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THE SNOWSHOE RABBIT ENQUIRY 1937-38

By DENNIS CHITTY and CHARLES ELTON

1. General Introduction.

IN THIS and the previous six annual reports (*The Canadian Field-Naturalist*, 47: 63-69, 84-86, 1933; 48: 73-76, 1934; 49: 79-85, 1935; 50: 71-81, 1936; 51: 63-73, 1937; and 52: 63-72, 1938) the progress of the ten-year cycle in abundance of snowshoe rabbits in Canada has been followed by means of a questionnaire enquiry and by statistical treatment of opinions on the relative change in one year compared with the one before. From conditions approaching a peak in 1931-32 it has been shown how, after this peak was reached, there set in a period of widespread, though not simultaneous decline, accompanied by epidemics. During 1936-37 some regional recovery had begun, which, despite great scarcity during 1937-38, was maintained and had started to appear in other sections of the country.

The results of this enquiry, consisting of the replies to questionnaires about comparative abundance from year to year, are mapped in the Bureau of Animal Population, Oxford University, where the detailed maps and records are available for reference. Duplicate copies of the replies to the Canadian Government enquiry, of the areas plotted on tracing paper over provincial maps, and of the final maps compiled from these tracings, are also being deposited in the National Parks Bureau, Ottawa. The enquiry now covers a large sample of the total range of *Lepus americanus* in North America.

2. Canada, (D.C.) Acknowledgements

The material consisted of 585 reports covering well over a half, but less than one million square miles of country.

1. 415 reports were received from observers through the National Parks Bureau, Department of Mines and Resources, Ottawa. We are much indebted to the Controller, Mr F.H.H. Williamson, and the Superintendent of Wildlife, Mr. Hoyes Lloyd, for their continued co-operation, and to the staff of the Bureau (in particular Mr. W. D. Taylor) for their work in collecting all these replies. We also wish to thank those who continue year after year to submit their observations. The following people contributed information: Royal Canadian Mounted Police (133 observers), Officers of the Provincial Game Departments (142), Superintendents and Wardens of the National Parks (75), other observers (65), including Taxidermists, Honorary Game Officers and Holders of Scientific Permits under the Migratory Birds Convention Act.

2. 149 of the annual zoological reports of the Hudson's Bay Company referred to snowshoe rabbits. These reports were supplied by courtesy of Mr. Ralph Parsons, the Company's Fur Trade Commissioner in Winnipeg, and are published by permission of the Governor and Committee in London. Mr. R. H. G. Bonnycastle has given much valuable help organizing the enquiry in Winnipeg.

3. 21 reports from the Maritime Provinces were kindly obtained by Dr. A. G. Huntsman from officials of the Biological Board of Canada.

Duplicates of the tracings are kindly being made by Mrs. Jane Baden-Powell.

Methods

The system adopted in these reports is to weight the replies from observers on a basis of the area to which the replies (increase, decrease or no change) are referred. It is not practicable to measure the true area covered and instead a count is made of the number of 30 mile squares in which lie all or part of the regions covered. This introduces certain errors: (1) when two entirely separate regions fall in different parts of the same square they are counted as overlapping one another and (2) the areas are exaggerated for example, Nova Scotia, area 21,428 sq. miles, overlaps 44 squares, area 39,600 sq. miles. The assumption is, however, that such errors occur at random among reports of each

TABLE 1

State of the Snowshoe Rabbit population in Canada, 1937-38
(number of squares.)

	Total	Increase	% Increase	Decrease	% Decrease	No Change	% No Change	Epidemic	% Epidemic
Yukon	64	2	2- 3	63	80-98	11	0-17	0	0
Northwest Territories.	174	16	5- 9	123	52-71	76	21-44	4	2
British Columbia..	269	130	26-48	139	27-52	109	13-41	0	0
Alberta	199	125	35-63	67	10-34	101	13-51	0	0
Saskatchewan	182	137	33-75	75	9-41	85	12-47	2	1
Manitoba ...	202	71	12-35	115	20-57	115	28-57	0	0
Ontario.....	352	155	26-44	170	28-48	134	20-38	6	2
Quebec &.... Labrador	339	114	23-34	204	50-60	65	14-19	0	0
New Brunswick.	38	13	3-34	34	34-89	17	5-45	1	3
Nova Scotia .	44	42	41-95	2	0- 5	26	5-59	0	0
Total	1863	805	23-43	992	31-53	739	16-40	13	0.7

