SUMMARY

Preface

As late as during the nineteenth century, the big predators were extremely disturbing to the rural people in great parts of Sweden. In the last part of this century and the first part of the twentieth century, the stocks decreased considerably and were close to extinction. About 1930 certain protective measures concerning the bear and the lynx made the stocks of these animals increase again. The wolf and the wolverine, on the other hand, have so far been completely unprotected and subjected to severe persecution. At the present time, there are some ten or twenty wolves, some hundred wolverines, three to fourhundred bears, a few more lynxes in this country. Fairly comprehensive complaints about damage caused by predators have lately been put forward by owners of domestic animals, in the first place by Lapps on account of losses in their herds of tame reindeer.

There have always been extremely great differences in opinion about the extent of the damage made by beasts of prey among reindeer as well as among big game. As a rule the damage is greatest during the winter. The aim of this study was to contribute to increasing the knowledge of the biology of these animals. Moreover the study was intended to form a basis for judging the above-mentioned problems.

The investigation was made possible by generous, economical support from different funds. Moreover personnel was placed at the author's disposal by the administrations of state and private forests. This help has made this interesting task so much easier for the grateful author.

Stockholm March 1966. *Bertil Haglund*

Winter Habits of the Lynx (*Lynx lynx* L.) and Wolverine (*Gulo gulo* L.) as Revealed by Tracking in the Snow

I. Method

The principal material for studying the winter habits of the four big predators in Sweden was collected between 1960 to 1964 by means

of tracking. The animals were tracked, as a rule, on skis by patrols consisting of two men.

Widely diverging opinions are met with in Sweden about the damage that these predators cause to the fauna and particularly to the herds of domestic reindeer. In order to obtain a basis for a policy concerning these predators, it was necessary to collect a comprehensive material. The method of tracking animals in the snow seemed to be the most effective method. Naturally, the fact that such a study can be performed only during the cold part of the year restricts the material. Periods of particular interest—such as the propagation period and the growth of the young—can be only slightly represented in such material.

Under the supervision of the present author, the field work was done by people carefully chosen among game wardens from the national parks and crown forests, from wood-industrial companies, among professional hunters, Lapps and other representatives of the local population. All the trackers were experienced hunters knowing how to perform their task. As a rule, the patrols consisted of one representative of the local population and one person in a more official position.

The task of the patrols was to search for tracks of any of the above-mentioned four predators and follow such a track as far as possible without frightening the animal. If the track was considered very recent, the patrol had to follow along the trace backwards for one day or more before it could proceed in the direction of the animal.

Observations were noted daily by answering questions according to the form seen on page 284. In order to obtain as uniform estimation as possible, each man was provided with identical instructions for filling out the forms. The animal to be tracked was chosen mainly at random when the men moved into a district where predators used to appear. They would follow the first track that they ran into. The work was not concentrated, e.g., to districts where exceptionally heavy predation in reindeer herds had taken place.

Technical Difficulties in Tracking

The difficulties which the patrolmen had were mainly due to the climate and the roughness of the roadless wilderness. Very often there were no possibilities of spending the night in houses. In many cases the trackings could not be completed on account of the fact that it was impossible to endure the field work for more than a restricted period of time.

The reasons for the most serious difficulties were the following:

1. Obliteration of the tracks on account of snowstorms or heavy snowing. Even slight wind could destroy the tracks in open areas on the mountain slopes or on bogs where the snow would be loose.

2. Cold weather following thaw which forms a crust so strong that tracking is made impossible or at least very difficult.

3. Towards the end of the cold season the snow will have melted over wide areas, e.g., on slopes towards the south and on surfaces having had only a very thin layer of snow. Especially the tracking of bears in the spring is often delayed or made impossible under such circumstances.

4. Herds of reindeer (*Rangifer tarandus* L.)—tame or semi-tame—and wintering groups of moose (*Alces alces* L.) may by tramping, at least locally, destroy the possibilities of tracking out interesting occurrences.

If interruptions due to any of the above-summarized difficulties were met with and it proved impossible to regain the track, so that no details were lost, the tracking was started over again and observations registered on a new form.

Measurement of Tracks

Whenever sufficiently accurate measurements of a track could be taken, this was done. Very often the snow was too loose or wet to allow any measurement. An old track might have thawed away or the wind might have altered it. Moreover, the track would be too indistinct in loose snow to measure. The measurements made were, however, of considerable value and provided information about the size of the animal. In some cases it was possible to distinguish between different individuals. The best measurements were those of the bear tracks. After the first winter, it was discovered that the length of the hind foot was the best measurement. The reason, among others, for this was that this measurement was the largest and its value not affected to any greater extent of a mismeasurement of a half or perhaps a whole centimetre. The track of the wolverine can also be measured with good accuracy in spite of the fact that this animal is only a partial plantigrade and this makes the measurement of the length less distinct. The soft paw of the lynx is widened in loose snow. This enlarges the surface of the track and consequently gives a large measurement. If the track is found on a hard surface, measurements of the width have proved to be 30 percent

smaller than in loose snow. On a hard surface the length of the paw of the lynx is a little greater than the width, in loose snow measurements will be the opposite. In other words, the size of the paw is adopted to the resistance of the snow.

Collection of the Material from killed Animals of prey

From the larger animals of prey [reindeer, roe deer (*Capreolus capreolus* L.), and moose] the lower jaw, one of the front legs below the knee and, if possible, the heart and the whole head was to be collected. From the season of 1961 to 1962, the material was extended to include the pelvis and parts of the backbone within the thoracic region. The reason for this was that lumbago had been observed within the reindeer herds and it was important to provide material for investigating whether parasites had occurred in the slain animals.

If the specimens of prey were fairly complete and the patrols not too far from a road, the men were supposed to collect the whole carcass. However, since the distance to roads were usually very long in most districts, only about 15 whole reindeer and roe deer could be collected. As a rule, the beasts of prey had left very little of small game suitable for research. Only one hare and a few half-eaten capercaillies were collected and analysed.

From the beginning it was not considered very important to collect samples of droppings from predators. Because of the fact that predators are rare and it is difficult to determine for sure what species the excrement derives from, it was not possible to obtain any comprehensive material from the whole country. However, as the work progressed, it was discovered that important conclusions could be drawn also from the analyses of droppings from the tracked animal. In the first place, one could find out what the animal in question had eaten the day before or perhaps a couple of days before the tracking had been started. Moreover, some details as, e.g., consumption of berries, vegetables, insects or small rodents could be revealed. Without an analysis of the excrements many of these details might never have been detected.

