leaves
Hypochaeris flowers
Rubus fruits
Gaultheria fruits
Vaccinium fruits
Animal material
April
May
June
July
August
% of total weight
% frequency of occurrence

FIGURE 7

Seasonal trends in the use of major foods by adult female blue grouse, by two week intervals, April 2 to September 16, over a 10 year period (1957-1966).


Food item
Pseudotsuga needles
Salix leaves
Pteridium fronds
Gaultheria leaves
Vaccinium leaves
Trifolium leaves
Hypochaeris flowers
Rubus fruits
Gaultheria fruits
Vaccinium fruits
Animal material
April
May
June
July
August
% of total weight
% frequency of occurrence

were eaten in greatest amounts during June when use of willow leaves was decreasing, and again in September by hens and chicks (Figs. 6 and 7). Small amounts of the leaves of salal (Gaultheria shallon), huckleberry (Vaccinium spp.) and clover (Trifolium sp.) occurred frequently in the early summer diet of adults (Figs. 6 and 7). Chicks consumed very little leaf material from salal or huckleberry (Fig. 8). The main food of adult grouse which remained on the winter range from June to October was foliage of Vaccinium (King, in preparation).

Leaves of different species were eaten in the order of their appearance in the spring, shortly after budding. This was apparent from the colour, size, and texture of the leaves in the crops. Thus willows were almost fully leaved when bracken was in the "fiddle-head" stage and began to appear in crops.

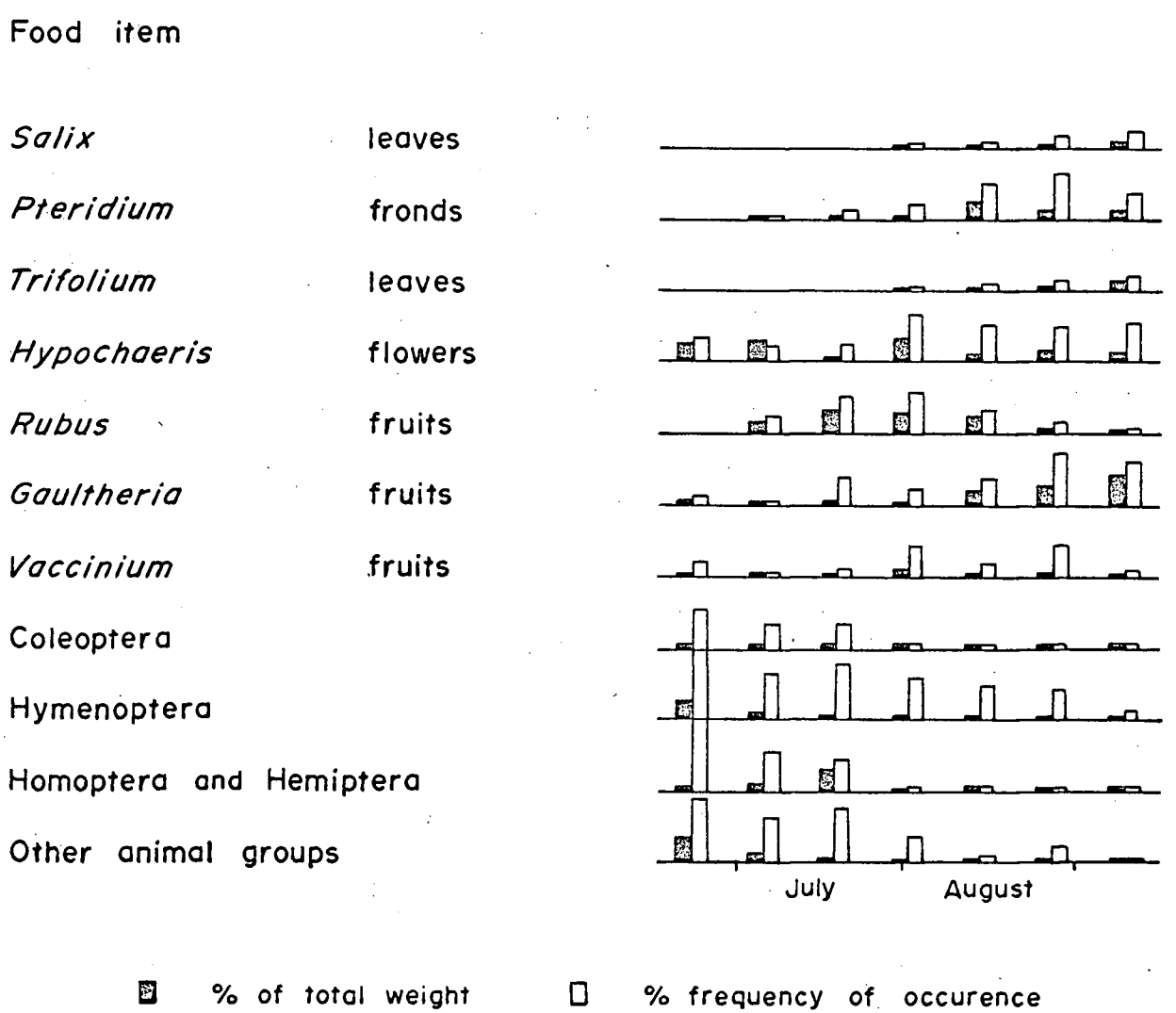
Leaves from the following plants were eaten infrequently and in small quantities: Rubus sp., Mahonia nervosa, Ribes sp., Rosa sp., Alnus rubra, Equisetum sp., Viccia sp., Plantago sp., Ledum groenlandicum, Crepis capillaris, Cerastium sp., Lactuca sp., Lycopodium sp., Selaginella sp., grass, and fronds of five species of ferns. One adult female had eaten fragments of lichens (Cladonia sp.).

Flowers

The flowers of a number of plants comprised a major part of the summer diet. Hypochaeris radicata flowers were eaten frequently, and more frequently by adult females (45 per cent frequency of occurrence) than by adult males (20 per cent f.o.).

FIGURE 8

Seasonal trends in the use of major foods by blue grouse chicks, by two week intervals, June 11 to September 16, over a 10 year period (1957-1966).