kind. Two theoretical advantages are (1) compensation for unequal distribution of observers, (2) a certain indication of the extent to which observers agree in their opinions. The first is obtained through giving equal areas the same significance whether they are covered by few or many observers, the second by expressing percentages between limits: e.g. "23—43% increase". This means that the squares overlapped by reports of increase were 43% of the whole but that only 23% were overlapped by increase uncontradicted by another type of reply. The method does not, however, state how much of the 23% was corroborated by two or more observers, nor to what extent the overlap between observers was real or only apparent.

RESULTS

The features of 1937-38 are shown in Figs. 1 and 2 and Table 1 and may be described under the following main headings;

1. *Scarcity of rabbits.* In most places numbers were so low that observers had difficulty deciding what change if any there had been compared with the previous twelve months (ending May 31st). In the figures this is reflected by a high percentage of no change reports (16-40%) and in a considerable overlap of two or three types of opinion. When changes in abundance are so slight it is questionable whether a report of no change can be considered as seriously conflicting with a report either of increase or decrease. Thus in Alberta and Nova Scotia the wide limits expressing increase are chiefly due to overlap with no change. The 35-63% increase in Alberta is made up of 125 squares, 37 overlapping with reports of no change, 10 with decrease, 9 with both. The percentage of increase uncontradicted by decrease is thus 53, compared with 35% when both no change and decrease are counted as being contradictory to increase. In Nova Scotia the revised figure is 91-95% instead of 41-95%. However, in Saskatchewan the correction amounts only to 47-75% compared with a previous 33-75%. Here, as in all the provinces further east except Nova Scotia, there is more overlap with decrease than with no change. This extensive disagreement therefore reflects a state of the rabbit population which presents real difficulties for analysis from subjective data.

2. *Continued decrease in Alberta and Saskatchewan.* During 1936-37 a certain amount of recovery took place in these provinces, particularly in Northern Alberta. The percentage of

squares reporting increase in the prairie provinces has been as follows:

	bottom of cycle		*recovery phase*	
	1934–35	1935–36	1936–37	1937–38
Alberta.....	17–34	15–35	18–56	35–63
Saskatchewan	3–30	6–30	12–44	33–75
Manitoba....	14–32	3–12	16–32	12–35

The figures for 1937-38 indicate that recovery has gone ahead for a second year in Alberta and Saskatchewan, but remained sluggish in Manitoba.

3. *Start of recovery in Ontario and the Quebec peninsula.* The map showing increase for 1936-37 was almost a complete blank for Northern Ontario and the whole Quebec peninsula. During 1937-38 patches of increase appeared, and although decrease reports were still in the majority for the third consecutive year it seems that some recovery may have begun.

4. *No recovery yet in Yukon, Northwest Territories or Northern British Columbia.* In 1934-35, while the provinces east of British Columbia were reporting high percentages of decrease there continued to be reports of increase from the North-west. In the two following years a steep decline set in, though snowshoe rabbit numbers still remained high in local sections of the Yukon as late as 1936-37. As might be expected from the later appearance of the "crash", recovery in these parts had not yet become obvious. In the Yukon and Northwest Territories reports of increase were practically negligible. In British Columbia the figure for increase (26-48%) requires further analysis.

As has been said in a previous report, the grouping of the figures by provinces is not a natural arrangement, but is the only procedure that can be carried out in the relatively short time between receiving the reports and sending the manuscript to press. In British Columbia there are areas, yet to be defined, in which fluctuations, where they occur at all, are not synchronous. It was not until one or two years afterwards that the decrease reported in 1934-35, south of a line from the tip of the Alaskan pan-handle to the Peace River, spread to any great extent north to the boundary. It was this same region, excepting an area of 18 squares north of the Peace River, from which signs of recovery were absent during 1937-38. The other 112 of the 130 increase squares referred to conditions in the central and south parts of the province—where increase also took place in 1936-37.