During the course of the tracking, it was sometimes difficult to decide why a predator had been digging in the snow and what it had found. By analysing the scats such questions could be answered. In some cases the devoured food could also be determined quantitatively. In 1961 the patrols were instructed to collect all droppings found. Nevertheless, no

greater amounts could be collected. One reason for this was the lynx' habit of covering its droppings.

The scats and the remains of the prey were sent to the National Veterinary Institute, Stockholm, for examination. The scats were examined for contents of parasites and after that sent to the University of Stockholm where two groups of students at the Zoological Institute analysed the contents. The remains of the prey were analysed in different respects at the National Veterinary Institute.

Additional Material from Predators

Some material was obtained from the Swedish Museum of Natural History and from The Research Station of the Swedish Sportsmen's Association at Boda (page 163). This material consisted of stomachs of lynx. The contents of these stomachs were studied.

Localisation and Character of the Tracking Districts

A map (page 101) shows the localisation of the districts in which the predators were tracked. These districts were chosen in the first place on the basis of presence of predatory animals. To some extent, the possibilities of getting experienced trackers also had to be taken into consideration. The character and function of the different districts can be summarized as follows:

I. This is the last district in Sweden in which wolves are still constantly found. Its population of wolverine is sparse, and only solitary lynx appear there. The elevation above the sea is 350 to 800 metres. The area was studied mainly from a helicopter.

II. This district was particularly suitable for observations of the wolverine. It borders on the high mountains in the west. Lynx occur in it and also fairly many bears. The district elevates from 400 to 1000 metres above the sea.

III. This is the national park district (the national parks of Padjelanta, Sarek, and Stora Sjöfallet). It was the most important district for this study and the area best represented in the material. Lynx, wolverine, and bears were fairly numerous. A few wolves were found but propagation had occurred only once during the five years of the present work. The district included high mountains in the west and extended into the conifer forest east of the mountains. Elevation above the sea was between 300 and 2100 metres. Bears were tracked up to 1300 metres above the sea.

IV. This district was included since it was known that lynx had preyed on herds of woodland reindeer. The district was situated within the conifer woodland. However, it included also a few woodless mountains. Its elevation above the sea was between 420 and 700 metres.

V. VI. VII. These districts formed an almost continuous territory in the upper part of the county of Jämtland. Many bears and lynx were found there and solitary wolverines. The wolverines might even have propagated some year. The districts were mainly coniferous but included also many woodless mountains. Towards northwest there were high mountains. Elevation above the sea was from 275 to 1200 metres.

VIII. This district was outside the territories for reindeer and close to the coast. It had a sparse population of lynx. Its elevation above the sea was between 200 and 400 metres.

IX. This district was located around the small national park of Sånfjället in the county of Härjedalen. It had a moderate population of bears and lynx and solitary wolverines, which might have propagated one year. Elevation above the sea was between 500 and 1200 metres.

X. This district was a low mountain area in southern Sweden covered by coniferous forests. It had a permanent stock of lynx and a dense population of roe deer. Elevation above the sea was from 250 to 400 metres.

Occasionally, animals—mainly lynx—were tracked also in other parts of Sweden. These animals were, as a rule, on long-distance travel.

Tracking Material Expressed in Figures

In the table on page 106 the result of the five years of tracking are summarized. Only 14% of the reports lack information about predators. However, this figure does not refer to days when bad weather forced the observers to stay indoors. Of the distance travelled during active and successful days, 37% concerns actual tracking. Search for tracks and travelling to and from the places for spending the night took the remaining 63% of the distance.

A diagram showing the distances for the different species of predators and distributed per month is found on page 108. It was particularly difficult to obtain a representative material from the higher altitudes during the months from November to January. The days were very short and it was severely cold. Therefore, especially the wolverine is poorly represented during the early winter months. The high figures for the

tracking distances between January and March are partly dependent on the comprehensive material from the lynx district in the southern part of Sweden. Down there the winter is shorter and limited mainly to these months. Furthermore, the days are longer. The bears were tracked mainly in April and May after leaving their winter dens between April 10 and May 20. After that it is no longer possible to track any animals even in Lapland. In the first snow in the autumn a few bears were tracked.

II. The Lynx (*Lynx lynx* L.)

The following weights of Swedish adult lynx were discovered primarily among animals from the County of Jämtland:

Adults: Mean weight of 13 males 17.9 kg; maximum 24.0 kg. Of 10 females 16.8 kg; maximum 22.0.

Yearlings: In December–January (hunting season) 20 young ones weighed between 8 and 11 kg, i.e., their mean weight was 9.4 kg.

Number of Tracked Animals

Geographic distribution of the tracked animals over the different districts is presented on the table on page 112. Lynx were tracked within all the districts. Except for district V to VII, they were all so far apart that every possibility of double counting was excluded. In estimating the values from districts V to VII, consideration was taken to the possible risk of double count. The number of tracked animals from each of these districts is definitely underestimated. The number considered correct is given in parenthesis. Very likely, the number of litters per year is also underestimated. Whenever two lynx walk together it is not always possible to decide whether the two are old animals or whether one is a female and the other a yearling. Probably propagation had been a little more frequent than is seen from the tables.

Alone one old male tracked in Hällefors in southern Sweden provided 24% of the total tracking distance. However, the mean values of this animal are very similar to those of the species as a whole. It is improbable that this overrepresentation gave rise to an error.

Activity, Rhythm, and Length of Travel

As has also been demonstrated by Saunders (1963), the lynx spends its daily rest—in general—in one bed only (a long time bed). For this

reason, this particular bed may be distinguished from others where the animal might have spent only a short while, e. g., a short rest during a long stroll in the night. By tracking between two successive beds one may therefore obtain a measurement for the activity of the animal per day.

A long rest during the light hours of the day is part of the daily rhythm of the lynx. About an hour before nightfall the animal leaves its resting place to go out hunting. Then during the darkest part of the night it goes to rest for a short while. After that it goes out for a new stroll and possibly hunts until it takes its day bed. However, the animal's hunting result will influence the daily rhythm. Sometimes the lynx will rest several times a night choosing different beds. Sometimes beds are used in the hunting preparations if located at game paths, e.g., hare trails.

The average length of the lynx' travel along the track (the cruising distance) was 19.2 km a day. This figure was obtained by dividing the total length of tracking (2371 km) by the number of day beds (123). Since the movement of the lynx was very regular the spread of the daily length of travel was not very wide.

However, of greater interest than the daily length of travel along a track, is the shortest distance between two days beds (the cruising radii). This distance demonstrates the speed by which the lynx will disappear or return to a certain district. In 78 cases it was possible to measure the shortest distance between a long rest during the day to the next one. These measurements are seen in the table on page 116. The mean value of the shortest distance between two successive day beds is 7.6 km. This shows that the animal disappears from one region to another with a considerable speed. It gives a spread of the predation which ought to be a prerequisite for keeping a sufficiently dense population of prey within the territory of lynx. Severe local predation will then be avoided.