Food item
Salix leaves
Pteridium fronds
Trifolium leaves
Hypochaeris flowers
Rubus fruits
Gaultheria fruits
Vaccinium fruits
Coleoptera
Hymenoptera
Homoptera and Hemiptera
Other animal groups
July
August
% of total weight
% frequency of occurence

This flower made up from three to six per cent (dry weight) of the food of both sexes over the summer (Figs. 6 and 7). It occurred in 50 per cent of the crops of chicks examined, and constituted 16 per cent (dry weight) of their summer food (Fig. 8). Stewart (1944) and Fowle (1960) also found flowers of Hypochaeris to be a prominent item in the summer diet of blue grouse.

Several species of flowers were eaten less frequently and in small amounts. These included those of Achlys triphylla, Mahonia nervosa, Hypochaeris glabra, Taraxacum sp., Agoseris sp., Mimulus sp., Viola sp., and Campanula sp. The flowers of Rubus ursinus and Gaultheria shallon were also eaten but have been included in the category of fruits and seeds because their fruits had begun to develop when they were eaten.

Fruits

The major items in the late summer diet of all grouse were a variety of fruits and seeds. From early July until the birds left the summer range, approximately 50 to 90 per cent of the food eaten by all grouse was fruits and seeds (Figs. 6, 7 and 8). Similar findings were reported by Beer (1943), Stewart (1944), Marshall (1946) and Fowle (1960).

The main species of fruits eaten were trailing blackberry (Rubus ursinus), salal, and huckleberry. All grouse consumed the fruits of the different species in about the same proportion and at the same time. Berries of trailing blackberry were taken most frequently and in the greatest quantities during

late July and early August, while peak use of huckleberries was slightly later (Figs. 6, 7 and 8). The fruit of salal was eaten in the largest quantities during late August and September although the flowers and developing fruit were eaten frequently from early June until the grouse left the summer range (Figs. 6, 7 and 8). The peak use of these fruits occurred in the order in which they ripened.

Other fruits and seeds which occurred less frequently were those of Mahonia nervosa, Fragaria sp., Pseudotsuga menziesii, Pinus sp., Juncus sp., Carex sp., Plantago sp., and Achlys triphylla.

Animal matter

Adult grouse on the study areas were almost wholly vegetarian. Animal food occurred in 5 to 10 per cent of males and females and constituted less than 0.4 per cent (dry weight) of their food during the summer. Animal material reported in the summer diet of adult blue grouse varies from 26.9 per cent (Mussehl and Finley, 1967) to 2 to 3 per cent (by volume) (Beer, 1943; Fowle, 1960). Invertebrates, first taken in early May, were eaten in small numbers throughout the summer. Insects eaten were Hymenoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera and Orthoptera. Other invertebrates taken were Arachnida (spiders), Isopoda, Diplopoda and Gastropoda. Ants were eaten most frequently, and were found in 60 per cent (18 of 30) of those adults which had eaten animals. Hemipterans were consumed by 14 per cent of these birds, and no other invertebrate

was eaten by more than two (7 per cent) of them.

In interior subspecies of blue grouse, grasshoppers and other invertebrates comprise a large portion of the diet of adults in the late summer (Beer, 1943; Stewart, 1944; Standing, 1960). These results are in contrast to the findings of this study.

Chicks ate members of all orders taken by adults and six additional ones; Homoptera, Isoptera, Odonata, Trichoptera, Psocoptera and Thysanoptera. With the exception of homopterans, all these were eaten infrequently. The insects most frequently consumed in June were Hymenoptera (mainly Formicidae) which occurred in 75 per cent of the chicks examined, Hemiptera and Homoptera (75 per cent) and Coleoptera (40 per cent). The most important homopterans were Cercopidae. The relative use of these invertebrates remained the same throughout July and August, and they were taken frequently (Fig. 4) although the percentage of the diet which they formed declined. Chicks continued to feed more frequently on animal material than did adults through the latter part of the summer, as is the case in other species of grouse (Helminen and Viramo, 1962). Rasmussen and Griner (1938) and Helminen and Viramo (1962) attribute the decrease in the frequency of occurrence of animal food in the late summer in the diet of juvenile grouse to the decreasing availability of invertebrates at that time. This may be so for blue grouse, for where invertebrates are abundant, as in dry forest habitats, the hens and chicks eat large amounts of

insects, particularly grasshoppers, during late summer and autumn (Beer, 1943; Stewart, 1944; Standing, 1960).

Grit

Mineral material is taken by grouse and is thought to be of importance for grinding food and as a source of minerals (Beer and Tidyman, 1942). Small quantities of grit were found in 13.4 per cent (110 of 820) of all crops collected between 1957 and 1966. The range in weight of grit found in crops was from 1.40 grams taken from a chick shot on August 31 to 0.003 grams from an adult female collected in mid-June. There was no consistent pattern among adult males, females and juveniles in the consumption of grit during the spring and early summer.

The ingestion of grit appears to have increased in August. This is in contrast to the findings of Beer and Tidyman (1942) and Fowle (1960) who reported large amounts of hard seeds replacing grit in the gizzards of some blue grouse taken from July until early September. Semenov-Tyan-Shansky (1960) states that the total weight of grit in the gizzards of European tetraonids is greatest prior to the onset of winter. The average weight of grit in crops showed an increase from 0.073 grams from April to July to 0.133 grams in August and September, but was not statistically significant ($t = 1.310$, 116 df). The frequency of occurrence of grit in crops collected prior to July 30 was 8.4 per cent. In August and September the incidence of grit increased to 19.7 per cent.

This difference is statistically significant ($Chi^2 = 4.49$) at the 5 per cent level. Fowle (1960) found grit in the crops of 11 per cent of 88 grouse collected from June to October, while Boag (1963) found grit in the crops of 22.5 per cent of the grouse he examined which were taken during September and October.

On Vancouver Island, blue grouse hens and broods migrate to their winter range in early September (Bendell and Elliott, 1967). The increase in the frequency of occurrence of grit in their crops may relate to a need for a winter supply of grit (Semenov-Tyan-Shansky, 1960), to a need for coping with rougher foods such as hard seeds (Korschgen, 1966), to a change in the degree of retention of grit in the gizzard (Beer and Tidyman, 1942), or to a combination of these. Changes in the texture of the foods eaten are associated with differences in the retention of grit in the gizzard (Semenov-Tyan-Shansky, 1960), and by mid-July the diets of adult males and females contained the greatest amounts of fruits (and thus of hard seeds), which were also heavily utilized by chicks at that time (Figs. 1, 2 and 3).

Diurnal rhythm of feeding

The diurnal rhythm of feeding was determined by examination of the weight of crop contents of birds killed at different times of day. The weight of crop contents of chicks was expressed as a percentage of the body weight of the birds to compensate for the effect of the size of the chick on the

amount of food consumed.