5. *Increase in Nova Scotia.* There seems to have been a marked recovery in this province, the only decrease reported being from near the border of New Brunswick. Elsewhere, particularly on Cape Breton Island, the bulk of the replies indicate a definite increase in numbers. In New Brunswick some slight recovery apparent in 1936-37 did not become more general. Many of the replies suggest that excessive killing for fox farms and for human consumption may be interfering with increase.

6. *Lack of epidemics.* During 1936-37 a few patches of epidemic were still reported, particularly in Quebec. In 1937-38 such reports were so few that it has not been worth while publishing a special map. There was a report from Fond du Lac, Saskatchewan, and north of it; one from Gogama, Ontario, one from New Brunswick.

3. UNITED STATES AND ALASKA (C.E.)

UNITED STATES

Through the cooperation of observers reporting through the U. S. Bureau of Biological Survey in Washington, D C. it has been possible to map for a fourth year something of the fluctuations of *Lepus americanus* outside Canada. The recurrent regularity of the ten-year cycle over much of Canada for at least 120 years (proved by examination of the Hudson's Bay Company's records), and the wide regional extent of the cycle, make it of great interest to know how far the cycle is maintained towards the edge of the snowshoe rabbit's range in the north-eastern United States and in Alaska. Also, although only a relatively small part of the range of *Lepus americanus* falls within the United States, the actual area is a huge one in which this species plays a considerable part in wild life inter-relations. The absence of any full historical records of fluctuations in the United States makes it all the more desirable that current cycles should be recorded over a large area by a standard method.

We wish to thank the Chief of the Biological Survey, Dr. Ira N. Gabrielson; and the Chief of the Division of Wildlife Research, Dr. W. B. Bell, for giving facilities; and Dr. H. H. T. Jackson of that Division, for organizing the questionnaires. Although the number of replies is not very large, Dr. Jackson has been successful in obtaining information of a high degree of reliability, by choosing observers with the right kind of opportunities and field experience. A particularly full report was supplied by the Wisconsin State Conservation Department.

The total number of replies was 55, of which 39 were mapped on the grid system, the rest mostly containing very useful records not in a form suitable for exact mapping *e.g.* the area