Territorial Behaviour

In the Hällefors district in southern Sweden one particular old male lynx was traced more than 500 km in all. Two of the single trackings covered more than 140 km each.

The different trackings for this particular animal are seen in the chart on page 118. Probably a narrower, more intensively utilized territory of about 300 square km may be distinguished surrounded by a margin

characterized by what may be termed district movements. These movements were not completely tracked. However, the lynx here evidently hunt and take contact with other specimens of lynx. The rutting place was altogether within the narrow territory and during the year when the area was tracked it was visited by four adult lynx. A female with two young tracked in December, 1962, for a total of 180 km seemed to have the same route of travel as the old male. No tendency towards a narrower movement territory for this group could be observed. However, the daily cruising distance was only $^2/_3$ of the old male lynx. It may be anticipated that the old male was the father of the group. In that case there must have been a real family group within a certain territory. Within the area where the big male had slain altogether nine roe deer, the female with her two young had also slain two roe deer. No other lynx had slain roe deer within this territory. Outside it, a total of six roe deer had been slain by adjacent lynx. Some occasional visit by a lynx in the border areas had included the hunt for a hare (*Lepus timidus* L.). Otherwise, outside the rutting season, only short visits had been made by lynx from adjacent territories.

The tracking material from the open Lappland wildnerness sparsely populated by game is not so continuous or to the same extent collected from familiar individuals, as the material from southern Sweden. However, it is evident that travels are still longer and the territories wider than in the southern part of Sweden. The river systems and big lakes are to some extent centres of the system of movement of the animals. The animals tend to move up and down parallelly to the valleys. The lynx also move to high altitudes in the mountains, in the national park of Sarek up to 1100 m above the sea level, which is about 400 m above the tree limit.

A lynx appeared temporarily in the Kolmården district in southern Sweden. There it went straight on for about 70 km. It hunted sparcely but took two hares in four days. Then it disappeared towards the south probably towards the district from where it derived.

The Hunting Technique of the Lynx

The lynx hunts according to a very regular scheme. It starts by localizing the prey by means of hearing and vision. Then it sneaks up to a suitable distance for attack. After that the attack is made very explosively. The lynx takes a few leaps and catches the prey.

As mentioned, the prey is often localized by means of hearing. The lynx will stand on hills trying to listen for the prey. In snow it will probably track a reindeer or a roe deer by vision. Sneaking up to the prey, the lynx shows great patience. Sometimes, in cases of feeding deer, the lynx will lie in one place and let the prey come closer as it continues to feed.

The table on page 128 shows the number of successful and unsuccessful attacks. It is evident that the lynx bases its attack on sneaking up and surprising. If this method fails, the chance of the lynx to succeed is dependent on whether the prey for some reason is unable to escape in a normal way. Starvation of an animal, snow conditions or local topography might favour the lynx. The table demonstrates that, if the lynx has not reached its prey within the first 20 metres, its risks of a failure are great. In 70% of the successful hunts the prey was caught before this limit. After this the effect of the attack diminished continuously except for the surprising fact that in attacks which last for more than 50 m the distances from 100 to 300 m gave a better result than the shorter distances between 50 and 100 m. Upon closer examination of the different cases, the reason will however be seen. Long but successful hunts by the lynx are favoured either by poor condition of the prey and/or by special topographic or snow conditions unfavourable to the prey. In such cases the lynx is able to detect, at an early stage, that a prolonged attack might be rewarding.

Hunting Co-operation between Different Individuals of Lynx

Usually females with young in areas where prey animals are to be expected seem to co-operate. The family spreads in a line with the young on the flanks. The method is evidently a way of training the young in hunting technique. Real co-operation with one animal suitably placed along a path and another animal frightening the prey was observed in two cases regarding the hare. In one case both the predators were adults. The map on page 133 shows this hunt.

Choice of Species

The table on page 166 demonstrates the lynx' choice of prey for the greater part of the winter as deduced from the tracking forms. With additional information from analysis of stomach contents and scats, the table shows that the lynx had attacked moose, reindeer, roe deer, hares, foxes (*Vulpes vulpes* L.), martens (*Martes martes* L.), ermines (*Mustela*

erminea L.), voles, lemmings (*Microtidae*-species), shrews (*Sorex*-species), capercaillies (*Tetrao urogallus* L.), black game (*Tetrao tetrix* L.), hazel hens (*Tetrastes bonasia* L.), and willow grouse (*Lagopus lagopus* L.). Successful hunts were proved concerning all these species except the moose, marten, and ermine.

Hunts for Reindeer and Roe Deer

In the middle of the winter the reindeer forms the essential part of the prey of the lynx in the northern part of Sweden. Since, nowadays, there are no wild reindeer in Sweden, all the reindeer belong to Lapps. In the southern part of Sweden, which does not have any reindeer, the roe deer, on the other hand, forms a considerable part of the prey in the midst of the winter. The two species of deer overlap only in small areas.

Among these two kinds of prey of the lynx, the number of unsuccessful attacks are fairly small. Of 64 attacks on reindeer, 45 resulted in kills, and of 35 attacks on roe deer, the result was 23 kills. On the other hand, the roe deer shows a greater ability to detect a sneaking predator. In nine cases, the trackers were able to state that the roe deer had detected the lynx at such an early stage that no attack had been attempted. If these case are included, the lynx failed in attacks on roe deer in about half its attempts. Even a 50% success is a high figure for a predatory animal.

Only in one case, a reindeer was able to detect the lynx at such a stage that no attack was made. Evidently the reindeer is not as observant as the roe deer. Probably this is the result of domestication. Moreover, the dogs used by the Lapps for herding the reindeer are very similar to predatory animals which may cause dangerous mistakes.

The lynx usually aims at solitary reindeer or at reindeer dwelling in the outer parts of the herds. And it seems easy for the lynx to sneak up. The reindeer are busy digging in the snow for food, usually consisting of lichens. The very short day of the Lappland winter forces the animals to work hard also during dawn and at night-fall. This facilitates the predators' hunting.

Normally, roe deer are found dead on the place of attack. Being heavier and stronger, reindeer might take a few steps before they fall.

On a few occasions reindeer were saved by abnormal behaviour. Thus, attacks on reindeer which had refused to escape, were interrupted on two occasions. No reason whatsoever for this could be observed

other than the fact that the reindeer had behaved abnormally calm. In some single case it appeared as if a certain lynx had specialized in killing calves.