Considerable variation in weights of crop contents occurred within each hourly interval. This variation may at least partially be a result of the influence of weather conditions on the feeding activity of the birds (Krafft, 1954; Peters, 1958). Crops which contained only trace amounts of food or which were empty were collected at all times of day.

All crops collected from 6:00 a.m. to 10:00 a.m. contained relatively little food. An increase in the average weight of crop contents occurred throughout the day. Feeding was intensified in the late afternoon and evening with greatest weights of crop contents reached after 7:00 p.m. (Figs. 9, 10 and 11). These results are similar to those of Krafft (1954), Peters (1958), and Seiskari (1962).

Bendell (1954) found daily peaks of activity in blue grouse at approximately 0300 to 0500 and 1900 to 2200, and attributed the greatest part of this activity to the foraging of females on or near the territories of males. No crops were available from grouse collected earlier than 0600, and the time required for passage of food from the crops of blue grouse has not been determined. Food eaten before 0600 (Caswell, 1953; Bendell, 1954) may mostly have passed from the crop to the gizzard by the time the grouse were collected. No evidence of the peak of morning feeding at approximately 0700 as suggested by Beer (1943) and Stewart (1967) was found.

FIGURE 9

Weight of crop contents of adult males, by hour.

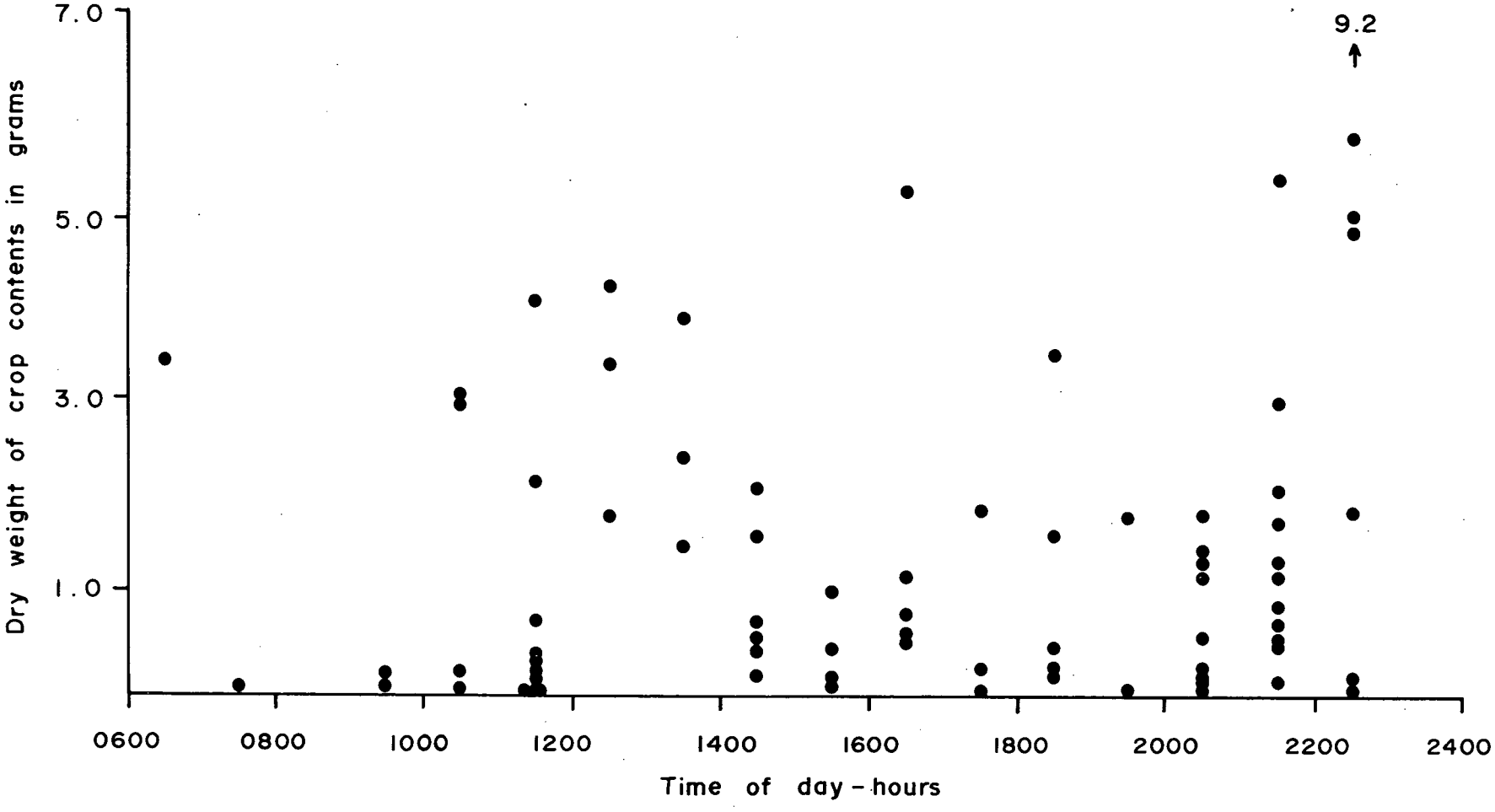

7.0
5.0
3.0
1.0
Dry weight of crop contents in grams
9.2
0600
0800
1000
1200
1400
1600
1800
2000
2200
2400
Time of day - hours

FIGURE 10

Weight of crop contents of adult females, by hour.