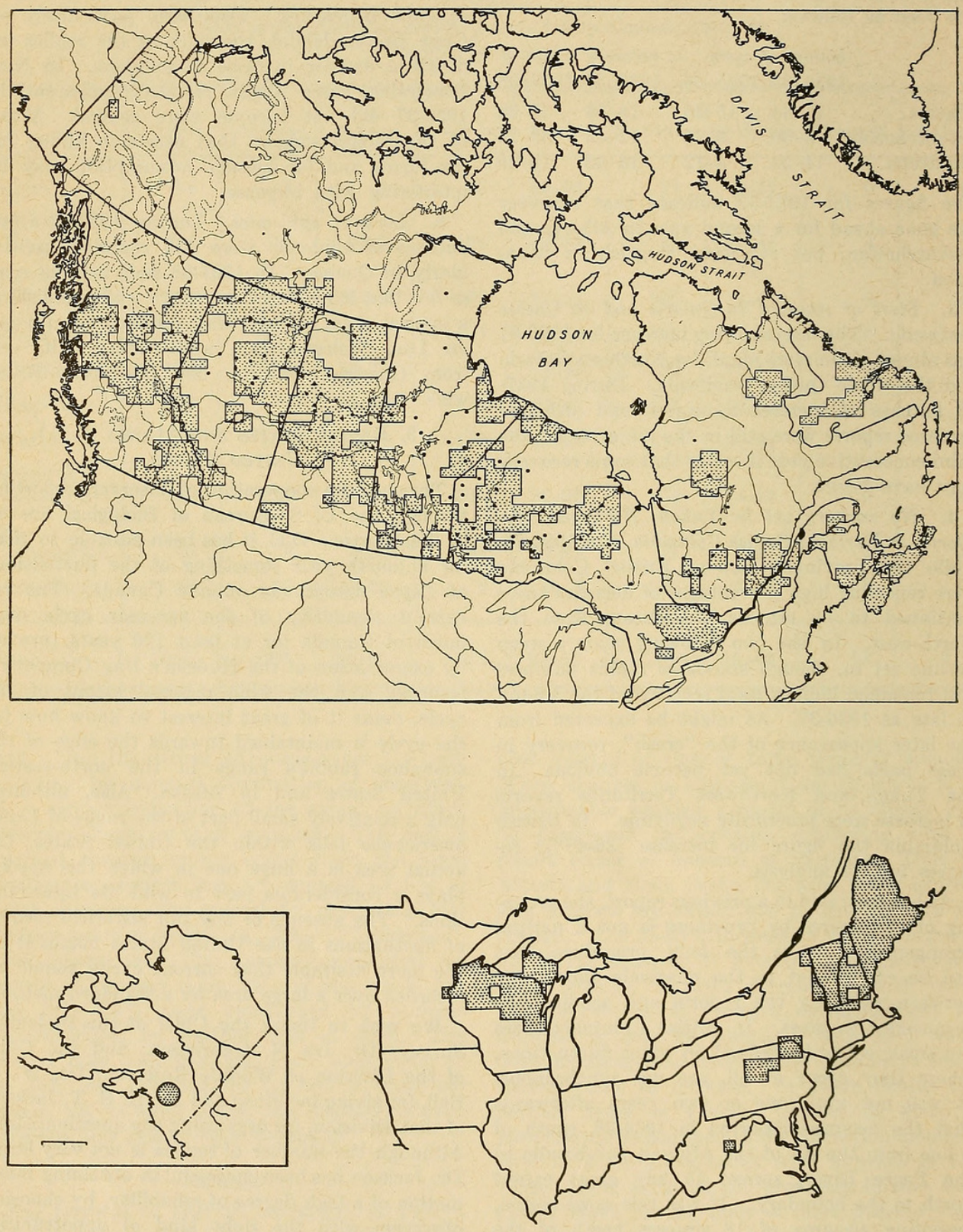
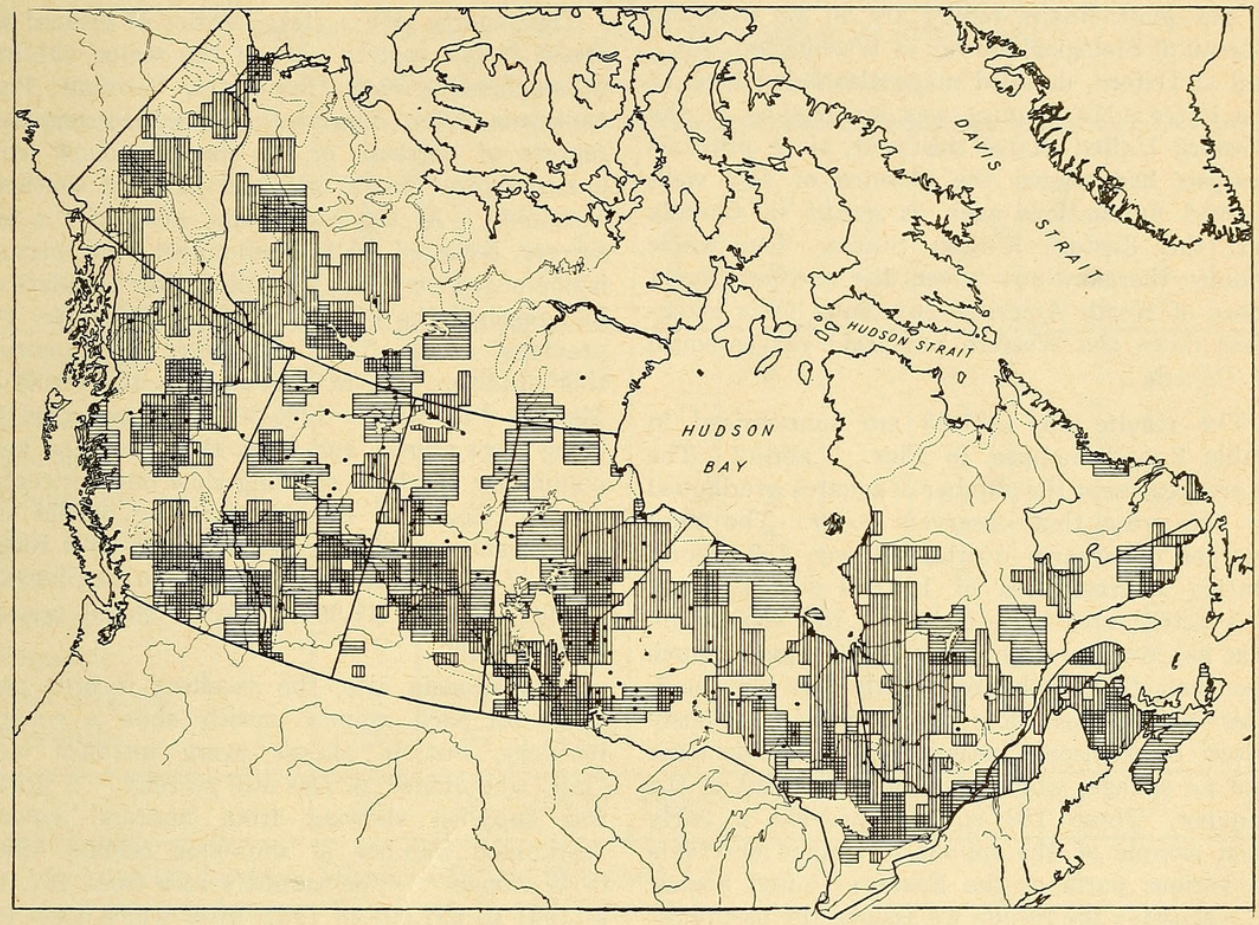


