THE ECOLOGY OF CERTAIN TERRESTRIAL SNAILS
AND
THEIR RELATIONSHIP TO THE LUNGWORM OF BIGHORN SHEEP

BY

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ABSTRACT

The distribution and abundance of terrestrial snails which inhabit the Rocky Mountain bighorn sheep (*Ovis canadensis canadensis* Shaw) ranges in the East Kootenay region of British Columbia were related to edaphic and climatic factors. Emphasis was placed upon those snail species which have been implicated as intermediate hosts of the sheep lungworm, *Protostrongylus stilesi* Dikmans.

Retinella electrina (Gould), *Euconulus fulvus* (Muller), and *Vitrina alaskana* Dall were found to be widely distributed on all ranges and were present in all but the driest plant communities. On low elevation ranges, *Euconulus* is the most abundant but *Retinella* is the most widely distributed. In alpine regions, however, *Vitrina* is the dominant species. These hydrophilic species were found mainly on organic soils under leaf litter or logs in aspen and coniferous forest communities where moisture conditions were suitable.

The relatively xerophilic species, *Vallonia cyclophorella* (Sterki), *Gastrocopta holzingeri* Sterki, and *Pupilla muscorum* (L.) are restricted to the dry, sandy soils of the bunchgrass communities, where they live under rocks. Of these species, *Vallonia* is the most abundant, but on the Columbia Lake range, *Pupilla*, which is restricted to this range, is almost as numerous.

The clay and silt soils of the bitterbrush communities appear to be unsuitable for the survival of any snails. Wide

temperature and moisture fluctuations, resulting in part from soil texture, appear to be the main factors limiting the occurrence of snails in these sites.

With the possible exception of Vitrina and Pupilla, the distribution and abundance of snails on the East Kootenay sheep ranges can not be explained by variations in soil calcium, even though calcium was shown to affect reproductive and growth rates.

Vallonia and Pupilla appear to be the most suitable intermediate hosts for sheep lungworm. However, no infected snails were found on any of the ranges and it was established that snails live in a habitat which is inaccessible to sheep. This indicates that terrestrial snails may not play a role in the life cycle of sheep lungworm in the East Kootenay region of B.C.

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INTRODUCTION

Certain species of land snails are believed to be intermediate hosts for Protostrongylus stilesi, the lungworm of bighorn sheep Ovis canadensis. Lungworm larvae, which are passed in sheep feces, penetrate into snails which, in turn, are ingested by the sheep with their food (Buechner 1960). This life cycle was proposed after Pillmore (Hunter and Pillmore 1954, Pillmore 1958) and Forrester (pers. comm.) found natural protostrongylin infections in snails of the following genera: Vallonia, Pupilla, Gastrocopta, and Euconulus. Additional evidence was obtained when they succeeded in infecting these snails with larvae obtained from sheep feces.

The lungworm is one of the major mortality factors of Rocky Mountain bighorn sheep (Forrester and Senger 1963, Moser 1962). It is thought that death is caused by pneumonia Pasturella sp. which errupts in lungs that have been weakened by lungworm (Buechner 1960). Between 1964 and 1968, sheep populations in the East Kootenay region of British Columbia suffered heavy losses in a die-off which was attributed to this lungworm-pneumonia complex (Bandy 1968). Other sheep populations in North America have a similar pathological history (Buechner 1960).

Since lungworm appears to be one of the major factors limiting sheep populations, and since the life cycle of the lungworm appears to involve a land snail, an understanding of the distribution, abundance, and ecological requirements of land snails may be necessary for the control of lungworm infestation and the management of mountain sheep. However, the relationship between snails, lungworm and sheep remains unknown because sheep have never been experimentally infected with infected snails. Nevertheless, land snails should be considered as possible intermediate hosts for P. stilesi since the life cycle of other protostrongylids has been shown to involve snails (Hobmaier and Hobmaier 1930, Gerichter 1948).

The small amount of available ecological information on terrestrial snails is of a very general nature. This is unsatisfactory since, in a group as diverse as terrestrial molluscs, it is reasonable to expect large differences between the requirements of species. The ecology of western North American snails, including the suspected intermediate hosts of P. stilesi, has been particularly neglected. The following information has been obtained mainly from studies done elsewhere, mostly in Europe.

Soil moisture appears to be the most important ecological factor determining the distribution and abundance of terrestrial molluscs (Hunter 1964). Active snails have a rapid water loss because they have a moist, permeable skin and a method of locomotion which depends on the secretion of a watery slime (Howes and Wells 1934). Although snails possess a capacity for enduring great changes in water content (Wells 1944), they are restricted to environments where they can replenish water losses (Kuhnelt 1961). Molluscs lay eggs only where the moisture content of the soil is sufficiently high (Carrick 1942, Herzberg and Herzberg 1962) since eggs are easily killed by desiccation (Hunter 1964, Whitney 1938). Generally, the highest mollusc populations are found in moist areas (Likarev and Rammel'meier 1962) but, in contrast, Strandine (1941) found that populations of the snail Succinea ovalis decreased when soil moisture increased.

If moisture is available, terrestrial molluscs have a relatively wide temperature tolerance because they have a capacity for acclimation (Roy 1962) and, unless the air is fully saturated, they can thermoregulate by means of surface evaporation (Hogben and Kirk 1944). Actual temperature tolerance limits for any species have not been established but some molluscs have been found active at 32 F (Mellanby 1961) and 85 F (Hogben and Kirk 1944). Eggs and young are more sensitive to temperature than adults. Cold temperatures greatly retard the development of these immature stages (Whitney 1938, Herzberg and Herzberg 1960) while temperatures in excess of 72 F kill eggs (Carrick 1942).

When the climate becomes severe, most species of snails require some form of shelter which can hold a suitable microclimate (Likarev and Rammel'meier 1962). Rocks, logs, and leaf litter provide suitable shelter (Ingram 1941) but litter is preferred because it maintains the most stable microclimate (Burch 1956).

Since snails require a large amount of calcium for shell material and physiological processes, Boycott (1934), Van Cleave (1952), Baker (1957), Lozek (1958), and others believe that a lack of calcium is the factor most often limiting snail distribution and abundance. Oughton (1948) found a positive correlation between soil pH and snail distribution but pH and soil calcium are not always correlated (Lutz and Chandler 1946). Burch(1956), the only worker to measure soil calcium, found a strong positive correlation between soil calcium and snail distribution and abundance.

As a group, land snails eat fungi, algae, lichens, green or decaying vegetable material, and live or dead animal matter (Newell 1967). It is unlikely that there is any area that does not have sufficient quantities of at least one of these food types to maintain a population of snails (Boycott 1934).

Land snails do not appear to be greatly influenced by other animals or by pathogens since the effect of competition, disease, and predation appear to be negligible (Boycott 1934, Newell 1967). However, Mead (1961) describes a virus which limits populations of the giant African snail *Achatina fulica* and Cain and Sheppard (1954) showed that the song thrush *Turdus ericetorium* was a significant predator of the snail *Cepaea sp*.

In summary, the literature reports that soil moisture and calcium are the limiting factors of terrestrial snails. These factors are determined largely by plant cover, climatic, factors, and the edaphic factors of parent material, texture, and organic matter content (Lutz and Chandler 1946).

The objectives of this study then, are: (1) To determine the relative abundance and distribution of certain species of snails inhabiting a sheep range; (2) To determine the ecological requirements of important species; (3) To assess the importance of these biotic, climatic, and edaphic factors to the distribution, abundance, reproduction, and growth of certain species of terrestrial snails; and (4) To determine if snails act as intermediate hosts for sheep lungworm.

DESCRIPTION OF STUDY AREA

Location

The study area is located in the East Kootenay region of south-eastern British Columbia between the upper Kootenay and Columbia Rivers and the western slopes of the Rocky Mountains (Fig. 1). Within this area, the investigation was restricted to ranges used by bighorn sheep and particularly to those ranges which were involved in the recent die-off. Emphasis was placed upon low elevation (approximately 3000 ft.) winter ranges which are located at the western bases of the Stanford and Hughes ranges.

The winter ranges can be divided into discrete units (Fig. 2). Of these, the Premier Ridge range was studied intensively while the Columbia Lake, Radium-Stoddart, Bull River, and Estella ranges received extensive treatments. The extent of the summer range is unknown but alpine areas in the drainages of Sunken, Wildhorse, Lewis, Diorite, Ram, and Mutton Creeks were considered representative and were briefly examined.

Physiography

Most of the Premier range is located between elevations of 2850 and 4406 ft. (870-1340 m) on a ridge (Fig. 3) which rises above the Kootenay River bed to the west and is separated from the mountains to the east by Premier and Quartz Lakes and by Wolf Creek. The Ridge is about four miles long by one and a half miles wide (6.45 x 2.42 km) and extends in a north-south direction. On the western side of the Ridge, the terrain is gently sloping except for two series of 100 to 150 ft. (30.5-45.8 m) high cliffs or steep, rocky slopes located between the

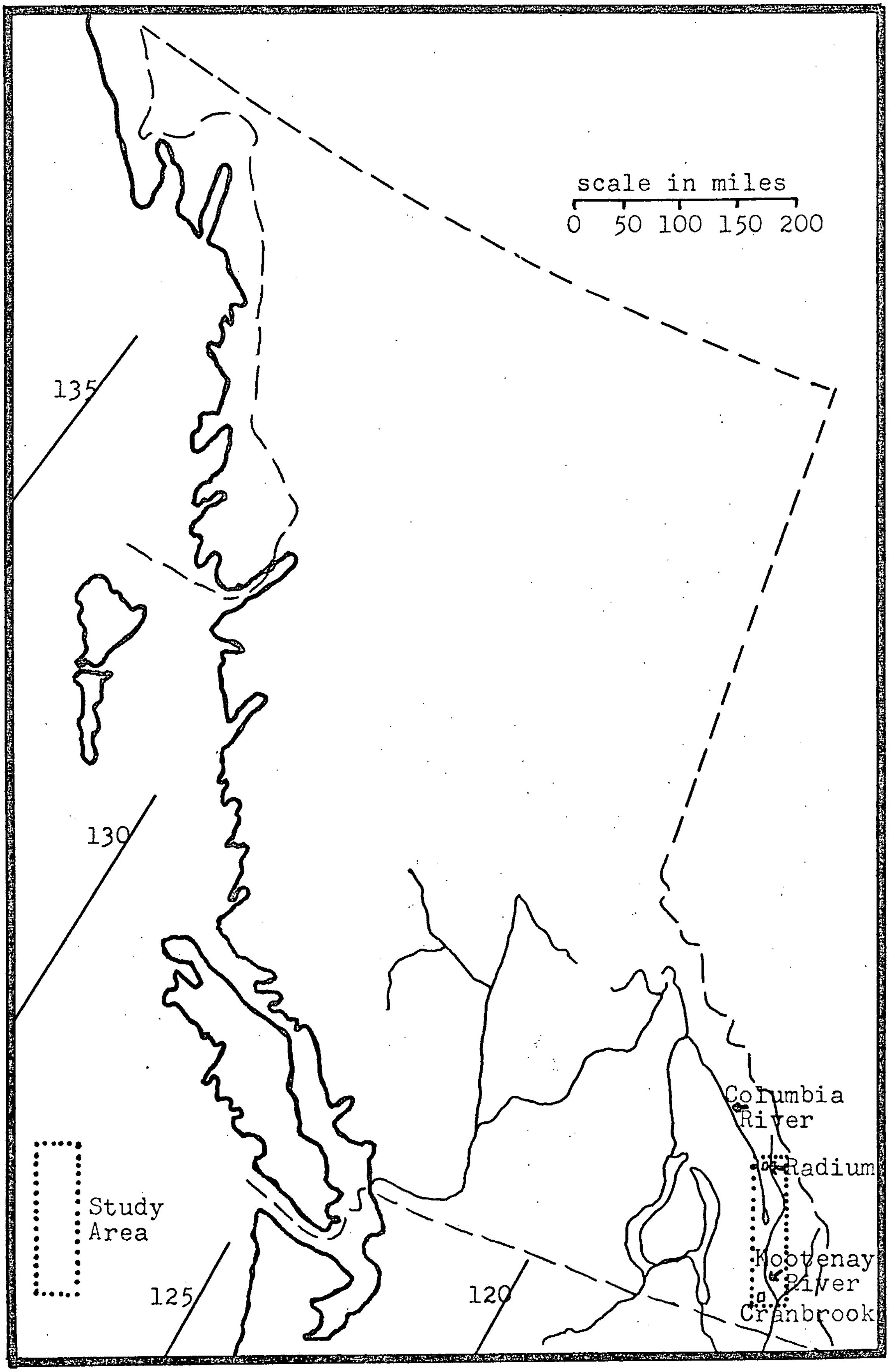


Fig. 1. An outline map of British Columbia showing the location of the study area in the East Kootenay region.