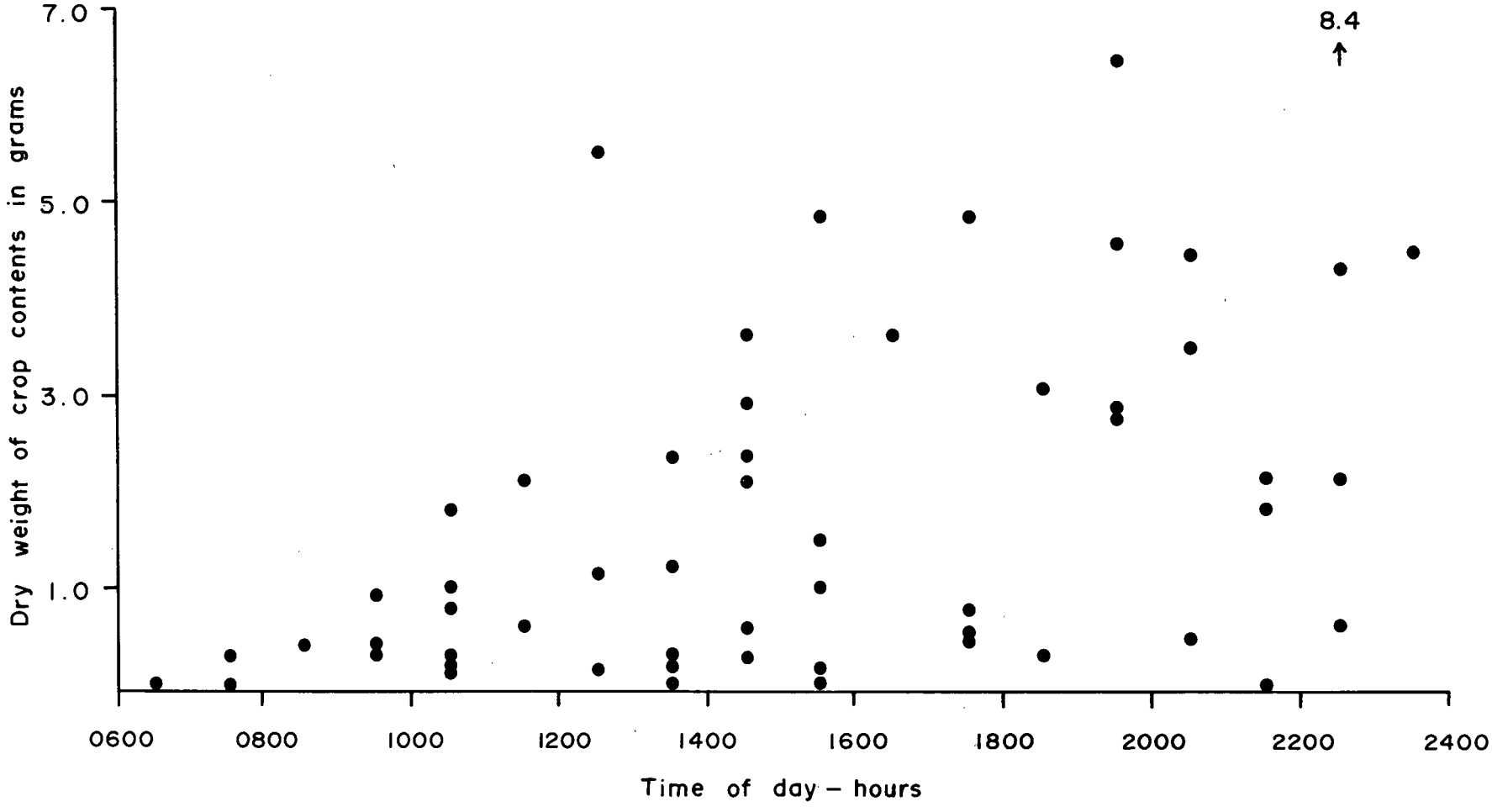
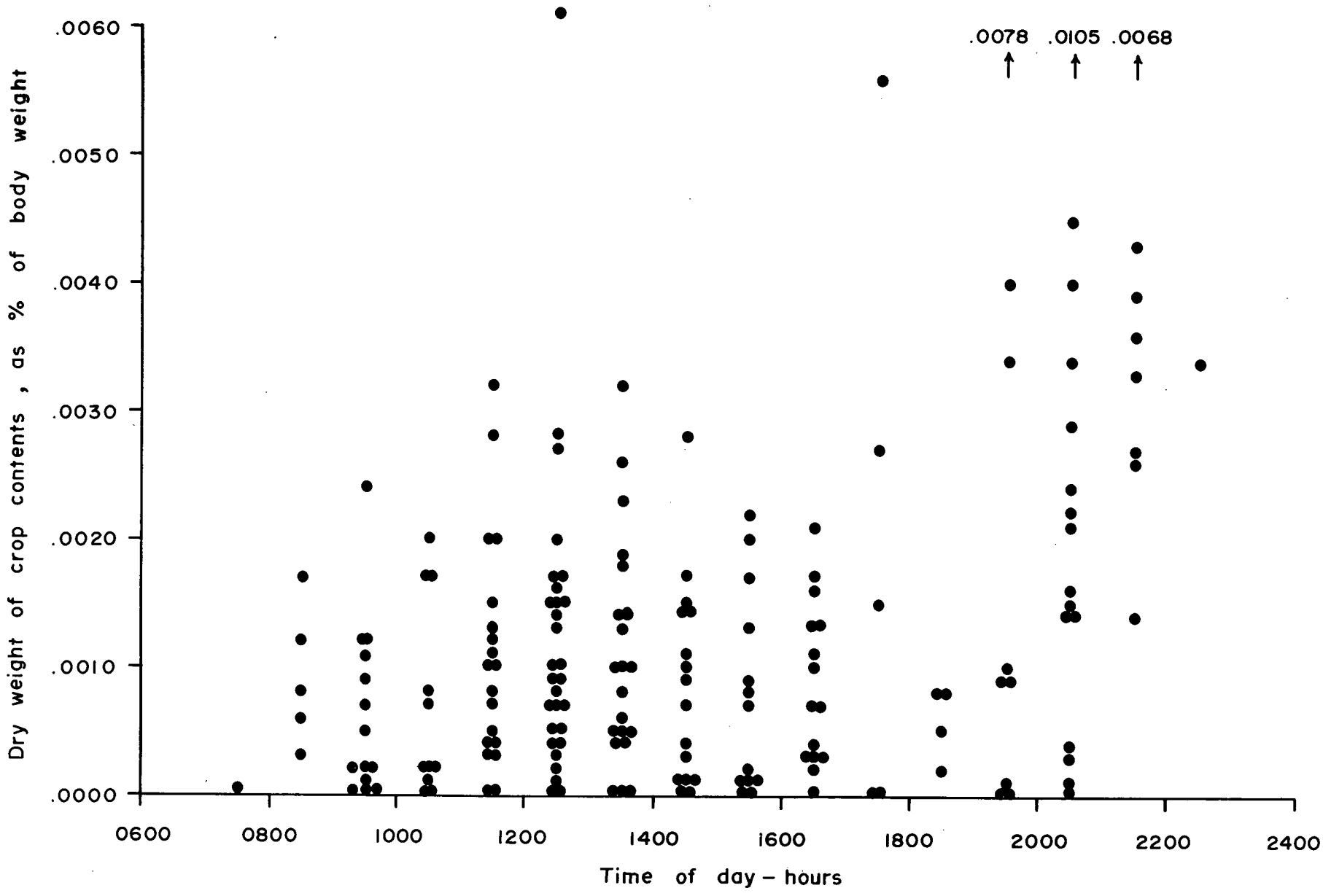

7.0
5.0
3.0
1.0
Dry weight of crop contents in grams
8.4
0600
0800
1000
1200
1400
1600
1800
2000
2200
2400
Time of day – hours

FIGURE 11

Weight of crop contents of chicks, by hour.