Fig. 1. State of the snowshoe rabbit population in 1937-38. Dotted areas are groups of squares overlapped by areas of observers reporting relative INCREASE in 1937-38 over 1936-37. Larger black dots are Hudson's Bay Company posts. Broken lines in Canada show main vegetation zones. Thick black lines are Province or State boundaries.



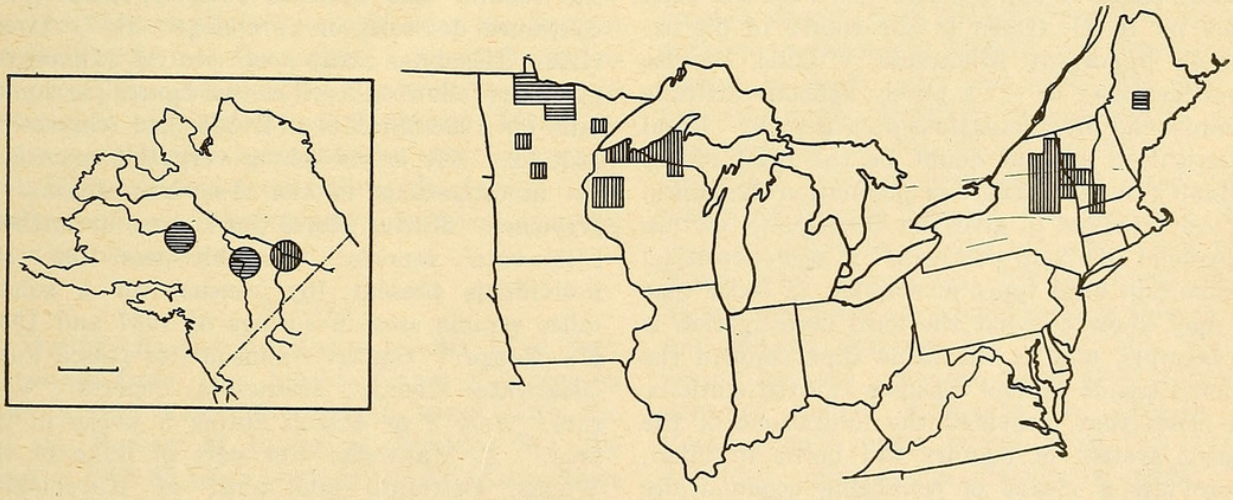


Fig. 2. State of the snowshoe rabbit population in 1937-38. Vertical hatched areas, are groups of squares overlapped by areas of observers reporting relative DECREASE in 1937-38 over 1936-37. Horizontally hatched areas, NO CNANGE.