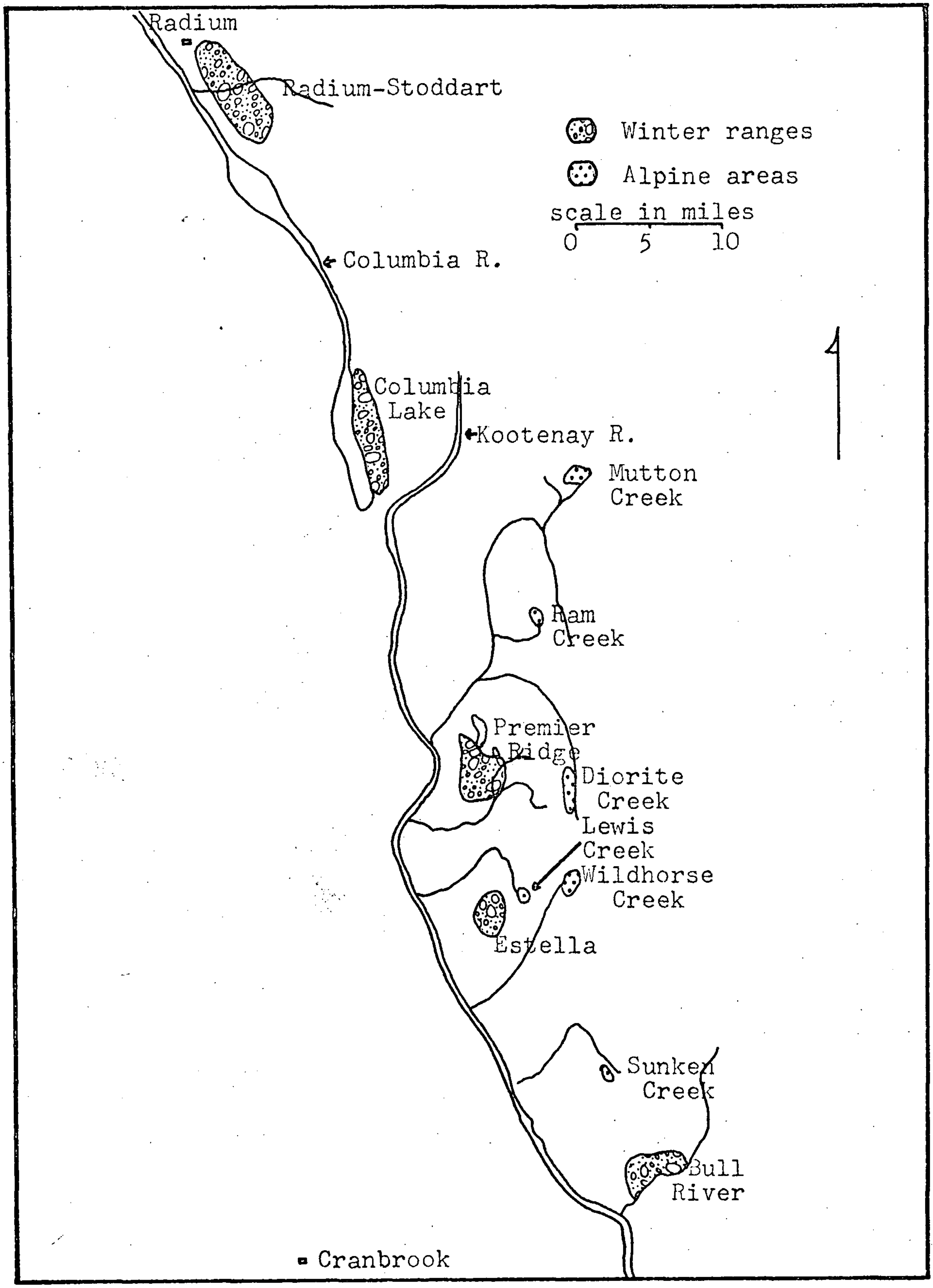
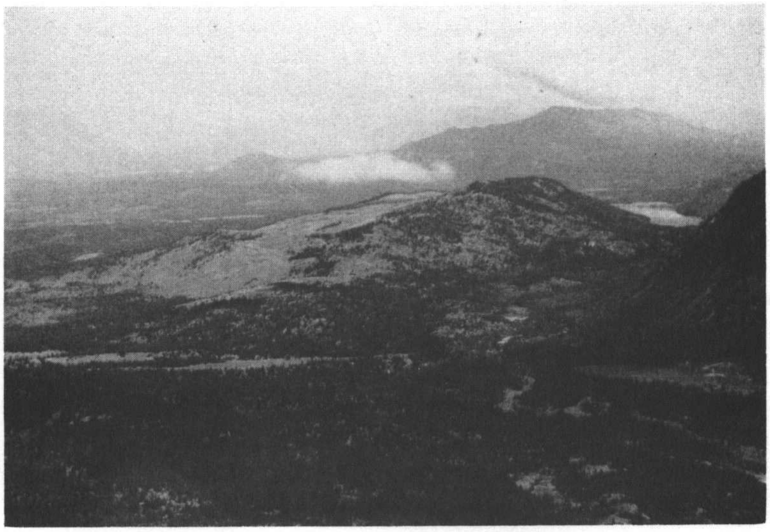


Fig. 2. The location of sheep winter ranges and alpine areas studied.

Figure 3. The Premier Ridge winter range.



3000 and 4000 ft (92.8-120 m) levels. On the eastern side, the topography is steeper and is dissected by deep gullies which contain water only in the spring. In addition, there is another series of cliffs above Quartz Lake and on the eastern side of the Ridge crest. South of Quartz Lake and east of the Ridge, between Wolf Creek and the mountains, is another part of the range known locally as the "Badlands". This is a series of step-like rock outcrops which lead up to the talus slopes at the foot of the mountains.

The Radium-Stoddart and Columbia Lake ranges are located on gently sloping river terraces and alluvial fans with a west to south-western exposure. Between the terraces and the mountains, there are an extensive series of rock outcrops and steep, rocky slopes. A few permanent creeks have formed deep gullies following geological faults.

The Estella range is situated on the west to south-westerly exposed flank of the Estella Mountain between the elevations of 4500 and 6000 ft (1370-1830 m). There are a few areas which are almost level and a few cliffs on the lower part of this range but the topography is generally steep and unbroken.

The Bull River range is located on a few flat river terraces and the steep, rocky, north bank of the Bull River Canyon with a south to south-western exposure. There are no dry cliffs similar to those which are present on the other low elevation ranges.

Geology and Soils

Calcareous Paleozoic rocks are the parent material of soils on the Radium-Stoddart, Columbia Lake, Ram and Mutton

Creek ranges. These rocks are composed of the limestones, dolomites, shales, and quartzites of the McKay, Jubilee, and Beaverfoot-Brisco formations (Henderson 1954, Leech 1954, 1958).

The Premier Ridge, Estella, and Bull River winter ranges and the remaining summer ranges are underlain by weakly or non-calcareous, Precambrian argillites, quartzites, and dolomites of the Aldridge, Fort Steele, and Creston formations (Leech 1958).

During the Pleistocene, a glacier moved down the valley which, when it receeded, left behind a till. Streams from the mountains, entering main rivers in the valley, formed fan-like deposits of alluvial material (Kelly and Holland 1961). The sand, silt, till, gravel, and alluvium formed in this manner cover the sheep range below 3000 ft (Leech 1954, 1958).

Vegetation

On the basis of aerial photographs, the B.C. Fish and Wildlife Branch (unpubl. rept.) described and mapped six basic plant communities which occur on Premier Ridge (Fig. 4):

(1) The *Purshia-Bromus-Stipa* (Bitterbrush) community is the most extensive, covering about 80% of the western half of the Ridge. Bitterbrush, *Purshia tridentata* and cheatgrass, *Bromus tectorum* are the dominant plants on the dry, gently sloping hills but Columbia needlegrass, *Stipa columbiana* and bluegrass, *Poa sp.* occur in moist hollows and gullies. Fig. 5 illustrates a portion of a bitterbrush community.

(2) The *Agropyron-Koeleria* (bunchgrass) community is found on dry, steep, rocky slopes and cliffs with a south or south-western exposure (Fig. 6). The plant cover, consisting mainly of bunchgrass, *Agropyron spicatum* and June grass, *Koeleria cristata*,

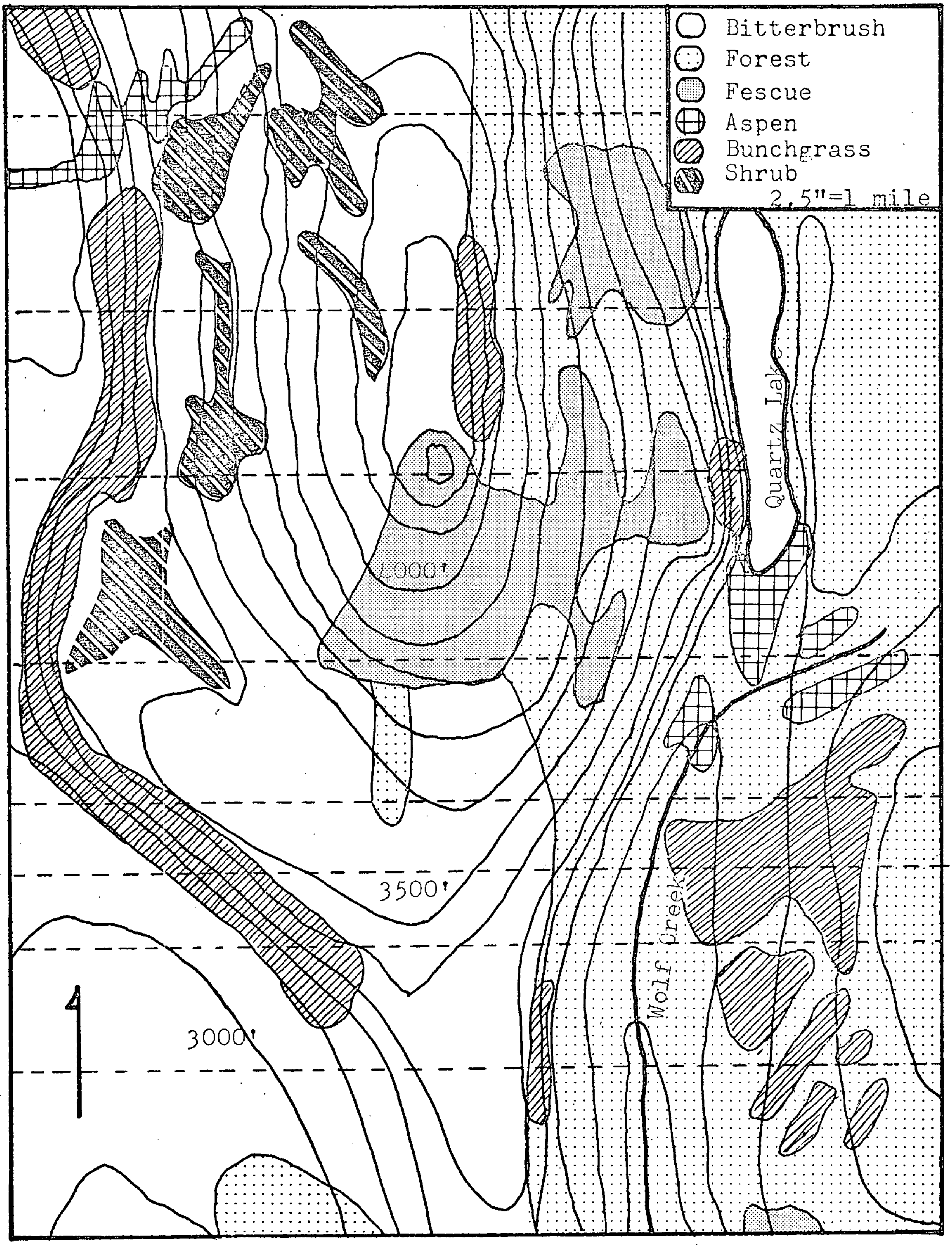


Fig. 4. The distribution of plant communities on Premier Ridge. Modified from unpubl. rept. of B.C. Fish and Wildlife Branch. Dashed lines are transects established to sample snails.

Figure 5. A Purshia-Bromus-Stipa (bitterbrush) community.

Figure 6. An Agropyron-Koeleria (bunchgrass) community.

is usually sparse but on ledges of rock outcrops the bunchgrass is frequently quite dense.

(3) On moist, gently sloping sites on the western half of the Ridge, the *Shepherdia* (shrub) community is present (Fig. 7). Soapberry, *Shepherdia canadensis* grows in dense clumps with bluegrass growing under and between the shrubs.

(4) The *Populus-Salix* (aspen) community is found in wet hollows and along waterways (Fig. 8). Aspen, *Populus tremuloides* is the characteristic plant and the litter produced by its leaves covers much of the ground.

(5) The *Pinus-Pseudotsuga* (forest) community occurs wherever there is sufficient moisture and covers most of the eastern half of the Ridge (Fig. 9). Lodgepole pine, *Pinus contorta* occurs in dense stands in moist hollows but Douglas fir, *Pseudotsuga menziesii* is more widely distributed. Except where dense stands of young fir are present, pine grass, *Calamagrostis rubescens* forms a heavy grass cover under the forest canopy.

(6) The *Agropyron-Festuca* (fescue) community (Fig. 10) occurs at the top of, and on the eastern side of the Ridge in areas which are drier than the forest but moister than the bunchgrass community.