The most common reason for unsuccessful hunting of reindeer and roe deer or even small game seemed to be the consistency of the snow. If the snow was slightly frozen and covered with a crust not strong enough to carry the lynx, successful hunting was impossible. There were examples showing that the lynx under such circumstances walked straight through areas with plenty of roe deer without even attempting to hunt. In other cases the roe deer were able to walk away calmly from the predator, which had no possibility of sneaking up unnoticed.

Hunts for Small Game

Swift start to get away is very important for a prey to escape an attack by a predator hunting according to the technique of a lynx. Generally, it may be said that small game are much more difficult to catch than larger and heavier ones. Of lynx' attacks on hares 35 % were successful. Among birds preyed by the lynx, capercaillies are the easiest to catch. In the present study 29 % of the hunts for these birds were successful. Black birds were never caught. Hazel hens and willow grouse were, on the other hand, attacked on 16 occasions, three of which resulted in kills, i.e., a percentage of 19.

The lynx usually locate hares by means of listening when the hares are on their feeding places. Probably, the lynx are able to hear the sound of the hares' nibbling. Passive waiting along hare trails might also sometimes result in kills. Such a method of hunting must however be based on dense populations of game. While Saunders (1963) noticed that 60 % of the hares were killed according to this method, the Swedish study shows only 35 %.

The lynx localizes the game bird by means of vision as well as by hearing. Some careless movement might have indicated the presence of a bird resting in the snow. Werner (1953) tells about a lynx which made an attack towards a hole in the snow where a skier had put his ski stick.

There is barely any doubt that the hare must be regarded as the basic prey of the lynx. Statistical proof of this has, in any case, been presented from Canada. The lynx of this country is, however, considerably smaller than the European lynx. But also in the U.S.S.R. (Naumov, 1955) it has been shown that the population of lynx very closely follows

the production curves of the hare (page 142). However, this also demonstrates the typical reaction of a predatory animal to be one year behind in time for the high peak of production.

The fact that the Swedish lynx are nowadays in the wintertime so predatious on deer (reindeer and roe deer) is most likely a fairly recent circumstance. This may depend upon the fact that there was a very sparse stock of small game in the northern parts of Sweden during the 1930's and 1940's. The fact that during the nineteenth century the deer in the southern and middle parts of Sweden were extremely sparse, but the population of lynx relatively dense, proves that the lynx is not dependent on the presence of larger animals.

The Lynx and the Fox

Many cases are known in which lynx have killed foxes. In many connections authors have pointed out the suppressive effect that the lynx has on the fox. In the reports for this study, there was not one single case of lynx having preyed on foxes. On the other hand, attempts at attacks on other predatory animals such as martens and ermines were reported. However, almost as a rule, the population of red foxes within the districts of this study was extremely low. Often it was more difficult to find a track of a red fox than of a lynx. The fact that the fox was afraid of the lynx was evident on several occasions when a fox made a very long jump over a track of a lynx or turned around and quickly disappeared in a different direction to escape. Probably this is normal behaviour of red foxes on contact with a fresh scent of the lynx.

Cases reported by Rådberg (1964 in a letter) and by many others in the literature have shown that lynx kill foxes by sneaking up and catching them after perhaps a short chase. It is also known in Sweden that lynx may go down into fox dens and kill red foxes there. One such hunt was tracked in the present study. However, one body of a dead fox was located which had most likely been killed by a lynx. Within the Hällefors district half-devoured young of red foxes were found during the summer in the vicinity of fox dens in territories known to have lynx. In two stomachs of lynx, the contents contained remains of fox including hairs.

From adjacent districts, finally, the present author received written reports on two red foxes killed by lynx. These reports gave an exact description of the episodes. Among hunters and wild-life people within the districts where lynx are present, the general opinion is that the

lynx keep the red foxes away. Occasionally, the lynx gets a chance to catch a fox, or kill it in some accessible den. Cut-off fox tails left in the track seem to be a sign of lynx hunts.

Concluding Remarks on the Predatory Habits of the Lynx

Previous statements in this study on the predatory habits of the lynx are based on the tracking reports. They are, however, supplemented by the results of analyses of scats and of stomach contents. The results are seen in Table 10 on page 166. The analyses of scats concern samples from tracked animals. The number of new preyed animals given in the table concerns only such animals as were not reported from the trackings. This means that they must have been killed before the trackers started their work. The stomach contents, on the other hand, have no connection with the trackings but originate from lynx shot during the winter season; most of them from middle part of Sweden (county of Jämtland).

For estimating the effect of the predation on the fauna, it is important to know whether the "active days of the lynx" observed by the trackers are representative of the habits of the lynx all winter. The observed days should not be considered "average days" but days of activity of the lynx. Days during which the animals did not move are generally not represented in the tracking reports. The normal reason for inactivity of the lynx is the weather. Lynx are known to be quiet and lacking initiative in bad weather. Their hunting technique depends upon vision and hearing which must be ineffective during blizzards and in whirling snow. It seems plausible that this kind of weather was met during at least between 20 and 30 % of the winter season. Uncritical judgement of the present material may result in an overestimation of lynx' activity.

Hunting Habits in Different Parts of Sweden

The observations of lynx predation, made by the trackers, were classified for three different regions (Table 5 page 143).

1. Areas in which the reindeer population is dense during the winter season. They include most of the land in northern Sweden that has lynx at the present time.

2. Areas in the South with lynx population and plenty of roe deer. Reindeer do not occur in these areas.

3. Areas where neither reindeer nor roe deer are present. Such areas are only found in some east sections of the northern counties. There

the lynx are very rare. Compared with Regions 1 and 2, Region 3 is underrepresented.

The table demonstrates:

1. A larger number of animals killed per unit of time in the reindeer-region (Region 1) than in the other regions.

2. Short movements in Region 3 combined with low effect of hunting efforts.

3. Difficulties for the lynx to catch small game in the northern areas (Region 1 and Region 3) on comparison with Region 2 in the southern part of Sweden.

In Region 1 reindeer is the most common prey (66 % of the kills). On comparison with the result of the hunting activity demonstrated by the lynx in southern regions of the country (Region 2) where the animal lives in conditions more typical of the species (a relatively abundant stock of small game and plenty of a small species of deer, which in size is very well suited as prey for the lynx) it seems to be clear that, *in the reindeer region, the lynx show surplus hunting activity, not necessary for their livelihood. This surplus hunting does not occur in the other regions.*

The material from Region 3 (only small game as prey) is small and insignificant. A lynx yearling which had a week before lost his mother on account of hunters, contributed to about 25 % of the total tracked distance. The average length of the daily travel rises from 14.4 to 15.3 km if this tracking is eliminated. The result of the hunts, however, do not proportionately change by this elimination, since the young lynx had been successful in catching a ptarmigan.