too large or else not defined accurately. Copies of the questionnaire replies are on file with the Bureau of Biological Survey at Washington, D.C., and at Oxford, detailed maps also being kept at the latter. No enquiry was undertaken in the Western United States this year, since previous analysis had shown the absence of any well-marked fluctuations such as occurs in Canada and the Eastern United States. The whole enquiry therefore now covers the northern forest zones of North America, but omits their extensions down the Western mountain ranges south of Canada.

The results for 1937-38 are summarized in Table 2 and mapped in Figs. 1 and 2. The figures represent the number of squares overlapped by the areas that observers cover. The total number of squares overlapped was 152, representing a gross area of 136,800 square miles. The actual area was, owing to the convention that *any* overlap counts as a whole square, much less than this, probably a little less than half. This exaggeration does not, however, seriously affect comparisons between increase, decrease and no change, which are the main point of the enquiry. These 152 squares provide a fairly good sample of the opinion of trained observers in various parts of the Eastern United States In discussing the results we assume the usefulness of the sampling and of the opinions. We may note that the only alternatives at present to the use of this intelligence system of sample subjective comparative opinions are (1) small local samples based on real censuses (such as have been taken by R. G. Green in the course of his extremely important Minnesota Wildlife Disease Investigations), or (2) a purely agnostic attitude towards wild life fluctuations on this scale. Local investigation will no doubt be the chief means of finding out the nature of population dynamics, but nevertheless it gives an inadequate picture of regional trends in numbers. It seems essential to maintain both types of enquiry, in order that we may know of what the local investigation is an example, and at the same time confirm the regional trends by real censuses at fixed stations. We claim that, provided the limitations of the present system of enquiry are borne in mind, it provides a means of canalizing economically and quickly and with the minimum of distortion by the coordinator, the opinions of experienced field observers over a very wide area. The more numerous the samples the better, provided the observations are still of a high quality. In this respect the United States enquiry is still capable of useful expansion in the direction of some of the Canadian results which now show in some zones a chain-mail pattern of observed areas.

The reports give a clear verdict of general increase in the eastern part of the region (Maine, Massachusetts, New Hampshire, Vermont, Pennsylvania, West Virginia). There are very few reports of decrease or no change except from north-eastern New York, and parts of southern Vermont. At the same time, none of the observers recorded high abundance: the picture is one of recovery just beginning after populations had reached the bottom of their cycle after the previous crash. Two examples will illustrate this situation. C. M. Aldous (for the whole of Maine): "In winter 1935-36, hares reported as being very scarce, and since that time the hare population has been showing slow but noticeable gains." Logan J. Bennet cites the official kill of snowshoe rabbits in Pennsylvania as a rough index of abundance from 1930-37: 20,602; 26,245; 19,890; 23,139; 17,995; 8,659; (closed season 1936); 2,420.

In Wisconsin also, the excellent records provided for each county mostly show a general recovery, but in almost every instance only "fair" abundance, or else still scarcity. A graph was supplied showing from hunters' reports "estimated number of snowshoe rabbits killed in Wisconsin". The numbers rose from 437,183 in 1931 to 631,007 in 1932, after which they fell steadily to 60,081 in 1937. Although these figures may provide only a rough measure of abundance, they illustrate the scarcity still existing in the winter of 1937-38. In Minnesota the reports also indicate scarcity, with either continued decrease, or no change. R. G. Green (Lake Alexander area, north-central Minnesota) gives the following April census figures per square mile for 1933-38; 478, 374, 356, 246 (corrected), 151, 32. (He is publishing very full reports of his investigations in the *American Journal of Hygiene*). Marius Morse (for an area in northern Minnesota) reports: "Probably less than 100 individuals present (by census) on 4 square miles sample area in springs of 1937 and 1938. No change." Gustav Swanson (for Itasca Park, Clearwater County, Minnesota) reports: "Very rare. Only 3 or 4 seen during 5 weeks in the area." J. Manweiler (for part of Lake of the Woods, Beltrami, and most of Koochiching counties, northern borders of Minnesota), on the basis of extensive trapping and tagging and other field work, states: "Generally we found that the cycle of the snowshoe hare was delayed from one to two years over that in Wisconsin... Since the winter of 1936-37 the snowshoe hare has been extremely scarce throughout our region and at the present writing does not seem to have

TABLE 2.