Figure 7. A <u>Shepherdia</u> (shrub) community.

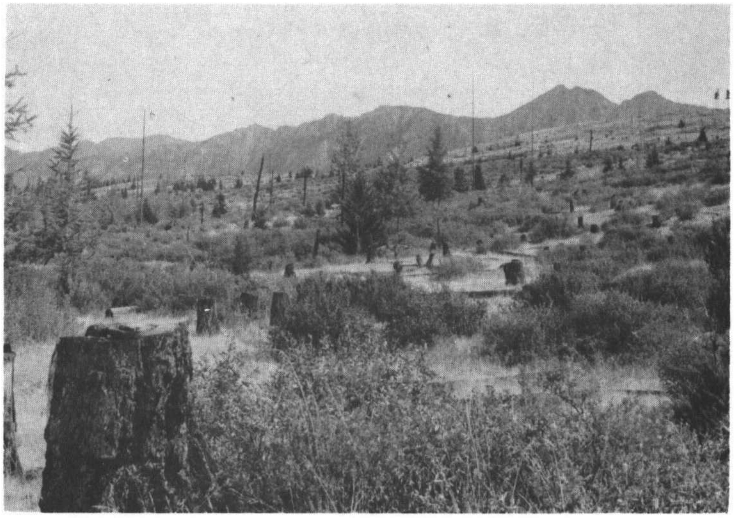


Figure 8. A <u>Populus</u>-<u>Salix</u> (aspen) community.

Figure 9. A Pinus-Psuedostuga (forest) community.

Figure 10. An Agropyron-Festuca (fescue) community.

METHODS

Distribution and Abundance

Since the land snails on Premier Ridge are too small and numerous to study the whole population and too large to study by techniques used for soil microfauna (see Murphy 1958), a suitable sampling program had to be developed. Before this could be done, it was necessary to know the habitat of the snails.

Preliminary investigations established that these snails are not found in soil or vegetation and also suggested that the most abundant snail (*Vallonia*) was present only under loose, surface rocks. To test this and to measure snail density, an area where this species was known to be present was selected and ten transects 50 yards (45.8 m) apart were run through this area. At 25 yard intervals along each transect, all possible habitat within a three foot (.92 m) diameter circle was examined for snails. To determine the relationship between rock size and snail occurrence, another area where *Vallonia* was known to be relatively abundant was selected and the soil surface under rocks of all sizes examined. The frequency and number of snails found under each category of rock size was recorded.

Since plant communities are indicative of the edaphic and climatic conditions present (Krajina 1965), the plant communities on Premier Ridge were used as the basis for the study. Using the information gathered in the preliminary work, the following sampling program was adopted to determine the relationships between snail distribution and plant communities. Eight transects

(Fig. 4) running in an east-west direction were established so that they passed through all the plant communities on Premier Ridge with a frequency approximately proportional to the area occupied by each community. The two largest rocks in every 100 ft. (13.6 m) of each transect were selected and the area underneath examined for snails. The relative humidity of the depression was measured with a Bendix-Friez hand aspirated hygrometer and the soil temperature at a depth of one inch (2.54 cm) was measured with a pocket thermometer. The species of snails present and the numbers of live and dead snails were recorded. Any Vallonia lacking the aperture lip which is characteristic of adults (Whitney 1939) was considered to be immature. If no rocks were present in any section of transect, then an area of one square foot (.09 m^2) under any logs, leaf litter or grass occurring on the transect was examined. After the first transect, measurements of temperature and humidity were taken only where snails were present or after every tenth rock because the first method was too time consuming.

The transect technique was relatively inefficient in finding snails, so considerable time was spent selectively searching Premier Ridge and gathering data on microclimate and age ratios of snails. Most of the live snails were found in this manner.

During the summer of 1967, the other sheep winter ranges were visited and searched for snails in an attempt to obtain comparable data on Vallonia abundance. On each range, a number of rocks which appeared to be most suitable for Vallonia was selected in an area where the species was known to be relatively abundant and the soil surface under each rock was examined for snails.

Climate

In 1967, a meterological station was established in three important plant communities on the Ridge to obtain weekly measurements of the climate at ground level. The stations consisted of a maximum-minimum recording thermometer buried to a depth of one inch in the soil to avoid exposure to the sun, a rain guage, and three evaporimeters. The evaporimeters were made from a can four and one half inches (11.4 cm) long and three inches (7.7 cm) in diameter which was half buried in the soil. The can was filled to a calibrated mark with tap water and covered with a lid constructed so that rain was excluded but air had access to the water surface.

Another meterological station, consisting of a recording thermometer in a Stevenson screen, two ogopogo evaporimeters (Wilcox 1966), and two rain guages was established near Quartz Lake to measure the macroclimate in a bunchgrass community known to be inhabited by snails.

Soils

During the third week in September 1967, representative soil samples were gathered from all communities on Premier Ridge and from bunchgrass communities on other winter ranges to study the edaphic characteristics of each community. Samples weighing about 1.5 kg were taken to a depth of one inch from under rocks except in the aspen community where they were taken from under leaf litter. Five samples were obtained from all

Premier Ridge communities except the bitterbrush and bunchgrass communities, where 14 and 20 samples respectively were taken. The bunchgrass community was sampled heavily to allow comparisons between snail habitats while more samples were taken from the bitterbrush community to assess variability. The following numbers of samples were taken from other ranges: Columbia Lake 10, Bull River three, Radium-Stoddart one. All samples were placed in air-tight containers immediately after they were obtained.

Approximately ten grams of each sample were oven dried to determine soil moisture. Then, another ten grams were mixed with 20 ml of distilled water, stirred, and allowed to stand for 18 hours. The pH of the soil solution was measured with a Beckman "Zeromatic" pH meter. The soils were then air dried at room temperature for five days after which the organic content of each sample was determined by the Walkely-Black wet combustion method (Jackson 1958). This method used only 0.2 g of soil if the organic content was high. To determine error involved in this measurement, one quarter of the samples were chosen at random and the procedure repeated. Soil moisture and pH measurements were not duplicated because of the relatively large amounts of soil and the simple techniques which were used for these determinations.

Dr. C.C. Rowles, Head, Soil Science Division, hand textured and formed balls from each soil sample after it had been wetted. The consistence of the soil balls after drying at room temperature was described according to methods established by the Soil Survey Staff (1951). The samples were divided into classes according to their texture and organic content so that a total of 14 classes were established.

The ability of the soil to retain water was determined with a porous plate pressure extractor (Holmes et al 1967). Pressures of 4.8, 13, 58, and 215 psi were used. The water remaining in the soil, after being subjected to the lowest test pressure, approximates the water content after normal drainage. At the other extreme, water not extractable by a pressure of 215 psi is bound too tightly to the soil to be available to plants (Dr. J. De Vries, pers. comm.). A rubber ring, five centemeters in diameter by one centemeter high, was filled with soil from each of the 14 soil classes. An excess of water was poured on the plate and allowed to come into equilibrium with the soil. The plate and the soil were placed in the extractor at 4.8 psi for one week. The moisture remaining in the sample, after that time, was determined by measuring the weight lost upon oven drying at 105 C for one day. This was repeated at 13, 58, and 215 psi.

Calcium

Since the literature considers a low level of calcium to be a major limiting factor for snails, the effect of calcium on the distribution of snails inhabiting sheep ranges was investigated. This was done in two ways: (1) The amount of calcium in the soil of each plant community was determined by leeching five grams of each soil sample with 250 ml of 1.0 N ammonium acetate and measuring the calcium content of the solution with a Perkins-Elmer "303" atomic absorption spectrophotometer. The distribution of snails on Premier Ridge was then related to the distribution of the plant communities. (2) A series of experiments were devised to experimentally test the effect of calcium on survival, reproduction, and growth of *Vallonia*.

Ten flower pot colonies were established in the following manner: A rolled, five centimeter long wick was made from cheesecloth and was wedged into the hole in the bottom of a three inch (7.5 cm), clay flower pot. The pot was covered with a Petri dish and placed into the neck of a quart jar which was one quarter filled with water. This arrangement provided a suitable humidity for snails. The bottoms of the pots were covered with washed sand. To five of the pots, approximately one gram of powdered calcium carbonate was added. Five *Vallonia* which had been maintained in stock colonies were placed in each pot. Colonies with calcium in the substrate were fed lettuce which had been rolled in calcium carbonate to approximate vegetation that had been grown on calcium rich soils. Control colonies were fed an equal amount of unaltered lettuce. Once a week, the snails were fed, the water level brought up to the mark, and the eggs and dead snails counted and removed. Eggs were placed in a separate pot to obtain data on hatching time.

At the end of the experiment, surviving snails were stored in 70% alcohol to prevent decay of the soft tissues. Snails from colonies with added calcium were kept separate from the controls. To determine if snails without access to calcium lost the mineral from their bodies while producing eggs, both groups of snails were ground to a powder, dissolved in excess hydrochloric acid, and the calcium content of the solution determined with a spectrophotemeter.

Any difference between the colonies might have been due to the carbonate rather than the calcium. To test this, six more colonies were established. A mixture consisting of four parts magnesium carbonate, one part magnesium hydroxide, and "n" parts water was added to the sand of three colonies. These snails were fed lettuce which had been rolled in the magnesium mixture. Otherwise, these six colonies were treated in the same manner as the previous ten.

To test the effect of calcium on growth, ten colonies of a different type were established. They consisted of a four dram vial with the bottom filled to a height of one centimeter with compressed, water-saturated, cotton batting and sealed with a screw lid. The cotton was covered with washed sand with five colonies receiving approximately 0.2 g of calcium carbonate. Two young snails that were sufficiently different in size so that they could be easily separated were taken from stock jars and placed in each colony. These were fed once a week with plain or calcium covered lettuce.

The greatest width and length of the snails were measured every week with a occular micrometer in a dissecting microscope. The two measurements were added to give an index of snail size and the average daily growth rate of each snail was calculated. This method of assessing growth is similar to that used by Whitney (1938) and Strandine (1941).

Parasitism

Live snails were examined for the presence of lungworm larvae by the method of Gerichter (1948), Kassai (1958), and Forrester (1962). Snails were placed in a Petri dish and activated with a fine spray of water. The Petri dish was then inverted and the feet of active snails examined with a dissecting microscope using reflected light and a magnification of 40 diameters. Snails were kept in flower pot colonies for 30 days to allow any larvae present time to develop and then were re-examined.

An attempt was made to infect snails with larvae obtained by the Baerman technique (Cable 1958) from sheep feces. The larvae were placed on the soil substrate of a colony of 25 snails which were examined two and six weeks later.

RESULTS

Distribution and Abundance of Snails

The most important species of land snails[1] found on the East Kootenay sheep ranges are shown in Fig. 11. These represent three molluscan families: Zonitoidae, Vallonidae and Pupillidae.

Zonitoidae

The Zonitoidae includes *Retinella electrina* (Gould), *Euconulus fulvus* (Muller), and *Vitrina alaskana* Dall. These species are the most widely distributed snails in the East Kootenay (Table 1). They live under the shelter of rocks, logs, or leaf litter, but are most abundant where such shelter occurs in moist hollows. Of these, *Euconulus* is the most abundant while *Retinella* is the most widely distributed. *Vitrina* is the least abundant except on alpine ranges where it was the one species commonly found. Relative abundance is shown by counts of 87 *Euconulus*, 73 *Retinella*, and 39 *Vitrina* which were made during the transect sampling.

Vallonidae

Vallonia cyclophorella (Sterki) is the only representative of the Vallonidae on the sheep ranges. It is present on drier parts of all sheep ranges except the Estella and alpine

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1 Unless qualified the term "snails" refers to live snails and snail shells.

Figure 11. The important snails on East Kootenay sheep ranges. In a clockwise direction starting from the left: Vitrina alaskana, Euconulus fulvus, Pupilla muscorum, Retinella electrina, Vallonia cyclophorella, Gastrocopta holzingeri. The 1 mm line shows scale.

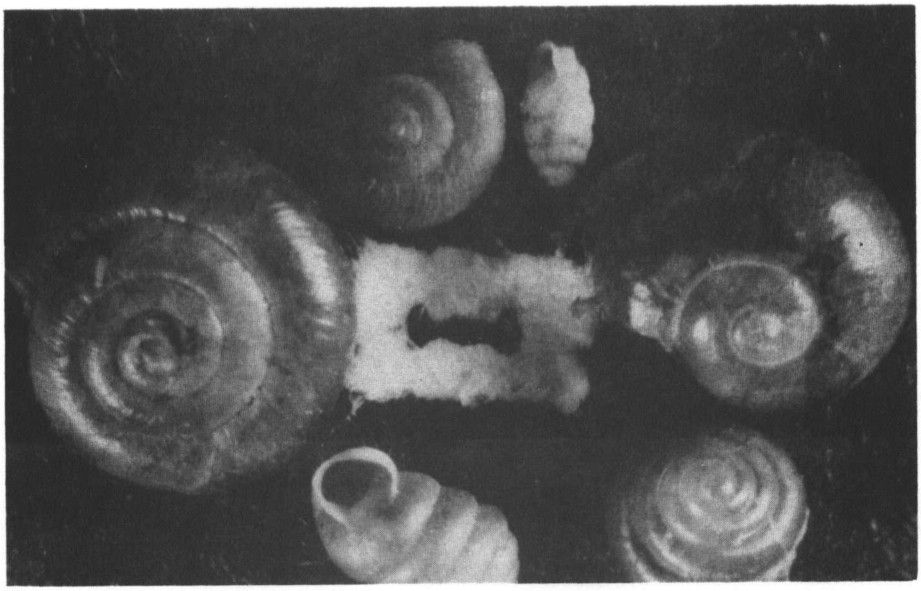

Table I. Distribution of snails on East Kootenay sheep ranges.