The number of attacks per killed small animal is in the reindeer area 4.00, in the small game area 4.50 and in the roe deer area only 2.22. The difficulties of the lynx in the northern areas 1 + 3 seem to be the depth of the snow, which is normally much less in Region 2. The similar figures for small game hunting in Regions 1 and 3 indicate that this explanation is correct. Probably the lynx had difficulties with their food supply in Region 3, where smaller game is usually very sparse and deer is absent.

Does the Lynx Kill More than Once During a Night?

The table on page 149 shows the distribution of animals killed by lynx on different days. Eighty daily records of successful hunts by the predator is divided into:

Thirty days during which reindeer were killed. In 9 cases more than one animal was killed during the same night.

Fifty days during which other game ("natural game") was killed. In 7 (8) cases more than one prey was killed during the same night.

By studying the different occasions on which more than one prey was killed during one night's hunting, it is found, concerning *natural game,* that only in one single case has the lynx really prolonged its hunt. This means that he killed, ate, rested for a short while and then started out again—apparently without any reason—and then killed another prey. In the other cases, the second prey either "exposed" itself to the lynx, e.g., a hare or roe deer just passed the predator lying down on its first prey, or the prey was some smaller game and the lynx had a whole family to support. In that case two kills a night might seem reasonable. As far as the *reindeer* are concerned the behaviour of the lynx was different. As a rule, the predator could locate the next prey from the previous kill. Then it reacted by slaying spontaneously and perhaps almost reflexively. Such reflex action was also observed sometimes when the lynx, seemingly without any reason, turned aside from his wandering direction and made an attack into the snow from 15 to 20 metres away and then tranquilly returned to his trail. No trace of game was seen in the snow. Probably a game bird (capercaillie?) had flung itself out of a tree. The lynx was then unable to resist this absolutely hopeless attack.

Normally the lynx does not kill more than one prey a day during the winter season; generally not that much. In rare cases, when two or more animals are slain, this is due to the fact that game has exposed itself as very easy prey. It is not "prolonged hunting". In the reindeer herds the lynx are wintertime offered a biotope rich in food and easy prey. Consequently, hard and—for the species—not typical hunts some times occur resulting in kills of several deer during one night.

Hunting Habits of the Lynx During Different Periods of the Winter

The big predators' hunting possibilities seem to be strongly influenced by the changes in snow conditions during different periods of the winter. The number of kills monthly are given in the table on page 154. In order to avoid very small figures for comparison, the material was divided into only two groups; one for the deer (reindeer and roe deer)

and one for smaller animals. It should be observed that the table only gives the exact number of kills per group and month. The idea of it is not to show the hunting activity. The material clearly demonstrates great variations in the hunting habits during the course of the winter. From October to November small game predominate as prey. From December to January there are about as many deer slain as smaller animals. In February six times as many deer as smaller animals are slain.

Because of this great tendency and suspicion that the migrating reindeer herds offer greatly varying possibilities to the lynx during different parts of the winter the tracking reports were scanned for presence of deer (table on page 153). The precence of reindeer was, however, very regular and even in all the northern areas where the investigations were made. As far as roe deer are concerned, there is no reason to suspect any differing abundance during the winter, since most of the tracking were made in the same areas and no regional movements are known which might influence the hunting possibilities of the lynx. Therefore, it may be concluded—as the figures distinctly demonstrate—that *the predation of the lynx changes from smaller animals to deer towards late winter (between February and April).*

As mentioned above, the lynx specializes strongly in preying hares. In order to understand the hunting habits of the lynx, this specialization is of a certain importance. The incidence of the hare fluctuates considerably—in conformity with the populations of other small game—during different parts of the year. A maximum occurs in the early autumn and a minimum in the spring. This means that the lynx is gradually deprived of its most important prey as the winter progresses. A similar decrease occurs among the tetraonids which—next to the hare—are the most important group of prey among the smaller game. In regions where reindeer and roe deer offer an easy prey during the winter, it seems, however, very natural that the lynx to a great extent change their hunting habits to preying on these bigger animals. This change is probably facilitated by the depth of the snow and also by the weakness of the deer.

The Killing Technique of the Lynx

The lynx usually attacks larger animals (reindeer and roe deer) by jumping up on the victim's back. From there it aims the killing bite at the neck or throat, using paws and claws to hold the prey. If it does

not get the right grip or lands too far back, the lynx might injure the prey severely with its claws. In most cases, however, the wounds from the claws will appear only as pricks of a needle. If successful in getting the correct position, the lynx aims its bite at the throat with the utmost precision.

Once in a while the lynx might, however, attack its victim directly from the front, putting its teeth into the throat while holding the prey with the front paws. This method seems to require particularly favourable conditions as far as darkness, depth of snow and topography are concerned. Moreover, it might possibly be used in preying animals with locomotor difficulties.

Circulatory disturbances indicative of suffocating was a normal finding among the reindeer and roe deer sent in for examination. Possibly, this was the result of a persistent grip over the throat. In spite of the fact that the reindeer as well as the buck of a roe deer is a strong animal capable of fighting before suffocated, no trace of death struggle could be found at the site of killing. The shock from a heavy predatory animal's explosive attack might naturally also play a certain role.

Utilization of Prey

In utilizing large prey the lynx does not follow a rigid pattern of behaviour. It seems normal for the lynx to rest a while within sight of the slain prey. Oftentimes the throat is torn open by the grip over the throat. On such occasions the lynx might eat the neck and the shoulder. Normally, however, the thigh and perhaps also the small of the back is preferred. The injuries to the roe deer are similar. However, since its body is smaller the injuries become greater. A group of three lynxes devoured a medium-sized roe deer in two meals.

Among Swedish hunters, the general opinion is that a lynx will separate the head of a roe deer from the body and carry it away. Nevertheless, not in one single case of 23 killed roe deer and 45 reindeer, were the animals found without heads. On the whole, the lynx does not carry away a large animal or parts of it. Nor does it have any greater instinct to dig down animals or parts of them. Larger prey is never covered or dug down. Even small game are dug down very carelessly.

The present author is consequently of the definite opinion that the lynx does not normally decapitate its prey of reindeer and roe deer.

Probably, this current misunderstanding has been caused by the fact that foxes may separate and carry away the head of roe deer killed by lynxes.

A normal meal of a lynx seems to consist of two kg of meat or perhaps slightly more. A hare is estimated a normal meal. Consequently, a reindeer or a roe deer would cover the requirements of a lynx for several days. The table (page 171) demonstrates 40 cases in which the trackers had been able to decide definitely whether the lynx had eaten once and then continued its walk or it had returned once, twice or several times.