Records of Snowshoe Rabbit population trends in the Eastern half of the United States, 1937-38.
(number of squares overlapped by observers' areas.)

	No. of observers	Total no. of squares	Increase	% Increase	Decrease	% Decrease	No change	% No change	Epidemic	% Epidemic
Maine	4	49	48-49		0		0-1		0	
Massachusetts	1	1	1		0		0		0	
Michigan	2	14	7		6-7*		0		0	
Minnesota	4	13	0		2		11		0	
New Hampshire	1	4	4		0		0		0	
New York	1	10	0		9-10†		0		0	
Pennsylvania	1	9	9		0		0		0	
Vermont	3	17	11-17†		0-4		0		0	
West Virginia	1	1	1		0		0		0	
Wisconsin	21	34	24-33*		0-8		0		0	
	39	152	105-121	69-80	17-31	11-20	11-12	7-8	0	0

* 1 overlap between Michigan D. and Wisconsin I.
† 3 overlaps between New York D. and Vermont I.

increased any whatsoever." This area lies very near the western limit of the species in Minnesota.

To sum up: the snowshoe rabbit populations in the Eastern States are still near the bottom of their cycle. In the eastern parts of the region recovery was definitely under way, as also in Wisconsin and parts of Northern Michigan. Minnesota lagged behind these other areas. If the United States cycle follows the typical Canadian one, we may expect continued increase now for several years.

ALASKA

During the last five years reports have been received from the Alaska Game Commission and a few other observers in touch with the U. S. Bureau of Biological Survey. For the season 1937-38 there are four reports from officers of the Alaska Game Commission, received through the cooperation of Mr. Frank Dufresne, Executive Officer of the Commission at Juneau; one from Mr. J. W. Warwick of the U. S. Biological Survey at Fairbanks; and one from Mr. Harry J. Liek, Mount McKinley National Park, through courtesy of the U. S. National Park Service. The only district for which a continuous sequence of records for five years has been obtained is Fairbanks (Tanana River) and surrounding country. Here snowshoe rabbits increased steadily until 1935-36, remained abundant without decreasing in 1936-37, but began to show disease in April, May and June 1937 and were less abundant (Warwick) or no change (Game Commission) in the season of 1936-37. This cycle has evidently followed the same general course as that in Canada, but the peak (1936) was two years later than the main peak in the North-West Territories (1934). Parts of the Yukon remained at a high level as late as 1936 but showed decrease by 1937. Mr. Warwick notes that the previous crash after abundance occurred round Fairbanks in 1924-25 The Commission's report which gives "no change" for fifty miles round Fairbanks, adds: "Still plentiful, but thinned out in adjacent regions to north and west."

North of this, in the country round Fort Yukon on the Upper Yukon River, there was fair abundance in 1936 (following increase in 1933-34, 1934-35,—no record for 1935-36), but decrease in 1937-38. These records indicate that the rabbit decrease had finally begun to take place