.0060
.0050
.0040
.0030
.0020
.0010
.0000
Dry weight of crop contents , as % of body weight
.0078
.0105
.0068
0600
0800
1000
1200
1400
1600
1800
2000
2200
2400
Time of day – hours

The highest weights of crop contents were from birds taken during or after the evening peak of activity reported by Bendell (1954). The large number of adult males with small amounts of food in their crops during this period can be at least partly explained by males feeding at night after cessation of hooting (Stewart, 1967).

Crop content weights of chicks tended to remain more constant throughout the day than did those of adults. This suggests that chicks fed more constantly than did adults, which would be in keeping with their greater food requirements for growth as well as maintenance. It supports field observations of Beer (1943), Bendell (1954), Fowle (1960) and Zwickel (1967).

DISCUSSION

A number of points must be considered in sampling crops for analysis of food habits. Seasonal changes in the availability of major foods affects their utilization. Thus, date of collection can greatly influence the apparent importance of different foods and results should be related to time of collection. For example, fruits of Rubus, Vaccinium, and Gaultheria ripen from late June until August. The peaks of utilization of these fruits occurred in the order of their ripening. Samples taken in June will show Rubus as an important food and those taken in August will contain mainly Gaultheria.

There is danger in comparing foods eaten with quadrat samples of species of plants. The degree of utilization of plants is probably more dependent upon the time, and amount of production of acceptable parts, than upon the numerical occurrence or ground cover of individual plants (Hungerford, 1962).

Age and sex of the birds collected must be considered. Dietary differences between adults and juveniles have been shown for many species of birds (Rasmussen, 1938; Beer, 1943; Stewart, 1944; Perret, 1962; Boag, 1963; and others). The use of different foods, or the different degree of use of the same foods, by adult males and females has also been shown by Seiskari (1962), Perret (1962), Korschgen (1964, 1966) and others, as well as in this study. Pooling of the foods eaten by adults and juveniles, or of males and females may thus obscure

differences in the feeding of age or sex classes.

Fowle (1960) did not find the same selective feeding of grouse as found here because he did not consider the seasonal nature of food habits and generalized from a sample taken in late summer. Further, he reported that chicks ate fewer berries of Rubus and more of Gaultheria than did adults, and he attributed this to the chicks being on an animal diet when blackberries were ripe, and later selecting Gaultheria fruits. However, this apparent greater selection of Gaultheria by chicks than by adults can also be explained by the amount of food eaten at different ages, and by what is seasonally available. As chicks grow, they eat more. Thus, items taken in late summer are eaten in greater quantity than those eaten in June and early July, and they will appear to form a greater portion of the diet than is actually the case, if the data from young and old chicks are pooled as was done by Fowle. Averaging the weekly percentages which each food comprises reduces this error. If this is done, the relative use of fruits is seen to be similar in adults and chicks (Table 3).

The lesser use of Vaccinium fruits by males than by hens and chicks (Table 3) can be explained by the earlier departure of males from the summer range and the late ripening of this fruit. Although flowers and developing fruit of Gaultheria were eaten frequently from early June until all birds left the summer range, they did not constitute a large percentage of the diet until they ripened in late July and August.

Table 3. Amount of fruits in the diet of adult and juvenile grouse, by average of weekly percentages of weight and frequency of occurrence.

Fruit	adult males		adult females		juveniles	
	%wt.	%f.o.	%wt.	%f.o.	%wt.	%f.o.
Rubus	23	21	18	41	16	26
Gaultheria	20	48	24	52	15	37
Vaccinium	1	20	9	28	5	24

Availability and selection of foods

Diet may reflect the relative availability of foods (Trautman, 1952; Peters, 1958; Fowle, 1960; Perret, 1962; Robel, 1964; and others) or a combination of what is available and the preferences of the species (Yocom and Keller, 1961; Boag, 1963; Korschgen, 1966). There is obviously some selection of foods by blue grouse for the following reasons.

In spring, females ate considerably more decidious leaf material than did males. Since the most abundant food available in spring from 1957 on at Lower and Middle Quinsam Lakes was conifer needles, hens clearly selected new leafy vegetation. In experiments on captive grouse, Siivonen (1957) found that hens supplied with early green foliage ate it "immediately and ravenously", while males were rather indifferent towards this food. The marked seasonal changes in the diet of adults (Figs. 1 and 2) show that the grouse were selecting parts of various plants as they became available.

A number of plants which were abundant on the summer range were not used as food. These included pearly everlasting (*Anaphalis margaritacea*), fireweed (*Epilobium angustifolium*, Canadian thistle (*Cirsium canadensis*), and western red cedar (*Thuja plicata*). These and other plants were thus selected against as food items.

Hens with broods are most frequently found in moist areas on the summer range (Elliott, 1966; Lance, 1967). Vegetation protected by cattle exclosures at water sources received constant

use as food for ruffed grouse (Hungerford, 1957). Broods of blue grouse may also frequent moist areas for this reason.

Finally, the percentage of ground covered by main food plants on the summer range could not be related to their frequency of occurrence or percentage by weight as foods (Table 4). Newton (1967) found similar results with bullfinches (Pyrrhula pyrrhula), in that the composition of their diet was not directly related to the availability of the various seed species which they fed upon.

For these reasons, the conclusion was reached that blue grouse select plant foods on the summer range. This contradicts Fowle (1960), who found a rough parallel between per cent frequency of occurrence of plants on his study area and their volume in the diet of the grouse.

Selection of food appears to be directed towards food types, such as leaves, flowers, and fruits, rather than to particular species. Within each food type, the degree of use of suitable food species seems related to their availability and condition. Leaf material was taken in greatest amounts shortly after budding, and peak use of fruits seems to coincide with their peak of ripening (Figs. 6, 7 and 8). The fruits which were eaten most frequently and in greatest quantities (Rubus ursinus and Gaultheria shallon) were those which were most common on the summer range (Tables 3 and 4). Less common fruits (Vaccinium spp., Mahonia nervosa, and Fragaria spp.) were eaten in amounts corresponding to their relative abundance on the areas. Similar

Table 4. Comparison of the percentage frequency of occurrence of major food plants on the summer range and in the diet of grouse, during August.