Species of snail	Range: Bull River	Estella	Premier Ridge	Columbia Lake	Radium-Stoddart	Rocky Mt. Alpine
Retinella electrina	+	+	+	+	+	+
Euconulus fulvus	+	+	+	+	+	+
Vitrina alaskana	+	+	+	+	+	+
Vallonia cyclophorella	+	-	+	+	+	-
Gastrocopta holzingeri	-	-	+	+	+	-
Pupilla muscorum	-	-	-	+	-	-

+=present
-=absent

areas. Vallonia inhabits space under loose, surface rocks on steep rocky slopes, and especially on ledges of rock outcrops (Fig. 12). In 65 sample-circles in Vallonia habitat, this species was found under rocks 13 times but never on the surface of the ground.

The abundance of Vallonia in an area depends upon the size of rocks present since snails are most numerous under large rocks (Table 11) for reasons which will be discussed later. As the largest rocks are generally found on rock outcrops, this is possibly why snails are most abundant there.

On dry slopes, Vallonia is the most abundant snail. In habitat sampled by the circle-transect method, the density of this species was $0.03/ft^2$ ($0.0032/m^2$), probably the average density of Vallonia in suitable habitat on Premier Ridge. In optimum areas on Premier Ridge, over 100 snails of this species were found under a single rock but this was not commonly encountered.

Table 111 list the frequency and abundance of Vallonia under selected rocks on each of the winter ranges. This data should be suitable for comparing snail abundance between ranges since the largest rocks in what appeared to be the most suitable snail habitat were selected.

Vallonia are most abundant on the Columbia Lake and Radium-Stoddart ranges where snails were found under 54% and 75%, respectively, of the rocks selected. Large concentrations of snails were found on both ranges but this more commonly occurred on the Columbia Lake range. Vallonia are much less numerous on the Premier Lake and Bull River ranges where snails were found

Figure 12. Typical *Vallonia* habitat.

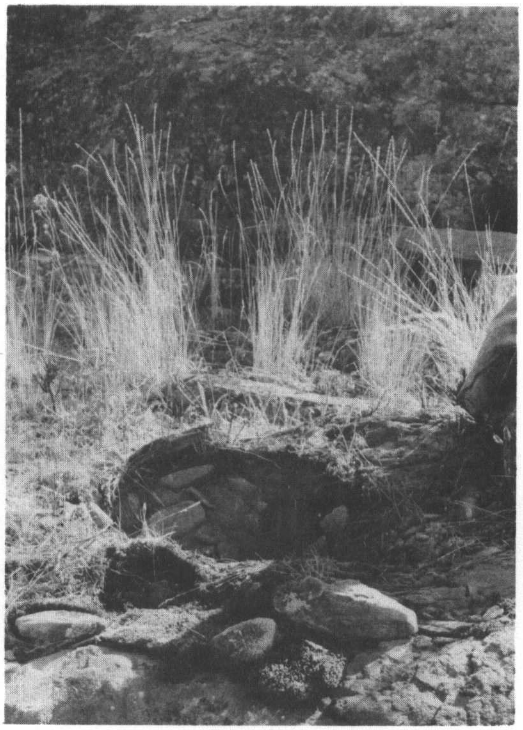

Table II. Relationship between the occurrence of Vallonia and rock size.

Rock size ($inch^2$)	Sample size	Snail occurrence	Occurrence (%)
1-4	100	0	0
5-8	100	0	0
9-15	100	0	0
16-24	72	1	1.4
25-48	78	6	7.9
49-63	43	7	16.4
64-99	34	12	35.3
100+	25	11	44.0

Table III. Abundance of Vallonia under rocks on sheep winter ranges.

Range	No. of Rocks sampled	Snail frequency (%)	Avg. No. snails/rock
Bull River	78	24.6	0.5
Premier Ridge	72	39.2	11.3
Columbia Lake	41	54.7	24.1
Radium-Stoddart	64	75.0	7.2

only under 39% and 24% of the rocks selected and where large concentrations of snails are scarce. There may not be as much habitat for Vallonia on these ranges since the Bull River range lacks the cliffs which are the most suitable habitat for this species and the cliffs on the Premier Ridge range are less extensive than those on the two northern ranges.

Pupillidae

The family Pupillidae includes Gastrocopta holzingeri Sterki and Pupilla muscorum (L.). The distribution of Gastrocopta appears to be similar to that of Vallonia except that Gastrocopta was not found on the Bull River range. The apparent absence of Gastrocopta from this range might be due to the difficulty in finding this minute snail. Gastrocopta are nowhere abundant, being found mostly in groups of one or two, but on the Radium-Stoddart range, groups of five to ten were common and one group of 30 was found.

Pupilla muscorum is restricted to rock outcrops on the Columbia Lake range where it occupies the same habitat as Vallonia and Gastrocopta. On this range, Pupillla is widely distributed and relatively abundant. In optimum areas, concentrations of over 200 Pupilla, as well as an equal number of Vallonia, were found.

Other Land Snails

Other land snails which were found in a wet aspen grove on the Estella range and in sedge meadows along Wolf Creek included specimens of Succinea haydoni Binney, Cionella lubrica

Muller, *Zonitoides arboreus* (Say), and *Catinella avara* (Say). Although Burch (1962) considers *Catinella* to be restricted to margins of water, it was found four times on Premier Ridge at least one-half mile from water.

Amphibious snails

The following species of amphibious snails are present on the vegetation surrounding creeks and sloughs in the East Kootenay: *Planorbis simularis* Baker, *Aplexa hypnorum* Linne, and *Lymnea gàlla* (Tryon). One specimen of *Allagama ptcychophora* (A.D. Brown) was found on the edge of the Bull River range. This snail is abundant in dense grass under deciduous trees along stream banks, but it is rare on the sheep range.

Relationship between Snails and Plant Communities

The distribution of snails in six plant communities on Premier Ridge (Fig. 13) is based on data obtained from transects through the communities. In addition, large areas of each community were searched in a less systematic manner but the results were essentially the same.

The aspen community contains the largest populations of Retinella, Euconulus, and Vitrina. At least one specimen of the three species was found in every site where aspen litter was present, with the greatest abundance occuring in dense aspen forest. Similar observations were made by Karlin (1961) and Bettle (1957, 1960).

The forest and shrub communities support moderate populations of Vitrina, Retinella, and Euconulus but these snails are concentrated in the bottom of moist gullies. Few snails are found on the dry forest floor.

Vallonia is restricted mainly to bunchgrass communities on Premier Ridge and also on the other ranges studied. On ranges where Gastrocopta and Pupilla are present, they are also restricted to this community. Vallonia, Gastrocopta, and Pupilla are not nearly as abundant in the bunchgrass community as are Euconulus and Retinella in the aspen community.

Snails are scarce in the bitterbrush community. Retinella was found only ten times and Vallonia nine times in 730 samples. Vallonia was found in transitional sites between bunchgrass and bitterbrush communities. Snails are also rare in the fescue community. No snails were found on transects and even selective searching in this community produced only a few specimens of Retinella.

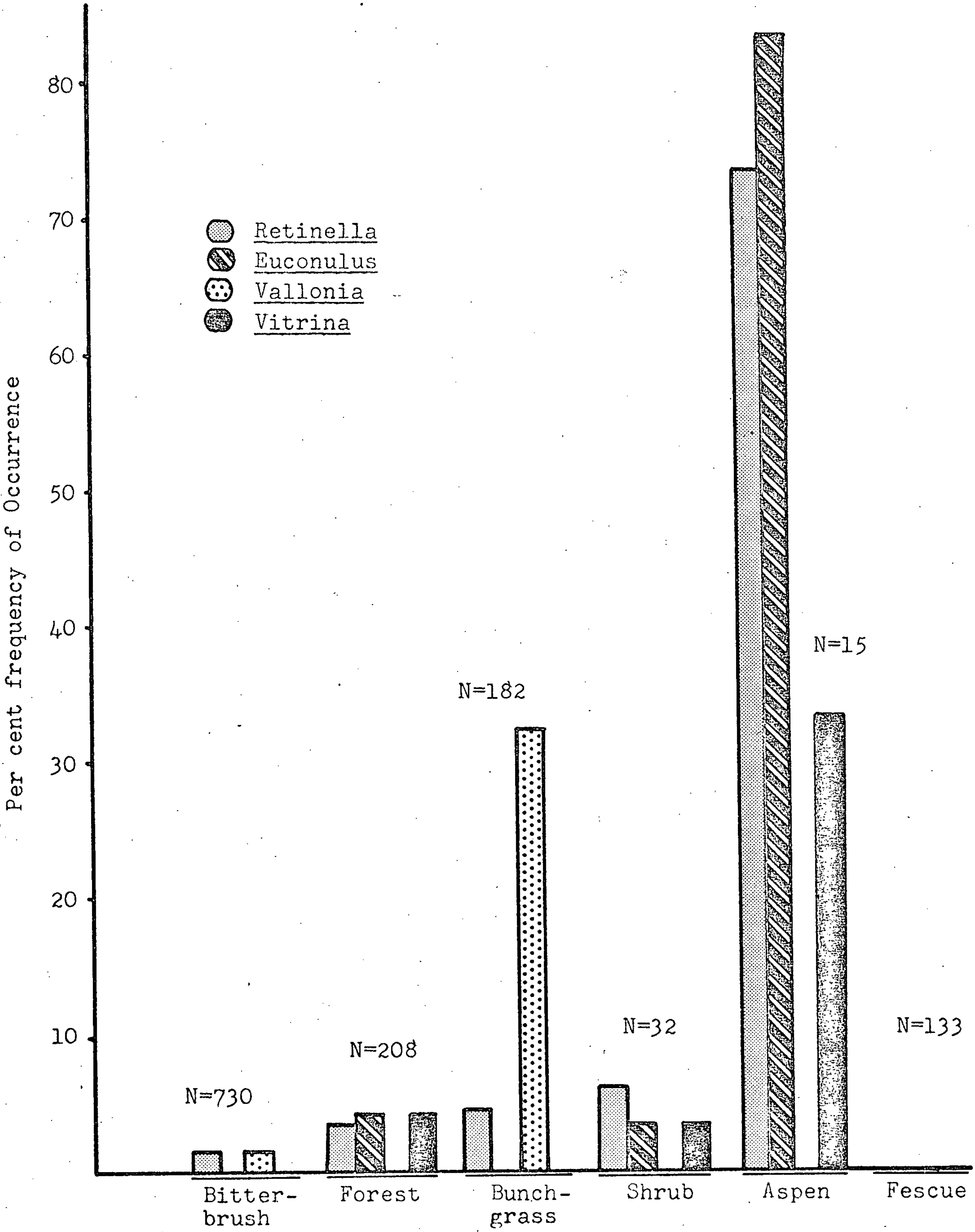

Fig. 13. Distribution and abundance of snails in Premier Ridge plant communities.

Effect of Climatic Factors on Snail Distribution and Abundance

Arid conditions, which are characteristic of the summer climate (Table IV) of the winter ranges, appear to have a strong depressing effect on *Vallonia* populations. This is illustrated by Fig. 14 which shows the survival of *Vallonia* during the summer months of 1966 and 1967. The general pattern appears to be one of a decreasing population as increasing temperatures and evaporation destroy the ability of marginal habitats to maintain a suitable microclimate for the snails. The initial sharp population decline probably results from the death of young and eggs since Whitney (1938) has shown that these immature stages of *Vallonia* are more susceptible than adults to desiccation. As the climate between May and July became more arid, the per cent of young in the live snail population decreased, but the per cent of young found dead increased markedly (Table V).

After July, the population consists of adult snails aestivating in good habitat. Enough rain usually falls in June to allow these snails to survive until the rains and cool temperatures of late August and September permit them to become active and start reproducing again. The population then increases until the cold temperatures of November force the snails into hibernation.

The amount of rain in July probably determines the size of the snail population later that year and next spring. In the East Kootenay, May, June, and August are relatively wet months but July is one of the driest and the warmest. A summer with adequate precipitation during July should enable more adults to survive the rigors of summer so that there is a rapid population

Table IV. Temperature and precipitation at the Quartz Lake weather station.

	Mean temp. (°F)		Mean ppt. (inches)	
Month	1966	1967	1966	1967
May	m	49.7	m	m
June	56.0	58.8	1.14	5.05
July	63.1	67.1	1.08	.57
August	60.9	70.3	2.13	tr
Sept.	60.9	63.5	.15	.52
Oct.	m	45.2	m	1.58

m=missing

Table V. The percentage of young snails in the Vallonia population on Premier Ridge during summer 1967.