by 1937, in the Canadian Yukon and in the Upper Yukon and Tanana regions of Alaska. To the south, in the country around Copper Center in south-central Alaska, increase and abundance still continued ("expected to reach top of cycle this winter of 1938-39"). To the west, in the region around McGrath, on the Upper Kuskokwim River, there was no change ("no apparent increase from low point in cycle," the last recorded peak being in 1926-27). This record indicates a complete failure to recover during the last cycle period. This area is near the limit of range and of suitable habitat (for the country here is "willow bush and stunted spruce"). Mount McKinley National Park reported increase, the previous cycle peak having been 1925, with great scarcity in 1928. Some good notes on *Lepus americanus macfarlani* in this Park have been published by J. S. Dixon (*Fauna of the National Parks of the United States* Fauna Series No. 3, pp. 194-6, 1938). Another paper, by C. B. Philip (*J. Mammalogy*, 20: 80-86 1939) contains valuable parasitological records from the snowshoe rabbit in Alaska (including the demonstration of tick-borne tularemia in snowshoe rabbits in the Fairbanks area). His notes on reproduction and abundance are also valuable, and we agree with his comment that the Alaskan cycle presents local irregularities, and that the forecast by one of us (C. E.) in 1936, failed to anticipate the delay of a year or two in the onset of decrease in the Alaskan populations. For the present, it is clearly most profitable to continue collections of records for a good many years, in order to find out how far and why Alaska differs in its snowshoe rabbit periodicity from the main part of Canada.

4. SUMMARY

585 reports for the season 1937-38 were received from Canada. This year was the second of a patchy recovery in snowshoe rabbit numbers in northern Alberta, Saskatchewan and central British Columbia. In Manitoba, Ontario and the Quebec peninsula recovery was much less far advanced, and in the North-west there was none. These stages of recovery correspond to the sequence during 1933-37 in which the decline set in. Increase was definitely under way in Nova Scotia, but not in New Brunswick. The great scarcity of rabbits, which still prevails generally in Canada, has led to much more confusion in the estimates of relative abundance than has been the case in past years.

55 reports were received from the United States. They indicate that the bottom of the cycle had been reached and that recovery had begun over wide areas in the Eastern States. But showshoe rabbits were still scarce generally. Six reports from Alaska indicate that decline had set in in some places, but abundance still continued in others.

SOME NEO-TRIASSIC AMMONOID FAUNAS OF THE PEACE RIVER FOOTHILLS, B.C.

By F. H. McLEARN

IT IS NOW possible to distinguish the Karnian and Norian parts of what, in previous publications, has been called the *Halobia* zone of the Schooler Creek formation. Some of the identifications of species and genera are only provisional, but the faunal lists give a fair idea of the succession.

The earliest fauna of the *Halobia* zone, probably of late Karnian age, includes *Stikinoceras kerri*, *S. robustum*, *Sirenites*, n. sp., *Styrites* cf. *haugi* Gemmellaro, *Placites*, *Juvavites*, *D.* (*Anatomites*) *humi*, *Gonionotites?*, *Malayites*, *Miltites?* and *Dimorphites*. A little higher is a late Karnian or Tropitan fauna with *Sirenites* n. sp., *Tropites*, *Juvavites*, *Juvavites?* cf. *carlottensis* (Whiteaves), *J.* (*Anatomites*) and *Gonionotites*. Much higher is a fauna which also appears to be of late Karnian age. It includes *Sirenites* n. sp., '*Palicites*', *Styrites* cf. *haugi* Gemmellaro, *Styrites* n. sp., *Juvavites mackenzii*, *J. mertoni*, *J. bococki*, J. (n. subg.?) n. sp., *J.* cf. *kellyi* Smith, *Gonionotites*? and *Griesbachites*. It is not possible to recognize the three foregoing faunas in all sections.

Yet higher is a fauna of Norian age with *Cyrtopleurites* cf. *bicrenatus* Hauer, *Cyrtopleurites* n. sp., *Pterotoceras* n. sp., *Drepanites*, *Placites*, and a species of *J.* (*Anatomites*) with ribbing like that of the *continui* group of *Juvavites*. Yet higher is a Norian fauna with *Sirenites* cf. *elegantiformis* Diener, *S.* n. sp., *Distichites* of both *megacanthi* and *compressi* groups, *Himavatites* cf. *watsoni* Diener, *H.* n. sp., *Helicitites* cf. *geniculatus* Hauer, *Hel*, n. sp., '*Heraclites*' cf. *ariciae* Mojsisovics, *Placites*, *Pinacoceras* of the group of *P. parma*?, *Phormedites*, *Parajuvavites*, *Isculites* cf. *decrescens* Hauer and *I.* cf. *smithi*,