Species of food plant	On summer range % ground cover	adult males % f.o.	adult females % f.o.	chicks % f.o.
Rubus ursinus	3.2	25	33	27
Pteridium aquilinum	15.4	50	42	58
Hypochaeris radicata	1.9	50	58	50
Gaultheria shallon	12.8	50	63	57
Salix spp.	6.2	25	18	11
Pseudotsuga menziesii	9.3	25	12	6
Vaccinium spp.	1.7	50	44	35

findings were reported by Beer (1943). Hemlock needles were eaten on the winter range in the same relative proportion as these trees occurred in relation to other conifers (King, in preparation).

The frequency of occurrence of invertebrates on the summer range was measured in order to relate their abundance to the degree of utilization in the diet of grouse. The relative abundance of invertebrates was determined by different methods during May, June and July of 1958 by Stiven (1961), and by F.C. Zwickel in July on 1962, at Middle Quinsam Lake. The invertebrates found in the crops of chicks collected during June and July were compared with the results of these samples (Table 5). Invertebrates were eaten in their order of abundance in the field. This suggests that young chicks feed on animal material as it is available. Rasmussen and Griner (1938) showed that the insects most frequently eaten by young sage grouse (Centrocercus urophasianus) were those most available in the area. By late July the diet of juveniles closely resembles that of adult females in type and kind of food eaten (Figs. 2 and 3, Table 6).

In 1958 Stiven sampled invertebrates from both the vegetation and the ground surface with an aspirator, while in 1962 Zwickel used a sweep net and took only those on plants. The greater similarity between the diet of chicks and the invertebrates taken by sweep net suggests that the invertebrates eaten were obtained largely from the vegetation and not from the

Table 5. Comparison of the per cent frequency of occurrence of major invertebrate groups on the summer range and their use by grouse chicks, June and July, 1957 through 1966.

Invertebrates	on summer range		in crop contents (105 crops) June - July (1957-1966)
	sweep nets (1962)	aspirator (Stiven, 1961)	
Hymenoptera	93	94	78
Hemiptera & Homoptera	42	100	58
Coleoptera	48	31	35
Diptera	29	69	14
Arachnida	10	100	17
Isopoda	0	38	13
Myriapoda	0	13	6
Lepidoptera	0	31	8
Orthoptera	5	*	5

* Stiven excluded members of the order Orthoptera, although he collected them.

Table 6. Comparison of major food items in the early September diet of adult females and juveniles.

Food	adult females (41)*		juvenile males (45)		juvenile females (36)	
	%wt.	%f.o.	%wt.	%f.o.	%wt.	%f.o.
Pseudotsuga needles	1.6	12	0.8	7	0.7	6
Salix leaves	1.5	20	4.4	12	2.9	32
Pteridium fronds	13.6	40	9.1	40	16.1	50
Trifolium leaves	8.2	16	8.9	17	18.5	22
miscellaneous leaves	0.7	14	0.6	17	1.0	22
Hypochaeris flowers	9.4	60	12.9	57	16.0	55
Rubus fruit	12.4	10	0.5	2	0.1	3
Gaultheria fruit	41.0	70	41.1	51	30.7	61
Vaccinium fruit	6.2	23	4.1	22	8.1	35
animal material	0.1	8	1.1	20	0.3	33

* Sample size

ground. Zwickel (1967) observed that chicks pecked at the vegetation for insects, but seldom at the ground. Isopods and myriopods, which are found almost exclusively on the ground, were taken by chicks. There must therefore have been some feeding upon invertebrates from the ground surface.

Nutritional basis of food selection

The dietary differences of adult males and females have been mentioned previously (Figs. 1 and 2). The transition from winter to summer foods occurs earlier in hens than in cocks, and results in differences in the nutrient composition of their diets. These differences appear to be related to differences in the biology of the sexes.

Requirements for protein and minerals increase over those necessary for maintenance levels during periods of ovulation, moult and growth of birds (Hill, 1944; Siivonen, 1957; Korschgen, 1964 and 1966; and others). Evidence has been presented (Gelting, 1937; McCann, 1939; Sadler, 1961; Korschgen, 1964 and 1966) to show that gallinaceous birds adjust their diets to meet their current requirements.

Values for the nutrient composition of the major food items in the spring and summer diet of Vancouver Island blue grouse were obtained from the literature (Table 7). These were used to determine the trends in the nutritional value of the diet of adult blue grouse, resulting from seasonal variation in the use of the main foods. Data from Stiven (1961) were obtained from plants and animals which were collected in June of 1958 at

Table 7. Nutrient content of major foods of Vancouver Island blue grouse*.

Food item	Protein	Ether extract	N-free extract	Crude fiber	Ash
Pseudotsuga needles	6.5	7.8	62.7	19.9	3.2
Salix leaves	8.8	2.6	60.2	21.0	7.4
Pteridium fronds	12.9	2.4	49.2	27.0	8.5
Hypochaeris flowers	14.4	5.4	53.5	14.0	12.7
Rubus fruits	13.4	1.4	64.3	15.0	5.9
Gaultheria fruits	9.2	2.0	63.8	20.0	5.0
Formicidae	66.8	2.9	23.7	4.0	2.6

* values for *Pseudotsuga* from Cowan *et al.* (1950), all others from Stiven (1961).

Middle Quinsam Lake. The material was therefore taken during the time at which it was utilized by grouse and from the same area on which the birds were collected. The differences in nutrient content of plants which have been shown to exist between plant parts, between areas, between vegetation from different aged stands, and between months (Cowan et al., 1950; Golley, 1961; West and Meng, 1966) should thus be minimal for these values.

The protein and mineral content of conifer needles (Cowan et al., 1950; Hoffman, 1961; Stirling, 1965; Ellison, 1966) is lower than that of all other main foods (Table 7), and the presence of large amounts of needles in the spring and summer diet of grouse will therefore decrease the relative amounts of these components in the diet.