	Live snails			Dead Snails		
Month	Young	Adults	Young(%)	Young	Adults	Young(%)
May	8	5	61.5	2	8	20.0
June	40	43	46.5	32	162	16.5
July	0	1	0	20	23	46.5
August	0	1	0	54	117	31.6
Sept.	0	8	11.1	39	67	37.8
Oct.	0	1	0	49	150	32.6

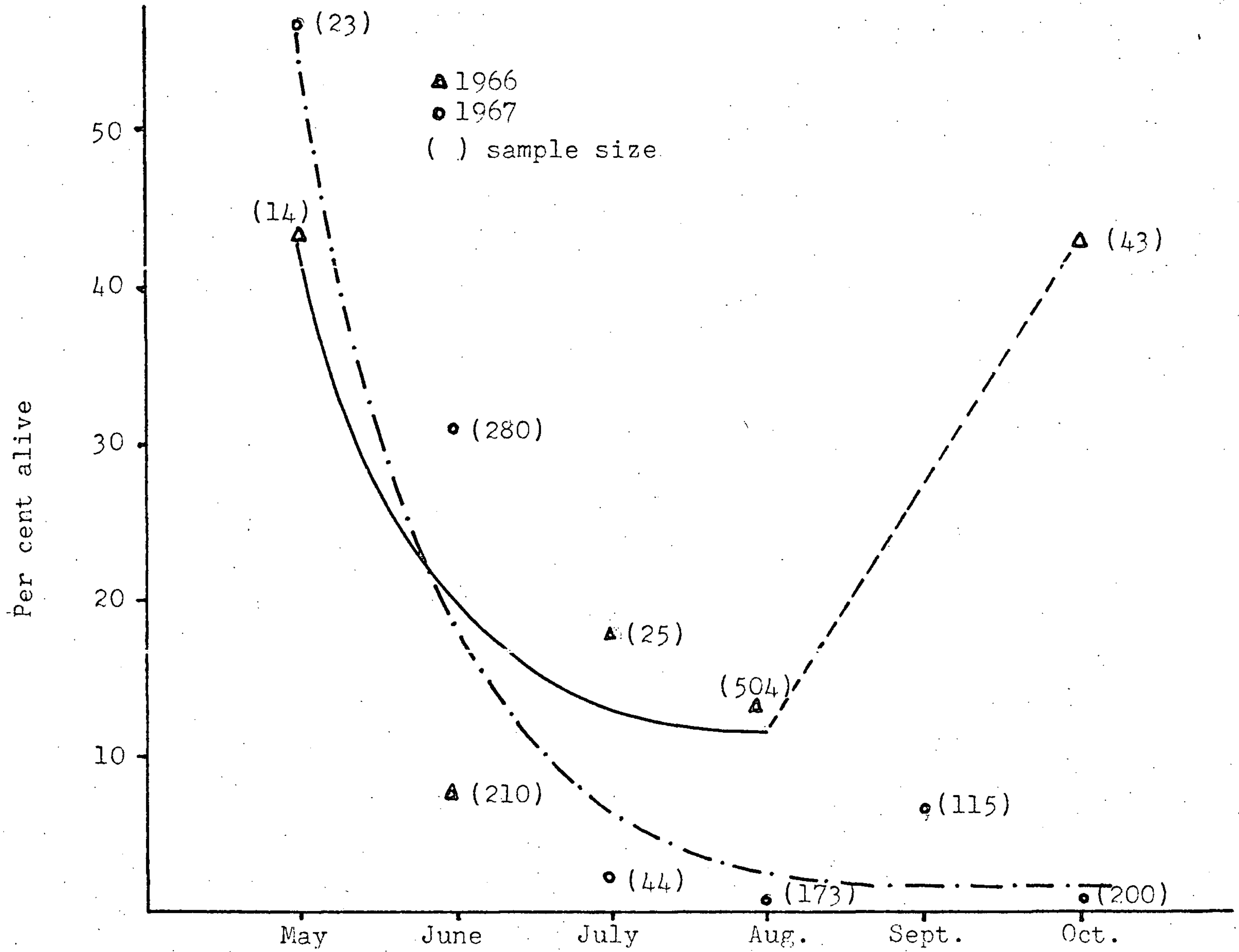

Fig. 14. The survival of the Vallonia population on Premier Ridge during the summers of 1966, 1967. Dashed line indicates estimated population increase.

increase in the autumn and a high starting population in the next spring.

The effect of summer precipitation on snail populations is shown in Fig. 14 where the snail survival is compared between the summers of 1966 and 1967. In 1966, the population apparently declined until July when it became stable or possibly increased. It began increasing after 1.8 inches of rain fell in the last three days of August. The rain appears to have stimulated the snails to come out of aestivation because none of the snails observed after the rain had the aperture sealed with the membrane which is characteristic of aestivating snails. Since 11 of the 18 live snails collected in October 1966 were young, it is believed that the increased population at that time was due to the young snails added to the population following the August rain. In 1967, June was wetter than 1966 and snail survival was higher, but since the rest of the 1967 summer was much more arid, the snail population declined sharply until late July and remained at a low level until at least mid-October. Snails observed at that time were still aestivating. Cold temperatures probably forced the snails to hibernate before there was a major population increase.

The climate of Premier Ridge is greatly influenced by plant cover (Table VI) and this may affect the distribution and abundance of snails. High populations of certain species in the aspen community may be partly explained by the cool and moist conditions found there. The climate under this dense forest canopy remained stable and moderate even during one of the warmest summers on record. In contrast, the climate of the bunchgrass community was the most arid and appears suitable only

Table VI. Microclimate in three Premier Ridge plant communities, 1967.

	Plant community					
	Coniferous forest		Bunchgrass		Aspen	
Month	Evap. (ml)	Mean temp. (°F)	Evap. (ml)	Mean temp. (°F)	Evap. (ml)	Mean temp. (°F)
June	504	64.5	556	68.6	108	54.5
July	906+	73.3	1034+	80.3	463+	61.5
August	1134+	76.0	1134+	82.9	994+	65.5
Sept.	967	m	1134+	74.0	664+	m
Oct. *	181	m	250	63.0	68	m

+=evaporimeters went dry during one or more weeks.
*=ten days only.
m=missing.

for Vallonia and Gastrocopta. The climate of the coniferous forest community was between the two extremes but closer to that of the aspen community. This may be a reason for the snail fauna of the two communities being similar.

Fig. 15 shows the relative humidities in habitats in which the four common species of snails were found. The hypothesis that these curves are all part of the same distribution was tested with the chi-square test. Statistically, there is no difference (P=.05) between the distribution of Euconulus and Retinella but the distribution of Vallonia and Vitrina are different (P=.01) from each other and from those of Retinella and Euconulus.

Based on this data, the land snails inhabiting the East Kootenay sheep ranges can be divided into three groups: obligatory hydrophils, facultative hydrophils, and xerophils. Other than the amphibious snails, the only obligatory hydrophil is Vitrina. This snail is restricted to habitats which, because of plant cover, drainage, or exposure, remain constantly moist. Young Vitrina avoid dry periods by burrowing in soil but adults, because of their large shell, are restricted to the soil surface where they are very susceptible to desiccation (Kuhnelt 1961). This may explain why this species was found alive only during the early spring when moist conditions are present.

Retinella and Euconulus are facultative hydrophils. They are found in many habitats and over a wide range of humidities but they are most abundant in moist areas.

Vallonia is relatively xerophilic, occurring in areas much drier than where the other three species are present. In

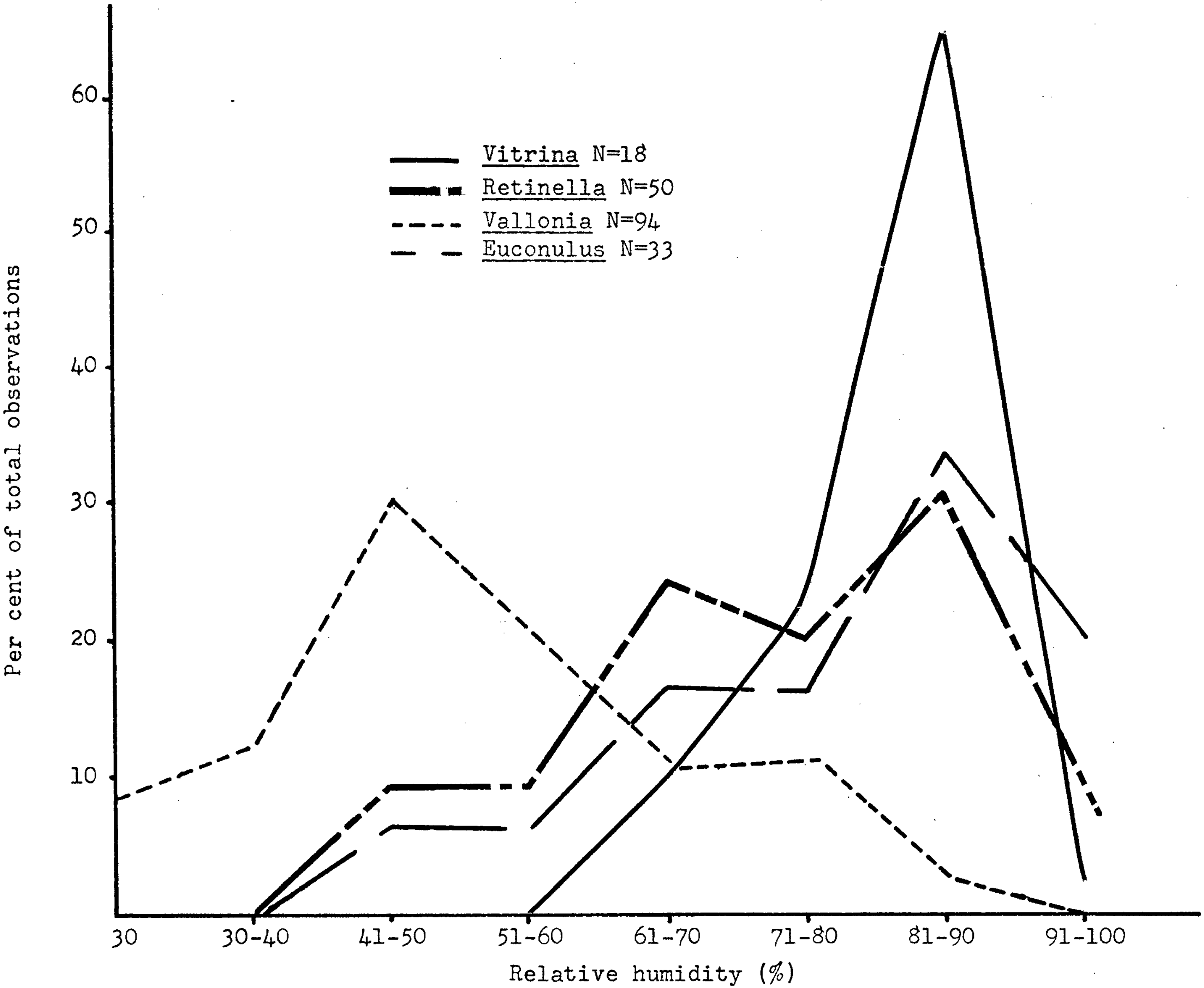

Fig. 15. Relative humidity in snail habitats.

contrast to Vitrina, Vallonia is not found where surface water accumulates. The few data available for Gastrocopta and Pupilla suggest that they have moisture requirements similar to Vallonia.

Fig. 16 shows the soil temperature in habitats of the four common species. Chi-square tests show that there is no difference (P.=.05) in the distribution of Vitrina, Euconulus, or Retinella but that the distribution of Vallonia extends significantly (P.=.01) further into habitats with warmer temperatures.

As arid climates adversely affect Vallonia populations, it could be predicted that Vallonia will be found in the coolest and moistest parts of its habitat. Fig. 17, which shows the regression of numbers of live Vallonia present on the temperature and humidity of the habitat, supports this prediction. The number of live Vallonia present is proportional to the relative humidity and inversely proportional to the temperature of its habitat. The best microclimate for Vallonia appears to be a high relative humidity and a low temperature.