The figures in the table show that it is common for the lynx to return to a killed roe deer at least once for a meal and after that go on. As for killed reindeer, on the contrary, one meal in connection with the kill seems to be the rule. This has to do with the previously mentioned surplus hunting in reindeer areas. It did even happen three times that lynxes killed reindeer without feeding on the bodies at all. The first time this happened was in connection with a very severe massacre on reindeer in Hotagen (in the county of Jämtland, deep snow conditions). In the second case two reindeer were killed, but only one of them was fed on. In the third case the lynx had very probably been frightened by the trackers just as it had slain a reindeer. Therefore, it had left the prey. Of course, small game are devoured much more completely. This is true especially of hares. In 23 controlled cases in which hares had been killed, the lynx had left only the paws (in certain cases only a few cm of the hind paws), the intestines and, in a few cases, the part of the nose with the front teeth, and a small part of the skin. Only once was a poorly nourished hare found dug down. In another case a piece of a front leg with the shoulder was found.

Tetraonids seem to be eaten more carelessly. Three of the eight recorded capercailles had been left half-eaten.

The wasteful manner in which the lynx utilizes killed deer (roe deer and reindeer) for only one or two meals is reminiscent of the fact that this animal originally was a small game hunter, particularly for hares. The lynx shows a very fixed pattern of behaviour which it is almost unable to modify. Its habit of hunting, eating where it kills, sleeping and then starting for its next hunt far away from the previous one, spreads the decimation of prey animals over a wide area. This keeps the density of small game at a level suitable for the lynx. As far as bigger game are concerned, the method seems uneconomical.

Why does the Lynx only Unwillingly Eat Carcasses?

In the present investigation, not one single case was noted in which the lynx had eaten carcasses. Although often passing places of previous kills, this predator seldom even gets close to a carcass. Nevertheless, the stomach contents of two lynxes shot at carrions, proved the presence of remnants of slaughtered pigs. The same thing was noticed in an analysis of excrements. The present author is of the opinion that the lack of interest in carcasses is not due to the circumstance that the lynx would require warm, fresh meat, but rather to the fact that frozen bodies are unfit or impossible for these animals to utilize. Its set of teeth are not suitable for crushing hard frozen meat. According to experience from zoological gardens, the lynx does not eat frozen meat.

How Do the Prey Animals React to Disturbances by the Lynx?

An answer to this question is of practical importance for estimating the trouble caused by lynxes in different connections. However, the trackers had great difficulties in finding this answer. In many cases lack of time on account of other important tasks made careful observations impossible. Nevertheless, some 30 cases were subjected to closer investigations. On the basis of these investigations, it may be said that the lynx' attack are the least disturbing ones made by big predatory animals. The animals seem to calm down as soon as the fright caused by the direct attack is over. The presence of lynxes in an area does not bother the prey animals very much. Not even animals having been forced to escape, are seriously disturbed. The loss caused to the reindeer herds is consequently that of actually killed animals and not that of disturbing and separating reindeer from the rest of the herd.

Notes on Rutting and Propagation

Usually the rutting time of the lynx is considered to appear towards the end of February and the beginning of March. The present material indicates that this period is slightly later. However, the material is small and scanty. From the 14th to 15th of March tracks from four adult lynxes aggregating together showed clear signs of rutting. Furthermore, touring couples of adult lynxes were noticed in the middle of March. Since this is very rare during other times of the year, it must also have been a sign of rutting. One male was killed by another lynx 20th of March. The reason for the fight probably was the rut.

One single litter of lynxes were believed to be born on the 10th of May (Rådberg 1959). Experience from zoological gardens (Zuckermann 1952, Palmgren 1920) proves that the gestation period lasts between 63 and 73 days. According to the literature (Werner 1953) the number of female lynxes is believed to exceed that of males. In field work, it is, however, not very easy to determine the sex of a lynx. The hunter expects similarities to, e.g., dogs or foxes and might, therefore, easily mistake a male for a female. The table on page 180 does not show a larger number of females. It should be noted, however, that the only group of lynxes (the Jokkmokk group) estimated for dominance of one sex or the other was determined exclusively by hunters. The present material gives no reason to believe that the females surpass the males in number.

The Development of the Lynx Kittens

A series of cases were studied (on the basis of statements in the press or other information) in which young lynxes had appeared close to human dwellings. These individuals were often found in very poor condition and easily killed. On a few occasions, the trackers also ran into lonely lynx kittens which apparently had had difficulties of nourishment.

Lynx kittens develop slowly. Trackings showed that the young stayed with their mother during most of the winter. Normally, the young will not part from the mother until the rutting period begins in March. In December they still suckle their mother. Their attempts at hunting are very clumsy at this time and they still rest in the same bed as their mother. Young lynxes shot during the hunting season in Sweden (December–January) weighed between 9 and 11 kg. Single kittens caught, as mentioned above, in the vicinity of human dwellings, weighed only between 6 and 8 kg, sometimes even less. There seems to be no doubt that these specimens were young of the year. Probably, their mother had been shot. The reason for their approach to human dwellings could have been search for rescue and perhaps food such as garbage or domestic animals (cats, hens, etc.).

The Lynx and the Roe Deer in Hällefors

In the southern part of Sweden (the roe deer districts) most of the tracking was carried out on ground belonging to Billerud's Industrial

Company in Hällefors. Since far back, this company has had a well-planned hunting management. Very accurate statistics of bag records have been compiled according to uniform rules. Consequently, it seems justifiable to consider the development of the bag records from year to year related mainly to the size of the stock. In 1953 the lynx appeared within the district after an absence of about 30 years. The first litter is believed to have been raised in 1957. The curves on page 185 show the bag records of roe deer (total number of animals 2,346) since 1939 for the whole district.

The marked declination of the bag records for roe deer in 1951 and 1957 is certainly related to difficult winter conditions. In spite of the presence of lynx, the stock of roe deer in the whole district increased. Not until 1959 could a negative effect of the lynx' predatory activity be noticed. After that the bag records decline rapidly and seemed to be stabilized at about 60% of the highest records from 1958 and 1959.

The effect of the lynx on the population of roe deer may be still better demonstrated by separating the bag record for areas with lynxes and areas without them. For the years from 1951 to 1964, the whole district is divided into areas free of lynxes and areas in which the lynx does appear (it must be pointed out, however, that the lynx areas are for the most part mountainous and therefore have severe winters). According to the curves, a steady increase appears in the districts which have no lynxes. In the others the bag records decrease to about 40% of the previous top results. However, also within these areas a stabilization and also a weak increase has occurred during the last few years. The curves indicate pressure on the roer deer exerted by the lynx. But it is necessary to keep in mind that there are many factors affecting the bag records. Bag records of the future and also further research from this district are definitely of the greatest interest.