The selection of broad-leafed material began when leaves first became available (Figs. 1 and 2). Their use by hens increased throughout April and was highest in mid-May (Fig. 7) which is the peak period for the beginning of laying (Zwickel, 1965), and use of leaves was greater by hens than by cocks during this period (Figs. 1 and 2). The food of males at that time was still largely conifer needles. The use of animal material by females was greater than that by males (Figs. 6 and 7), although invertebrates were not a major constituent by either weight or volume in the crop contents of any adult female. The protein and mineral content of the diet of females was thus considerably higher than that of males

during the reproductive season. A similar situation was reported by Korschgen (1964), who found a difference, which was greatest during the reproductive season, between the foods taken by male and female ring-necked pheasants (Phasianus colchicus). Marked changes in the nutritional value of the diet of the hens occurred during that period, but no such change was observed in the diet of roosters. The protein and mineral intake of ruffed grouse (Bonasa umbellus) increased when protein requirements of females increased during ovulation (Korschgen, 1966).

A comparison of the diets of adult and subadult males during spring and early summer showed that they ate essentially the same percentages of the different food types (Table 8). Few yearling males establish territories (Bendell and Elliott, 1967). Most move over what appears to be a relatively large home range, showing movements similar to those of females (Bendell and Elliott, 1967; Lance, 1967). The similarity of the diets of adults and yearlings further supports the concept that breeding and territorial behaviour did not impose a dietary strain upon males.

The occurrence of flowers and fruits in the diet of adults, both males and females, increased greatly during June (Figs. 1 and 2). By early July the amount of conifer needles eaten by both sexes decreased to less than three per cent (dry weight) of the foods eaten. The nutrient composition of fruits and flowers is high in protein and minerals (Table 7). The quality

Table 8. Food of adult and yearling grouse, April and May, 1957 through 1966, by percentage dry weight.

Food type	males adults	males yearlings	females adults	females yearlings
sample size	73	18	37	18
conifer needles	64.2	65.7	55.2	49.7
leaf material	31.6	23.7	41.4	48.3
flowers	0.6	1.2	0.3	0
fruits	3.0	9.3	3.0	1.9
animal material	0.6	0.1	0.1	0.1

of the diet of the hens remained high, resembling that of the reproductive season, while that of the males increased to a similar level.

During late May, adult males begin their annual moult with the replacement of the first primary feather. Growth of primaries 2, 3, and 4 is completed or in progress at the end of June, at which time moult of the contour feathers begins (Bendell, 1955b). There is some question as to when the moult of adult females begins. The onset of feather replacement is apparently related to the reproductive status of the birds. Höhn (1961) states that cyclic fluctuations in production of gonadal hormones, together with changes in the level of thyroid hormone, control the postnuptial moult of birds. Bendell (1955b) reported that adult females commenced the moult concurrently with adult males, while Boag (1965) found that breeding hens began moulting after termination of incubation, approximately four weeks later than males and non-breeding females. Nevertheless, by late June moulting is in progress for both males and females, and the process continues through August and September. An adequate supply of protein in the diet seems necessary for good feather development (Hill, 1944; Korschgen, 1966). The need to meet this demand may explain the abrupt transition in the diet of males, from predominantly needles to fruits and flowers which have high protein contents.

The diet of chicks from mid-July until they leave the summer range (Fig. 3) is similar to that of adults, with a

greater use of animal foods. A suitable diet for meeting the requirements of growth and moult, as well as for maintenace, is necessary for chicks. The late summer diet of chicks was relatively high in protein and mineral content. Animal material has a much higher protein content than the plant foods eaten (Table 7), but the energy expenditure necessary to capture sufficient invertebrates to meet the nutritional requirements of the growing birds may be prohibitive.

Influence of diet upon reproduction

The existence of a maternal influence on the viability and survival of galliform chicks was suggested by Young (1868, in Zwickel, 1965) and has been supported by the findings of Nestler (1946), Bump *et al.* (1947), Siivonen (1957), Jenkins *et al.* (1967) and Zwickel (1965). Yearly variation in the quality of the staple winter food is believed by some workers to be responsible for determining the condition of the hen, and through her, the viability of the chicks (Koskimies, 1955; Lauckhart, 1957; Boag, 1963; Jenkins, 1963). However, bobwhite quail (*Colinus virginianus*) were found by Nestler (1944) to show no statistically significant differences in fertility and hatchability of the eggs of birds maintained on winter diets of different protein levels. Dale and DeWitt (1958) state that pheasants kept on a low-protein winter diet were able to reproduce successfully during the following summer providing the reproductive diet was satisfactory.

Siivonen (1957) suggested that the change in overall quality of the diet of the hens in spring may be a factor in determining the reproductive success of tetraonids, and that the time of greatest importance was the three week period immediately preceding laying. The survival of red grouse (Lagopus lagopus) chicks has been found to be related to the amount of green heather available as food for breeding birds in the spring (Jenkins et al., 1967).

No difference was found in reproductive success of grouse from the different study areas during the same year, but mean brood size between years was significantly different (Zwickel and Bendell, 1967). The year of lowest chick survival on the study areas was 1962, when nesting was also delayed (Zwickel and Bendell, 1967). The foods of hens collected during April and May of the years 1960 through 1963 were compared between years to determine whether dietary differences occurred which could be related to delayed nesting or to the poor early survival of chicks in 1962. A higher percentage of conifer needles in the pre-nesting diet of hens would be expected in a year of late nesting and low chick survival, if the availability of food to hens was affecting their time of nesting or the viability of their chicks. No such difference in the use of needles by hens was found between 1962 and any other year, or between 1962 and the pooled values for all other years (t-test, 5% level). The use of all food types by hens was similar in 1962 to that in other years (Table 9). The diet

Table 9. Comparison of use of food types in the early summer* diet of females during year of poorest chick survival (1962) to the 10 year average values for the diet of females, as a percentage dry weight, and frequency of occurrence.

Food type (Sample size)	1962 (18)		10 year average (55)	
	wt.	f.o.	wt.	f.o.
conifer needles	31.2	74	36.8	64
leaf material	66.6	93	58.1	93
flowers	0.6	40	1.7	48
fruits	1.5	33	2.8	25
animal material	0.1	13	0.4	10

* during May and June

of hens as determined by this measure cannot therefore be related to the late hatch or to the poor early survival of chicks in 1962. No data for nutrient content of plants from the study areas are available from different years to determine yearly variation in the nutrient composition of the main food species occurred, as has been reported by Siivonen (1957) and Lauckhart (1957).