Another indication of the preference of Vallonia for cool and moist areas of its habitat is shown by its activity. Since snails withdraw into their shells if the climate is unsuitable (Hogben and Kirk 1944), they remain active only under conditions of optimum temperature and humidity. Table VII lists the temperature and humidity in sites where active snails were observed and the ratio of active to inactive snails present. The data indicate that snails are most active at, and hence prefer, relative humidities between 70 and 80% and temperatures below

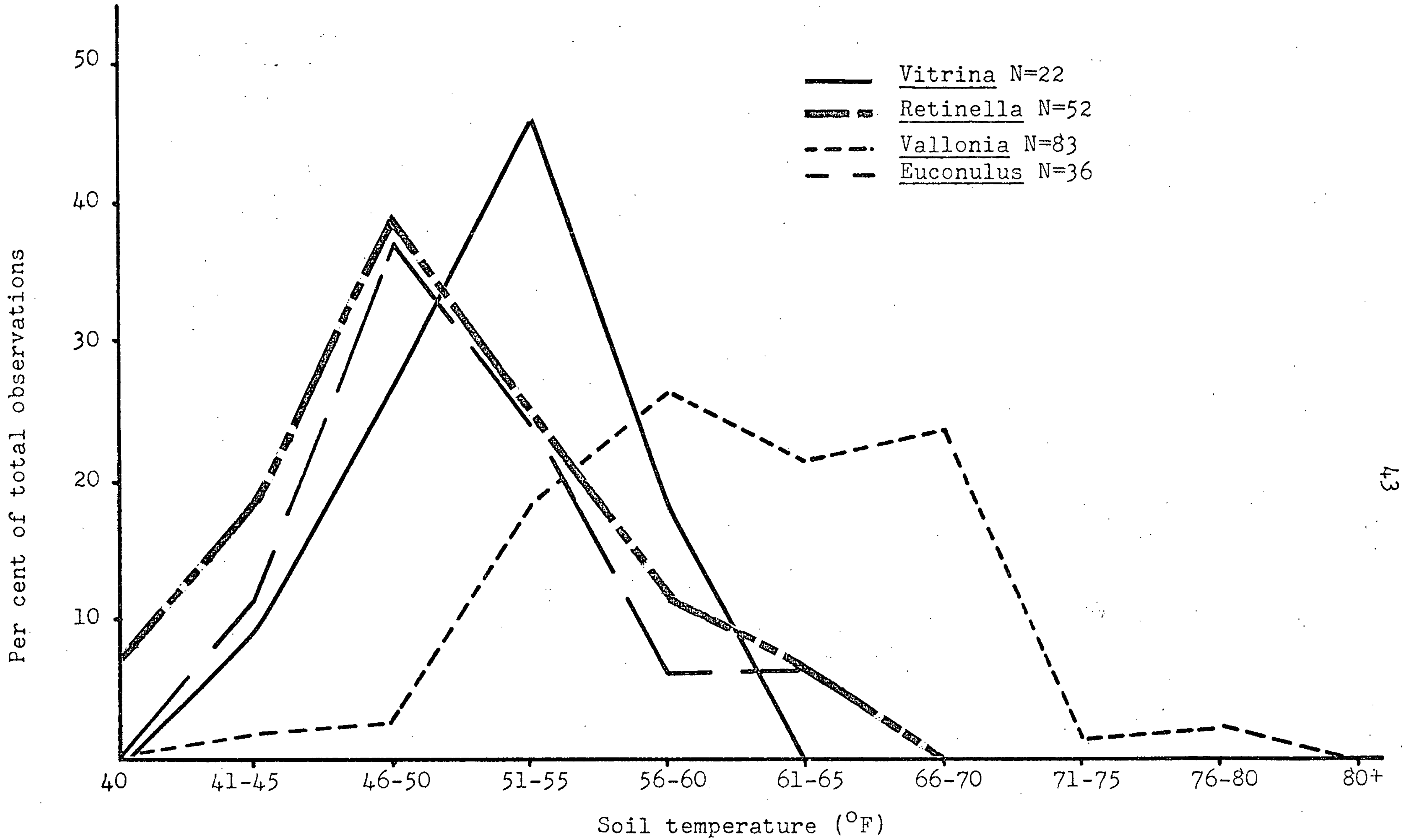

Fig. 16. Soil temperature in snail habitats.

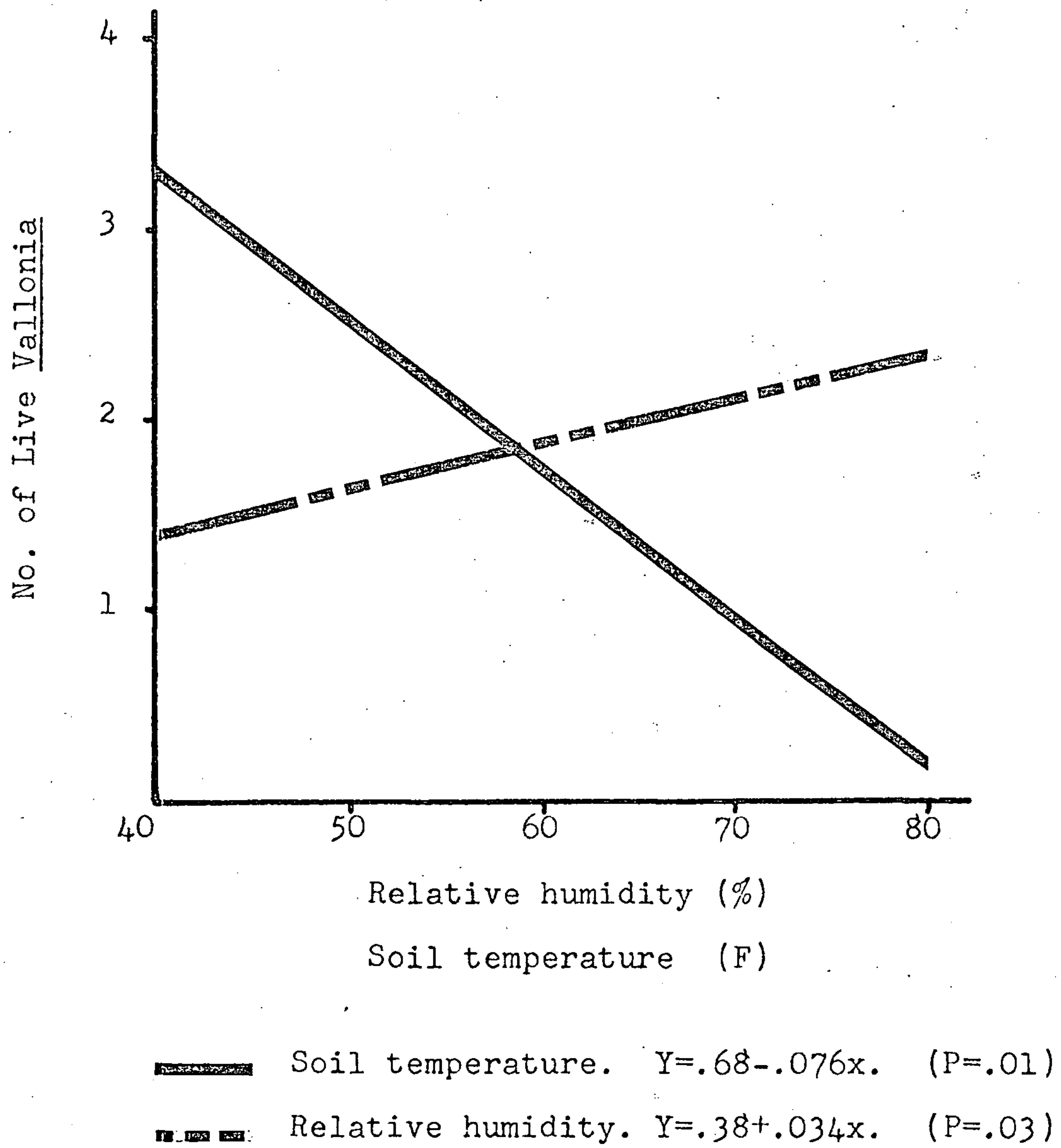

Fig. 17. The effect of temperature and humidity upon the occurrence of live Vallonia.

Table VII. Microclimate of habitats occupied by active Vallonia.

Soil temp. (°F)	Snails inactive	Snails active	Snails active / Snails inactive
< 56	2	28	14.0
56-60	10	35	3.5
66-70+	6	12	2.0
Relative Humidity %			
< 50	3	2	.7
50-60	20	19	1.0
61-70	12	12	1.0
71-80	1	10	10.0
80 +	1	1	1.0

55 F. The moisture preference, as shown by occurrence, differs from that indicated by activity because areas that maintain a constantly high humidity are probably too wet, at times, for *Vallonia*. These snails are restricted to sites where the average humidity is relatively low but they become active during occasional periods of high humidity.

The Effect of Edaphic Factors on the Distribution and Abundance of Snails

There are four basic types of soil texture on the sheep winter ranges: sandy loam, silt-clay loam, loam, and muck. Each type has a characteristic snail fauna. *Vallonia*, *Gastrocopta*, and *Pupilla* are restricted to sandy and gravelly soils which are typically found in bunchgrass communities (Table VIII). The highest populations occur on a very fine sandy loam, a type which is commonly found on the Columbia Lake and Radium-Stoddart ranges. This soil type is not as widely distributed on the Premier and Bull River ranges where *Vallonia* is correspondingly less abundant.

Fine textured silt and clay soils of the bitterbrush community support very few *Retinella* which are found mostly on silt soils at the bottoms of gullies.

The shrub and fescue commumities have a loam soil which contains an equal mixture of fine and coarse textured materials. On soil of this type, *Retinella*, *Euconulus*, and *Vitrina* are relatively widely distributed but they are not abundant.

Retinella, *Euconulus*, and *Vitrina* are most abundant on the muck soils of the aspen and certain densely vegetated forest communities. Soils are placed in this class if the inorganic component can not be determined. Any effect on snails is probably due more to the organic matter than to the inorganic particle size.

Generally, if the soil texture is suitable, snails are most abundant on soils with the most organic matter. Soils of the aspen community contain the most organic matter (Table IX)

Table VIII. Soil texture in relation to plant communities on sheep ranges.

	Per cent of soil samples in texture classes							
	aspen	forest	shrub	fescue	bitterbrush	bunchgrass (Premier)	bunchgrass (Columbia)	bunchgrass (Bull River)
Texture / Sample size	5	5	5	5	14	20	10	3
loam	-	20	100	80	14	15	-	-
very fine sandy loam	-	-	-	-	-	40	90	-
sandy loam	-	-	-	-	-	35	10	33
gravelly loam	-	-	-	-	-	10	-	67
loam-clay loam	-	-	-	20	29	-	-	-
silt loam-clay loam	-	20	-	-	43	-	-	-
silt loam	-	-	-	-	14	-	-	-
muck	100	60	-	-	-	-	-	-

Table IX. Mean pH, moisture, organic matter, and calcium in soil of the major plant communities.

Plant community	Sample size	pH	Moisture (%)	Organic Matter (%)	Calcium (ppm)
shrub	5	6.7	9.5	11.4	1600
aspen	5	7.4	34.5	21.3	3300
forest	5	6.6	11.8	14.0	1300
bitterbrush	14	6.9	4.6	4.7	1500
fescue	5	7.0	6.2	9.2	2300
bunchgrass (Premier)	20	7.2	5.0	8.9	2600
bunchgrass (Columbia)	10	7.8	6.0	10.9	3100
bunchgrass (Bull River)	3	7.7	3.4	3.6	3500

and the most snails. The shrub and forest community are similar to each other both in soil organic matter and in snail abundance. _Vallonia_ is most abundant on the ranges where the organic content of the bunchgrass community soil is highest. The Bull River bunchgrass community contains little organic matter and very few _Vallonia_.

A possible reason for the relationship between soil texture, organic matter, and snail abundance is that these edaphic factors largely determine soil moisture. Table X lists the per cent moisture remaining in representative soils from Premier Ridge after being subjected to 4.8 and 215 psi. Sandy soils hold the least amount of water at all pressure, but if organic matter is present, the soil remains relatively moist. Very fine sandy loams with much organic matter hold water well without becoming muddy because the sand particles permit excess water to drain but the organic matter retains enough moisture to prevent the soil from becoming dry. In contrast, muck, silt loams, and loams with a high organic content are wet at low pressures, while at high pressures, soils without much organic matter lose water rapidly. There are only two soils on Premier Ridge that are capable of maintaining stable moisture conditions: a highly organic, very fine sandy loam which maintains a constantly moist but not wet habitat; and muck which maintains a constantly wet habitat. It is on these soils where the xerophilic and hydrophilic snails are, respectively, most abundant.

Soil texture and organic matter also determine soil consistency. This characteristic is important for snails because a dry compacted soil offers little habitat while a loose soil

Table X. Moisture retention of soils from Premier Ridge.

Texture	Organic matter (%)	Moisture (%) 4.8 psi	Moisture (%) 215 psi
loam	5.0	42.0	12.5
loam	7.3	36.0	17.0
loam	13.2	49.5	25.5
very fine sandy loam	9.0	36.0	19.5
very fine sandy loam	11.9	35.0	26.0
sandy loam	4.9	22.8	9.1
sandy loam	5.5	34.5	16.0
gravelly loam	3.4	21.6	9.0
gravelly loam	6.2	26.8	11.7
loam-clay loam	4.0	30.0	11.4
silt loam-clay loam	4.2	25.5	10.0
silt	5.0	55.0	18.0
muck	28.1	72.3	32.2

has spaces and pores which can be utilized. The low organic clay and silt soils of the bitterbrush community become very hard while sandy and organic soils of the bunchgrass and aspen communities remain soft (Table XI).

On Premier Ridge, snails are most abundant in the two communities (aspen and bunchgrass) which have the most soil calcium (Table IX). However, the relationship does not hold for other communities. The forest has more snails than the fescue community, yet the latter community has twice as much calcium as the former. The greater abundance of Vallonia on some ranges can not be explained by the calcium content of their respective bunchgrass communities since the soil of the Bull River range has the highest calcium content but the smallest Vallonia population.