III. The Wolverine (Gulo gulo L.)

Considerable difficulties were met with in collecting representative material for the observation of the wolverine. One of the reasons for this was the sparse population of wolverines in most districts of Sweden. Moreover, it is difficult to collect material during the early winter in the mountains and the high plateau district. Nevertheless, during the last years, the trackers had orders to give priority to the wolverine whenever possible. The result was a tracked distance of 957 km or

about the same distance as the lynx was traced in the same districts (areas with reindeer).

The presence of wolverines in the districts studied is outlined on page 192. In Districts IV, VIII, and X, no wolverines were found.

Number of Tracked Animals

It is difficult to determine exactly how many wolverines are represented in the present material. This is, to some extent, due to the fact that the family group, which is most easily identified, does not keep together during the winter. Moreover, this species of animals is subjected to severe hunting. It is almost always difficult to decide whether a wolverine, which has been shot, has appeared among the individuals tracked.

The Table 12 page 192 contains fairly uncertain figures. However, the number of animals must be considered a minimum. Especially within the very vast district No. III, the number of wolverines must certainly have been much larger than that given in the tracking record.

Difficulties in Tracking the Wolverine

The wolverine is often found in the border districts between the forests and treeless mountains. In these areas it will also propagate. When the animals cross ridges or open moors their tracks might easily be obliterated by the wind. In such cases it was difficult to track for long continuous distances. During the late winter wandering routes are, to a great extent, determined by the localization of stored meat gathered and dug down after their own or other predatory animals' hunts, or found after accidents among the reindeer. Large amounts of meat are stored by the wolverine to live on when hunting becomes less successful.

Rhythm and Activity of the Wolverine

As other predators, the wolverine moves during the dark part of the day. However, its habits in this respect are very irregular. Among the four big predators, the wolverine is the commonest to be seen in bright daylight. Several times they were observed in daylight by the trackers without being frightened. As is seen from the following observations, this is true also of the propagation period. A female once left the den

at 12.30. Another time she came back at 17.30. A third time she left the den at 17.20. On the last-mentioned occasion, she had returned from her nightly strolling at dawn. This was noticed in the middle of April. In the beginning of May, another female was moving about with her young very frankly and unwarily in the middle of the day. Once, without being frightened, she left her temporary lair with her young at 5.45. The wolverine also rests more irregularly than, e.g., the lynx. It is difficult to determine which of its beds are actually day beds (long-time beds) and from them conclude, how far the animal in question has moved that day. However, a normal distance seems to be at least 30 km.

If snow conditions are suitable, the wolverine digs deep holes in the snow especially in the vicinity of kills in order to take care of the meat. Sometimes this animal might dig a deep hole under a killed reindeer and lie down to rest there.

Propagation Areas

The wolverine gives birth to its litter in February or March. Already at the height of the winter the territory seems to be picked out. At least sometimes, the territory is chosen because it includes the place where meat is stored for the winter. Such territories offer good possibilities for study. In four of them females with their litters could be closely observed. Two definite propagation dens and two areas in which propagation had most likely occurred were investigated. The wolverine does not seem to propagate in the same place year after year.

During the winter most of the wolverines live in the low mountains or in the coniferous forests bordering on the high mountains. In these areas a number of scattered reindeer spend the winter. They are left behind here after the autumn migration of the rest of the herds to their winter feeding areas, which normally are located hundreds of km from these districts. Single wolverines might now and then appear further down in the woodland, disturbing and hunting reindeer. However, nowadays the wolverine very seldom propagates at any distance from the mountains. The commonest propagation den is dug out in a hard snowdrift connected to rock formations or a heap of rocks left on the mountain planes. Nevertheless, dens might be found below the limit of the coniferous forests. In such cases the dens are usually located among the rocks in a slip below a mountain slide.

Distribution of the Winter Tracking

The table on page 108 shows that the distribution of the tracked distances during the winter was very irregular and that $^2/_3$ of the distances were tracked in March and April. This part of the winter offers more favourable conditions for tracking since the trackers are able to operate in the propagation territories where animals are constantly present. During the early part of the winter snow conditions, short daylight and severely cold weather hold the trackers back. The wolverine has the habit of moving along the same paths repeatedly—"the wolverine trails". They visit their caches of meat and old kills regularly. Also late-winter tracking gives a certain idea of what has previously happened, especially as far as food resources are concerned.

The Food of the Wolverine

The main winter food of the wolverine is reindeer (Table 1 on page 106). In the hunts tracked, no other species of game were killed except a few small rodents. The number of carcasses visited by wolverines was considerable and exceeded the number of killed reindeer three times. Most of these carcasses (85 %) were those of reindeer. But some of bears and moose which had been shot were also found. In a few cases hares and foxes had been dug up out of the snow.

Except for the successful and unsuccessful hunts for reindeer and hares given in the table, hunting occurred only to a slight extent. Shrews were killed and sometimes eaten, other times not. Lemmings were common food, but not dominating—in spite of the fact that these rodents were often abundant, especially in the spring of 1961.

The analysis of scats demonstrated the same kind of food. In only six cases of 38, no remains of reindeer were found. In ten of them remains of rodents etc. were found, the total number of which was 22 individuals—one vole, one shrew, 18 lemmings, and two "unspecified".

A certain amount of vegetables were found in the scats such as fragments of the greenery of lingon and blueberries, other "fibres and slices of plants", and certain fragments of coniferous trees, probably deriving from territory markings in trees and shrubs (cf. page 225). The wolverine is able to crush very strong bones (fig. 23 on page 198). In the scats, bone splinters up to 20 mm long were found.

Carcass or Produce of Hunt?

To a great extent the wolverine feeds on carcasses, which here means the bodies of animals earlier killed by predators or by accident. About 50 different old kills or remains of reindeer were found to have been visited by wolverines. In 15 of the 50 cases, the trackers could establish that the reindeer had been killed by wolverines. (Table 14 on page 200.) In most of those cases the killing and the visiting animal might have been the same individual. Sometimes the male of a family might kill a reindeer which is utilized by the female and partly carried off to the den for feeding the young.

Among the twenty other animals reported killed by other or unknown species of predators, seven were killed by the lynx. This figure is probably underestimated.

Nowadays, since there are practically no more wolves in the mountain regions, the lynx has taken over this animal's role of supplying the wolverine with meat if hunting conditions are unfavourable to the big marten.

Half the number of reindeer dead of unknown causes, were found in areas where the lynx is comparatively numerous and known to prey heavily on reindeer during the winter season. In some cases the lynx had visited the carcasses before the wolverine. It is believed that about 40% of these reindeer had been killed by the lynx. Only one of them was reported killed by accident (fall down a steep mountain).