Although all study areas were within 25 miles of one another, and all had been logged and burned, there were differences in their plant cover at the time when grouse were collected. The coverage by conifers on the areas differed, being lowest at Comox Burn during the period 1957 through 1966 (Zwickel, 1965). Artificial replanting of Douglas fir altered the natural pattern of plant succession on the areas (Bendell, 1954; Zwickel, 1965). The vegetation at Lower Quinsam Lake changed markedly between 1953 and 1957, (Zwickel and Bendell, 1967), with an increase in the amount of dense cover.

In order to determine the extent to which plant cover influenced the diet of grouse, data on foods eaten by the birds collected from the different areas were examined separately. The percentage of conifer needles eaten by hens collected at Lower Quinsam Lake from 1950 through 1952 and from 1957 through 1961 showed no significant differences at the 5% level (t-test) for any two week interval during the spring or summer. There was also no difference between the needle content of the diets of females from Lower and Middle Quinsam Lakes between 1957 and

1966, or between these birds and those collected at Comox Burn from 1962 through 1966.

The diets of males collected at Lower Quinsam Lake during the two sampling periods did show a difference in the percentage of conifer needles which they contained. During early May, adult males taken from 1950 through 1952 had eaten smaller amounts of conifer needles than had those collected between 1957 and 1961, and this difference was significant at the 10% level (t=2.042, 11 df). In late May and June, the difference between the diets of males from the two collection periods increased, and was significant at the 1% level (t=4.589, 37 df). During July, following the decrease in needles use (Fig. 1), no difference in the percentage of needles eaten by males from the two periods of collecting existed. There were no significant differences in needle consumption by males from Lower and Middle Quinsam Lakes from 1957 on. Insufficient adult males were collected at Comox Burn to test statistically the percentage of needles in their diet against that of birds from the other areas. The limited data available suggest that males at Comox Burn ate approximately the same amount of needles as did those from Lower Quinsam Lake between 1950 and 1952, and less than those males collected at Lower and Middle Quinsam Lakes after 1957.

These findings support the conclusion that females select foods other than needles during the reproductive season. Zwickel (1965) found no evidence of a relationship between mean

brood size and habitat type on these study areas. The selection of food by hens resulted in a similarity of diets despite the habitat differences between areas, and any dietary influence on reproductive success due to different availability of foods would therefore have been nullified.

Males showed a lesser degree of selection of food than did hens during the breeding season. When the males changed from a predominantly needle diet to one consisting mainly of fruits and seeds, areal differences diminished and the use of main types of foods became very similar. It therefore appears that when the nutritional requirements of grouse result in a selection of foods, the effect of the habitat on the diet is diminished. At other times, relative availability of acceptable food items seems to exert a stronger influence on their use.

In blue grouse, adult hens appear to produce more young than do yearlings (Zwickel, 1965; Bendell and Elliott, 1967) and the possibility that this may have a dietary basis was investigated. The main types of food eaten by adult and yearling grouse of both sexes, during April and May of the years 1957 through 1966 were examined (Table 8). April and May were chosen because this is the time of peak breeding activity, and the transition in the diet of hens occurred during these months. The amounts of the five types of food eaten by adult and yearling hens were virtually the same. Therefore, where both adult and yearling females were likely eating the same foods in every year, differences in reproductive

performance between adult and yearling hens were probably related to innate differences in their physiological capacity for reproduction, and not to the food which they ate.

Autumn migration

During late summer and autumn, blue grouse leave the lowland breeding ranges and return to their winter range in the mountains. Beer (1943) and Marshall (1946) suggest that this altitudinal migration may be related to the condition and abundance of fruits on the summer range and their ripening later at higher altitudes. However, on the study areas, adult males begin their migration in early summer and virtually all have left the lowlands by early August. The departure of the males occurs prior to and during the period of greatest abundance of the fruits of Rubus and Gaultheria, and their greatest use by hens and chicks. The time of depature of adult males from the summer range is related to the seasonal decrease in testicular volume (Bendell, 1955a; Simard, 1964). This strongly suggests that the altitudinal movement of males is caused by the physiological condition of the birds and is not related to the supply of food.

Most of the migration of hens and chicks apparently occurs in early September (Bendell and Elliott, 1967). The greatest amounts of Rubus and Gaultheria fruits were eaten by them in August and September (Figs. 7 and 8). There was no apparent decrease in the amount of fruits in the diet of hens or chicks which seemed related to the migration of hens with chicks.

Also, it appears that hens with brood migrate at about the same time each year (Bendell and Elliott, 1967) and migration is fairly rapid once it has begun (Lance, 1967). The evidence suggests that in hens and young, as in the cocks, physiological events are more important in migration than is the food supply.

SUMMARY

1. The crop contents of 875 blue grouse collected at three areas on Vancouver Island were analyzed to determine the late spring and summer food habits of the birds.
2. The transition from the winter diet to more succulent summer foods occurred later in males than in females.
3. The spring and early summer diet of adult females was mainly leaf material and flowers.
4. Adults consumed small amounts of invertebrates throughout the summer.
5. The diet of chicks consisted mainly of invertebrates until the birds were approximately three weeks of age. After that time plant foods predominated in the diet and by late summer the foods of chicks were very similar to those eaten by adults.
6. Over 80 per cent (by weight) of the diet of the birds examined was made up by the following food items: *Pseudotsuga menziesii* needles, *Salix* spp. leaves, *Pteridium aquilinum* fronds, *Gaultheria shallon* leaves, *Trifolium* spp. leaves, *Hypochaeris radicata* flowers, *Rubus ursinus* fruits, *Gaultheria shallon* fruits, *Vaccinium* spp. fruits, and animal matter.
7. The frequency of occurrence of gravel in crops increased in the late summer.

8. The weight of crop contents increased throughout the day, and the highest weights were from birds collected at dusk.
9. Blue grouse were found to select parts of plants while on the summer range.
10. The degree of use of food items within a food type was influenced by their availability and condition.
11. Chicks ate animal food in the order of abundance of the invertebrates in the field.
12. Invertebrates were taken mainly from the vegetation.
13. The protein and mineral content of the diet of females increased during the reproductive season due to selection of foods. They remained high during the period of moult, at which time the diet of males increased in protein and mineral level.
14. There were no apparent differences, in either males or females, between the diets of adult and sub-adult (yearling) birds which could be related to differences in reproductive performance of the two age classes.
15. The spring diet of hens could not be related to the poor early survival of chicks in 1962, or to the late hatch that year.
16. Selection of foods resulted in similar diets for grouse from areas which were different in terms of type and amount of vegetational cover.
17. The altitudinal migration of blue grouse in autumn appears to be caused by factors other than the food supply.

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