Table XI. Dry consistence of soil samples from plant communities.

Plant Community	Sample size	Per cent of samples soft	slightly hard	hard	very hard	extremely hard
shrub	5	-	-	60	40	-
aspen	5	60	40	-	-	-
forest	5	40	40	-	-	20
bitterbrush	14	-	-	8	8	84
fescue	5	-	-	40	20	20
bunchgrass (Premier)	20	25	35	35	5	-
bunchgrass (Columbia)	10	60	40	-	-	-
bunchgrass (Bull River)	3	-	-	67	33	-

Effect of Calcium on Snail Growth and Reproduction

Although the effect of soil calcium on snail distribution and abundance is not shown clearly from field data, calcium definitely affects reproduction of laboratory maintained *Vallonia* (Table XII). Snails provided with calcium carbonate laid 110 eggs while those without laid 53. This difference is highly significant (P.=.01). In contrast, there was no difference (P.=.05) in egg production between colonies provided with magnesium carbonate and that of the controls. Thus, egg production of *Vallonia* is being affected by the calcium rather than the carbonate ion.

Since only one adult snail died during the experiments, there was no difference in survival attributable to the presence of calcium but, after producing eggs, the shells of snails from the calcium colonies contained 32.5% calcium compared to only 27.5% for the controls. No statistical treatment is possible because there was no duplication. However, this suggests that snails deprived of calcium produce eggs by reabsorbing it from their shells and will eventually have to stop producing eggs or die.

Calcium also affects the growth rate of Vallonia. The relative growth rate was used since not all snails were of an equal size at the start of the experiment. The mean growth rate for snails provided with calcium was 0.024 mm/day compared to 0.017 for the controls and this difference is significant (P.=.05). Similar results were shown by Oldham (1929, 1934) who found that slugs and the snail *Helix pomatia* when provided with calcium produced shells nine times heavier than those without access to calcium.

Table XII. Effect of calcium and magnesium on egg production of <u>Vallonia</u>.

Number of eggs produced, July 5-October 2, 1967.

	With		Without	
Colony no.	$CaCO_3$	$MgCO_3$	$CaCO_3$	$MgCO_3$
1	11	12	5	7
2	31	10	12	18
3	28	17	15	15
4	23	-	6	-
5	17	-	15	-
total	110	37	53	40

Two way analysis of variance for data of table XIII.

Source of Variation	df	Sum of squares	Mean squares	F.
Calcium	4	306.6	76.7	25.7**
Colonies	1	324.9	324.9	6.1 nsd
Error	4	50.6	12.7	
Total	9	682.1		
Magnesium	2	44.3	22.2	.96 nsd
Colonies	1	.2	.2	.01 nsd
Error	2	46.3	23.2	
Total	5	90.8		

**= effect of calcium significant at 1% level.
nsd=no significant at 5% level.

Table XIII. Effect of calcium on growth rate of captive *Vallonia*.

	With $CaCO_3$ Average relative growth rate (mm[1]/day)	Without $CaCO_3$ Average relative growth rate (mm[1]/day)
	.0273	.00911
	.0179	.0236
	.0309	.0166
	.0294	.0191
	.0482	.0152
	.0235	.0183
	.0309	.0230
	.0207	.0295
	.0135	.0189
mean	.0242	.0173

1=length plus width

Analysis of variance for data of table XIII.

Source of variation	df	Sum of squares	Mean square	F.
Calcium	1	2.61	2.61	3.89*
Error	16	10.74	.67	
Total	17	13.36		

*=effect of calcium significant at 5% level.

Examination for Lungworm Larvae

Vallonia is the snail most capable of acting as an intermediate host for *P. stilesi* because it is the most common snail in the bunchgrass community which is most heavily utilized by sheep. On the Columbia Lake range, *Pupilla* is also found in this community and could be an intermediate host. *Gastrocopta* and *Euconulus* have been implicated as vectors but neither is abundant in areas utilized by sheep and,thus,are probably not involved in the life cycle of the lungworm.

However, snails do not seem to be infected. None of 417 molluscs examined (Table XIV) contained lungworm larvae and most of the *Vallonia* examined probably had access to lungworm larvae since they were taken from areas where sheep feces were abundant. Even 25 *Vallonia* experimentally exposed to hundreds of active first stage larvae failed to develop any infection. Microscopically, I have observed several larvae make contact with snails, but none penetrated or even attached to the snails. Under field conditions, the possibility of a snail being infected must be slight.

Table XIV. Molluscs examined for lungworm larvae.

Species of mollusc	Sample size
Vallonia cyclophorella	313
Pupilla muscorum	14
Euconulus fulvus	38
Retinella electrina	25
Vitrina alaskana	6
Catinella avara	2
Gastrocopta holzingeri	4
slugs	15
total	417

DISCUSSION

The Interaction of Climatic, Biotic, and Edaphic Factors in Determining the Distribution and Abundance of Snails

A snail, like all animals, must maintain the moisture content of its body within relatively narrow limits. For this purpose, the shell, operculum, and certain physiological mechanisms have evolved which protect the snail from desiccation and at the same time prescribe the tolerable ambient moisture range in which the species can survive. Through the evolutionary process, different species have developed differences in tolerances and have adapted to different ecological niches.

This is demonstrated by the snails on Premier Ridge. The hydrophilic *Vitrina* has a narrow distribution, being restricted to the uncommon very wet areas on Premier Ridge because of its preference for a high relative humidity. *Euconulus*, and especially *Retinella*, can survive drier conditions than *Vitrina*. As a result, they have a relatively wide distribution. *Vallonia*, and *Gastrocopta* seem to be restricted to relatively dry areas because they can not tolerate as much moisture. This was suggested by Whitney (1938) who noticed that *Vallonia* climb the walls of the terrarium and aestivate if conditions are too moist. I observed similar behavior in my captive *Vallonia*, while under the same conditions *Retinella* and *Euconulus* remained active. However, *Vallonia* still requires a substantial amount of moisture and is therefore restricted to areas which are never wet but remain relatively moist.

The distribution and abundance of snails on Premier Ridge can be most simply explained by the soil moisture patterns in the habitat. Soil moisture, in turn, is determined by soil texture, soil organic matter, and plant cover and is indirectly influenced by the parent material of the soil, climate, exposure, and altitude (Lutz and Chandler 1946). Thus, the distribution and abundance of snails is affected by a complex interaction of biotic, climatic, and edaphic factors and the preferences and tolerances of the different species.

Parent material, climate, and exposure influence soil moisture by affecting soil texture and plant cover. Soil texture is determined by the physical and chemical composition of the parent material and is modified by climate and gravity (Bunting 1965). Climate determines the general distribution of plant and animal life and is affected by exposure and altitude. It is important to consider these indirect factors when comparing snail distribution between widely separated areas, but within a restricted area such as Premier Ridge, the small degree of variation can be disregarded.

Soil texture influences soil moisture by governing the rate at which water drains from the soil. In light soils, water drains rapidly from the large spaces between sand particles but is held by capillary and hygroscopic pressures in clay and silt soils (Daubenmire 1959). Generally, fine textured soils hold more water but much of it is bound too tightly to the soil particles to be available to plants or animals (Osting 1956).

Soil texture also determines the consistence of the soil, which in turn affects soil moisture. Since clay particles are most cohesive when dry (Braun-Blanouet 1965), fine textured soils become compacted and dry during arid seasons. Water is slow to penetrate into the compacted soil and much of the water evaporates before soil organisms gain access to it. Also, because of slow drainage, the surface of fine textured soils becomes very wet and muddy during periods of heavy precipitation. Since the moisture content of fine textured soils fluctuates widely, they are, at times, too dry for hydrophilic snails and too wet for xerophilic snails. Thus, on Premier Ridge, the clay soils of the bitterbrush communityare unsuitable for snails. In contrast, almost all the water which falls on sandy soils penetrates immediately and the surface remains relatively dry. These soils are too dry for hydrophilic snails but suitable for xerophilic snails which seem to restricted to the bunchgrass community because it is the only community with sandy soils (Table VIII).

Besides affecting soil moisture, texture may also influence snails by modifying soil temperature. Clay soils have the greatest temperature fluctuations because they have less pore space and are poorly aerated. In contrast, coarse textured soils have uniform temperatures (Lutz and Chandler 1946) which are probably more suitable for snails.

Soil moisture is determined more by the presence of soil organic matter than by soil texture. Soils with a high organic content are always wet since organic matter may hold up to nine times its weight in water· a proportion considerably greater than that held even by clay colloids (Daubenmire 1959). These organic soils provide optimum conditions for hydrophilic snails but are too wet for xerophilic snails. However, if there is enough sand in organic soils to permit drainage, then they provide a suitable habitat for xerophilic snails.

Organic matter is important to snails for other reasons. It affects the drainage and temperature of the soil by increasing the pore space of fine textured soils and decreasing it in coarse textured soils. Since the food of Premier Ridge snails is decaying plant material (Newell 1967), the organic content of the soil might also affect the abundance of snails by influencing the food supply. This is probably more important in aspen forests since the deciduous litter is edible but less important in coniferous forests where the litter is inedible (Likarev and Rammel'meir 1962).

Plant cover affects the soil moisture level by influencing the microclimate at the soil surface. Soil moisture in a densely forested site is much greater than in exposed areas because a forest canopy reduces evaporation by moderating temperatures and wind, and by increasing humidity. Under forest cover, summer air and soil temperatures are approximately equal but in exposed areas, soil temperatures may be 50-60 F higher and evaporation may be increased up to 62% (Lutz and Chandler 1946). Thus, on Premier Ridge, even after a long dry summer (1967), there was still an average of 34.5% water in the soil of the aspen community and 11.5% in the forest community while the grass communities contained approximately 5% (Table IX).

Soil moisture probably determines snail distribution and abundance on Premier Ridge but it results from complex interactions between several factors (Fig. 18). Plant cover has the greatest effect on soil moisture because it reduces evaporation

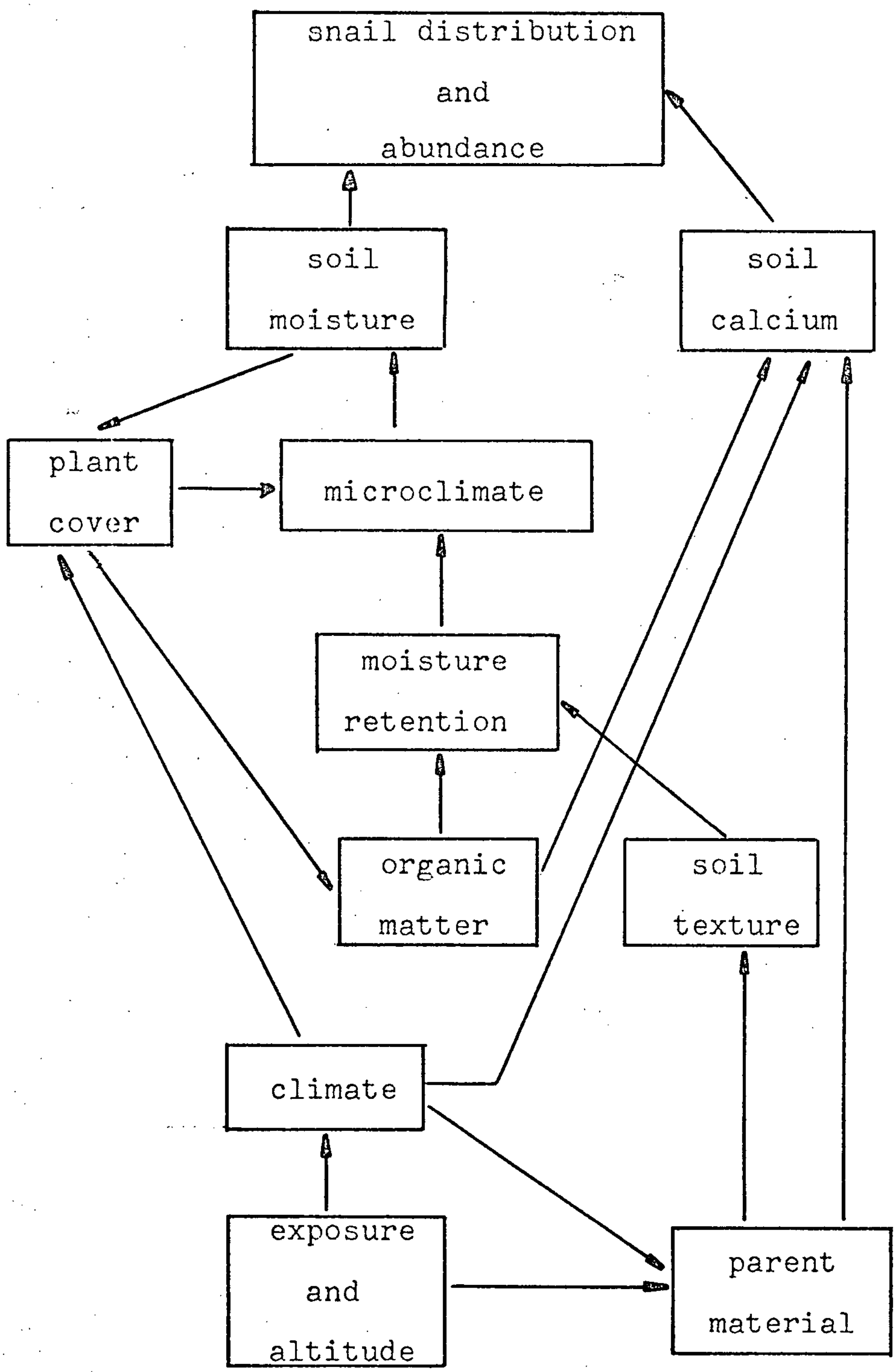

Fig. 18. Interaction of edaphic, climatic and biotic factors and its effect on the distribution and abundance of land snails.

and produces organic matter. Conversely, plant cover is determined largely by soil moisture (Braun-Blanquet 1965) which, if organic matter is neglected, is determined by soil texture. Trees require a soil of high water holding capacity to become established (Lutz and Chandler 1946), so they usually establish on fine textured soils. Trees greatly increase soil moisture by producing large quantities of organic matter and moderating the climate. This makes the site suitable for more trees and the site keeps getting wetter until it is suitable for hydrophilic snails.

In contrast, grasses establish on well-drained sandy soil because they are more efficient than trees in obtaining water (Lutz and Chandler 1946). Grasses do not add as much organic matter to the soil surface nor do they reduce evaporation to the same extent as trees. Thus, grass communities never get as wet as forest communities. Xerophilic snails apparently prefer the bunchgrass community as it occurs on well drained sandy soils which contain enough organic matter to maintain sufficient moisture.

Thus, while the distribution and abundance of snails on Premier Ridge can be explained by soil moisture patterns, the latter can be attributed primarily to soil texture. Therefore, soil texture appears to be a main limiting factor. Kunhelt (1961), summarizing land snail ecology, reached a similar conclusion.

Effect of Soil Calcium on Snail Distribution

Soil calcium is determined basically by parent material but it is modified by climate and plant cover. Thus, while soils derived from rocks such as limestone and dolomite are more calcareous than those from shales, argillites, or quartzites, climate, especially precipitation, governs the amount of calcium leeched from the top layers of soil and plant cover determines the amount returned in organic matter. For example, aspen and some other deciduous trees concentrate calcium in their leaves, thereby increasing the calcium content of the litter and the uppermost soil horizizons (Lutz and Chandler 1946).

As snail shells are composed primarily of calcium carbonate (Wilbur and Owen 1964), the amount of calcium required by a species depends on the size and thickness of the shell, which in turn is determined by the snail's habitat. Snails living in dry areas require a large, thick shell because water loss through a shell of this type is relatively small (Machin 1967). Moreover, when dry conditions dehydrate snails, the acidity of the blood resulting from water loss can be buffered with calcium mobilized from the shell (Robertson 1941). Therefore, calcium should have the greatest effect on the distribution of xerophilic snails since they should have the greatest requirements for calcium for the conservation of water. Snails living in wet areas are characterized by a small, thin shell and thus are relatively independent of calcium (Boycott 1934).

The habitat of the xerophilic Vallonia is restricted to the dry, highly calcareous soils of the bunchgrass community. It has the largest, thickest shell in proportion to its body size of the Premier Ridge snails and therefore it probably has the greatest calcium requirements. In the East Kootenay, where conditions for Vallonia appear marginal, the effect of calcium on reproductive rates may determine the success of this species since it produces more eggs and grows faster if calcium is available (Tables XII, XIII).

Yet, hydrophilic snails are also most abundant in the highly calcareous soils characteristic of aspen communities. These snails may select this community to meet their physiological requirements for calcium. However, as the level of calcium affects pH and the latter influences the rate and type of plant decay (Braun-Blanquet 1965), calcium may influence snail abundance through its effect on food supply.

Nevertheless, the abundance of snails in the two most calcareous communities of Premier Ridge does not mean that calcium is the most important factor because the calcium effect was not separated from those of other edaphic factors. Furthermore, while Burch (1955) found a strong positive correlation between snail distribution and soil calcium, the minimum amount of calcium found in any sample from Premier Ridge was greater than that in Burch's maximum sample. On Premier Ridge, calcium is probably less important for snails than soil texture or organic matter because all plant communities appear to have ample soil calcium.

However, on two of the East Kootenay sheep ranges, soil calcium may determine the distribution of snails. On the first area, the Columbia Lake range, the soils are derived from highly calcareous rocks and it is the only place where Pupilla was found.

Of the snails studied, Pupilla probably requires the most calcium since it has the largest, thickest shell, and since it is oviviparous (Pilsbry 1948) and must obtain enough calcium to produce the shells of its offspring. The only apparent difference between the xeric snail habitats on Columbia Lake and Premier Ridge, is that the former has much more calcium in its soils (Table IX). The presence of Pupilla there might, therefore, be attributed to this greater calcium supply.

The alpine area is the second place where calcium may limit snail distribution. Snails become more calcophilic with increasing altitude (Hunter and Hunter 1956), presumably due to the need for a thicker shell for protection from the harsh alpine climate. Yet, cold, wet alpine conditions create acid soils (Braun-Blanquet 1965) so that calcium may not be as available for snails. Vitrina, which has the smallest shell of any snail studied and presumably the least requirement for calcium, is the only snail abundant in alpine regions and it appears that a lack of calcium is the main factor limiting the occurrence of other species.

Thus, while some ecologists, (Lozek 1958, Boycott 1934) believe that snail distribution can always be explained by the calcium content of the substrate, it is less important than soil moisture since, in a suitable microclimate, snails should require little calcium. In accordance with Liebig's "law of the minimum" calcium should be considered to be a limiting factor only if other soil factors appear suitable.

The Role of Snails in the Life Cycle of the Sheep Lungworm

During this study the following information was obtained which supports the hypothesis that land snails act as intermediate hosts for the lungworm of bighorn sheep: Some species of snails implicated in the life cycle of this lungworm are relatively abundant in areas of East Kootenay ranges utilized heavily by sheep. These snails live in the bunchgrass community where sheep most commonly graze. Furthermore, lungworm larvae (Matekin *in* Pillmore 1958) and snails are both most active at low temperatures and high humidities. These conditions occur on sheep ranges when sheep are present during the early spring or late fall. Larvae-snail contact as well as snail-sheep contact is therefore possible.

However, evidence which refutes the hypothesis was also collected. If snails are an important intermediate host, large numbers of snails should be infected because all the sheep are heavily infected (Bandy 1968). Yet, no infected snails were found. Moreover, since snails live mainly under rocks, they are generally not available for sheep to ingest. It is possible that snails are being ingested with the grass sheep uncover when digging through snow. Sheep could turn over rocks with their feet and expose the snails. Dr. J.C. Holmes informs me that he found snails exposed where sheep were feeding in Alberta. Yet, it is difficult to understand how sheep could overturn the large rocks which cover *Vallonia*. Sheep might also ingest snails with the mud eaten in mineral "licks" but I searched six licks utilized by sheep and found no snails. This is not surprising since the lack of cover and the high proportion of clay in lick soils form an unsuitable habitat for snails. Some workers (Buechner 1960) have suggested that sheep select snails as a source of calcium but the amount of calcium provided by snail shells would be minimal and probably unnecessary since the soils themselves are calcium-rich.

It can be seen that, in the East Kootenay, the possibility of snails transmitting lungworm is slight. Even if there is a period when the snails are readily accessible to sheep, there is no area where the density of snails is great enough for them to become an effective vector. There is little chance of a snail becoming infected and little chance of a sheep contacting an infected snail.

This contradicts Pillmore (1958a:59) who stated "Our work has shown that several species of land snails belonging to the families Pupillidae and Vallonidae are essential intermediate hosts for lungworms of the genus *Protostrongylus* occurring in Colorado". His conclusions are based on two observations: (1) He found *Protostrogylus* larvae in the feet of snails inhabiting the sheep range; and (2) he infected certain snails with larvae from feces of bighorn sheep.

Actually his results are equivocal because Pillmore (1958) states that the three other species of *Protostrongylus* on the sheep range reported to use land snails as intermediate hosts can not be separated in the larval stage from *P. stilesi*. He considers that most of the larvae found in snails were sheep lungworm but he presents no substantiating evidence.

Pillmore once found 428 of 1300 *Vallonia* infected but this appears to be atypical, since Forrester (pers. comm.) found infections in only one of 300 Vallonia and in four of "several hundred" Euconulus. Furthermore, in the present study, no infections were found during the examination of 313 Vallonia. Even the results obtained from artifically infecting snails can be construed as negative evidence. Pillmore (1958) was successful in infecting only 5.8% of 4,056 Vallonia and Forrester (pers. comm.) could infect only 6.5% after many trials. If only 6.5% of Vallonia can be infected under conditions of high concentrations of snails and larvae, the proportion infected in the field must be much less.

The method of transmission which has been hypothesized for P. stilesi is not efficient. Yet, since most of the sheep in the East Kootenay (Bandy 1968) and most of the sheep in the world (Buechner 1960) are infected, a more efficient system of transmission must be operating. In the same family (Metastrongylidae) of nematodes to which P. stilesi belongs, some species have an intermediate host, some have a direct life cycle, and are transmitted prenatally (Jones 1967).

With sheep lungworm there is evidence to support all three types of transfer. Evidence for an intermediate host is based mainly on Pillmore's work which was discussed above. In addition, Pillmore (1958a) and Forrester (1962) have found some snails which the larvae of P. stilesi appear to have left. If so, this would indicate evolution towards a direct life cycle. There is also evidence of prenatal transmission of sheep lungworm (Pillmore 1959, Forrester and Senger (1964). Usually in this type of transfer, the larvae must pass out of the animal, molt, and be ingested by the pregnant female before it can pass to the foetus but Forrester and Senger (1964) found first stage larvae in the lungs of three lambs.

Since a parasite with a two host life cycle is considered primitive (Otto 1966), *P. stilesi* could be at a point where it is evolving towards a direct life cycle but still retaining its intermediate host. It could thus, utilize all three methods of transfer. Such a system would be most advantageous in different situations. A direct life cycle would allow rapid transfer during periods of high sheep density and favourable weather and would not be restricted to areas where a suitable intermediate host was present. Larvae using snails as an intermediate host would insure the survival of the parasite during periods when conditions were not suitable for direct transfer since larvae remain viable in snails for long periods (Geritcher 1948). Prenatal transfer would insure a wide distribution of lungworm but only a few parasites could be passed to the foetus because a heavy parasite load might kill the lamb before it gained strength and the host species thus could be exterminated.

SUMMARY

(1). *Retinella electrina*, *Euconulus fulvus*, and *Vitrina alaskana* are present on all East Kootenay sheep ranges. *Vallonia cyclophorella* and *Gastrocopta holzingeri* are restricted to winter ranges and *Pupilla muscorum* occurs on the Columbia Lake range only.

(2). *Vallonia* is most abundant on the Columbia Lake and Radium-Stoddart ranges while *Vitrina* is most numerous on alpine ranges.

(3). On winter ranges, *Retinella*, *Euconulus*, and *Vitrina* are most abundant under leaf litter in aspen communities but also occur under rocks or logs in all except very dry plant communities. *Euconulus* is the most abundant but *Retinella* is most widely distributed.

(4). *Vallonia*, *Gastrocopta*, and *Pupilla* live exclusively under rocks on rock ledges and steep rocky slopes within bunch-grass communities. *Vallonia* is the most numerous snail in this community except on the Columbia Lake range where *Pupilla* is equally abundant.

(5). *Vallonia* is most abundant under large rocks.

(6). *Vitrina* is an obligatory hydrophil, *Euconulus* and *Retinella* are facultative hydrophils, and *Vallonia*, *Pupilla*, and *Gastrocopta* are relatively xerophilic.

(7). *Vallonia* is most active at low temperatures and high humidities.

(8). *Vallonia* populations appear to decline in dry seasons but increase with autumn precipitation.

(9). Xerophilic snails are restricted to sandy soils, being most abundant on a sandy soil with a high organic content probably because it maintains a moist but not wet moisture regime.

(10). As a result of being constantly wet, muck soils have the largest populations of hydrophilic snails.

(11). Clay and silt soils of the bitterbrush community have wide temperature and humidity fluctuations and appear unsuitable for any snails.

(12). The effect of interaction of climatic, biotic, and edaphic factors on the distribution and abundance of snails is discussed. It is concluded that, because it ultimately determines soil moisture, soil texture is the main limiting factor for snails.

(13). *Vallonia* produce more eggs and grow faster of provided with calcium but there is probably enough soil calcium in all Premier Ridge plant communities to meet the requirements of most snails.

(14). *Pupilla* may occur only on the Columbia Lake range because of the greater amount of calcium there, while the lack of calcium on alpine ranges may restrict the snail fauna to non-calcophilic species such as *Vitrina*.

(15). The distribution and abundance of *Vallonia* and *Pupilla* make them the most suitable host for sheep lungworm but no snails were found infected and the habitats of sheep and snails do not overlap.

(16). Since snails do not appear to be vectors of sheep lungworm on East Kootenay ranges, the possibility of direct or pre-natal transfer is suggested.

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