The Hunting Technique of the Wolverine

The wolverine is not a skilful hunter. Its success depends on extremely favourable conditions—above all deep snow, which makes it difficult for the prey to escape. In certain snow conditions, the broad paws of this animal (normally between 12 and 20 kg) carry it so well that is is able to move much better than, e.g., the fox (between 8 and 10 kg).

Sneaking hunts ending in a surprise attack are rare. The general hunting technique is actually to try a chase whenever an opportunity is given. For lack of favourable conditions, the wolverine will often not even try to hunt.

The tracker often gets the impression that the wolverine is out trying to find something to eat rather than to prey for game.

For about one thousand kilometres of tracking, only nine successful

hunts for reindeer were reported (in some of them several animals had been killed). Seven hunts had failed. Among smaller game, six hunts for hares and one for capercaillies failed. No successful hunt for small game was noted.

Hunts for Reindeer

The tracking record did not reveal any cases of wolverines following reindeer herds or single reindeer for any long distances. As a rule, the wolverines had moved around aimlessly and seemed to have come across the reindeer more by chance, while scanning through the areas, than by continuous trailing. When the wolverine detects a reindeer, it attacks immediately without sneaking up. A longer or shorter hunt begins. If the wolverine does not reach its prey, it will give up the chase. Occasionally, a sneaking hunt, during which the wolverine has waited for its victim on some rock ledge, was recorded. The longest chases recorded were one km.

In a few cases the description of wolverine hunts seems to indicate that the wolverine had driven a herd of reindeer back and forth. When the herd turned, the wolverine took a short cut and tried to reach its prey. This type of hunting might probably occur essentially when reindeer appear in areas of comparatively favourable snow conditions, e.g., sparsely wooded pine areas or frozen lakes unwillingly left. On such occasions, three reindeer were killed on different days in one district. In another place four reindeer were killed during two days.

In most instances, chase hunting was carried on in difficult and deep snow. A large male wolverine appearing twice in a large herd of reindeer in feeding areas just below the low mountain district, killed seven reindeer the first time, and ten the next. Snow conditions were then particularly difficult for the reindeer. It was very easy for the wolverine to catch up with its prey.

Hunts for Moose

In the literature (Zetterberg *et al.*) it has been stated that the wolverine might hunt and even sometimes kill a moose (*Alces alces*). In spite of the fact that a fairly large number of moose appeared in the areas where the wolverine was tracked, this predator did not show any interest in the moose. No attacks were noted. However, immediately outside

District III, there was an attack on a female moose with calves. The cow died, but not until the wolverine had left the place of attack and the cow hade walked away about one km. The episode was carefully described (S. Widahl in a letter, 1963) and verified by photographs.

Within the reservation of Pecore-Hyce Teplow (1937–38) studied the matter and found that 36.7% of the wolverine stomach contents continual remnants of moose. He stated, however, that this was mainly the result of feeding on poached animals. Naumow (1955) gave a mean percentage of 27. The present author is of the opinion that the wolverine very rarely kills moose in Sweden and that this animal should not be counted among the predators which kill moose. In the case described above, the wolverine had a den in the vicinity. Perhaps its cache of meat had been used up, so that the wolverine was short of food for her young.

Hunts for Small Game

The wolverine's hunts for small game were all unsuccessful. On two occasions a wolverine dug up the body of a hare. Two bodies of foxes were dug out of the snow. In the district in which this happened the lynx was rare. Therefore, it does not seem impossible that the wolverine had also killed these animals. One successful attack on capercaillies resting in a snow bed was also reported by P. E. Kuoljok.

Six unsuccessful hunts for hares were tracked. Several of these hunts were fairly long, up to 5 km or more. As a rule, the wolverine loses the track of the hare on mountain ridges or mountain peeks where the snow is hard. On one occasion, a wolverine hunted a hare straight through a small herd of reindeer which was scattered by the hunt. No hunt for red foxes were noticed. One of the trackers (L. Arvidsson) mentioned in a letter, however, that he had seen in 1959 tracks of a wolverine hunting a red fox. "The fox had had great difficulties, sinking deep into the wet snow, whereas the wolverine had run easily on the surface." (According to Teplow, analyses of stomach contents proved that the food consisted of: moose and reindeer 72.8%, hares and other rodents 11%, tetraonids and grouse 5.7%, other predatory animals 1.8%.)

The Wolverine and the Track of the Lynx

The wolverine seems to show considerable interest in the tracks of the lynx. Without doubt this has to do with the fact that the wolverine

wants to feed on the prey left behind by the lynx. In 14 cases, the trackers noticed that wolverines had followed lynxes. The total length of these tracks was 77 km, i.e., a mean of 5.5 km per case.

However, this habit of the wolverine seems to be limited to the early winter (fig. 24 on page 207). Seventy of the 77 km mentioned above were tracked before the last of February, i.e., a percentage of 90. Only 215 km of the total of 958 km (23 %) were tracked before this date. Not one single time before that, did the wolverine hunt with success. It seems as if the wolverine follows the tracks of the lynx only when lacking food. Later in the winter when many carcasses are accessible, the wolverine does not seem to be particularly interested in the tracks of the lynx.

From what has been mentioned above, it appears firstly, that the wolverine has difficulties in hunting reindeer during the early winter, secondly, that the wolverine, on the whole, has difficulties in finding food during this time of the year when it has to shift its more comprehensive summer diet to a diet dependent on hunting results or carcasses, particularly of reindeer.

Once a lynx was noticed to come across a reindeer recently killed by a wolverine, and to eat of it.

Importance of Different Seasons

The table on page 208 gives the dispersion of the hunts and the hunting attempts of the wolverine during the time before and after February 1. It is evident from the table that no attempts at hunting small game had been successful. Furthermore, one single unsuccessful hunt for reindeer and a few visits to carcasses were noticed during the first period. This period comprised—as earlier mentioned—$^1/_4$ of the whole tracking material. The carcasses usually derived from animals killed by the lynx. In spite of the fact that 90 % of the tracking reports from this period indicated a fairly dense population of reindeer, not one single reindeer had beed killed by the wolverine. Nor were many carcasses found. Before the 1st of March the distance between each carcass was 23.9 km. In March this distance was 8.7 km, in April 12.9 and in May 7.1. The mean distance for the whole winter was 11.3 km. These figures give a good idea of how the number of preyed animals increases during the winter months in the Lapland wilderness. They also indicate that the wolverine positively reveals its prey to the trackers following

it. The hunting activity of the wolverine seems to decrease during the months of spring provided that a sufficient number of carcasses are available.

Normally, the wolverine's hunts for reindeer are almost completely restricted to the height of the winter probably because this predatory animal is dependent on particularly favourable snow conditions for its hunts. Possibly, a poorer general condition of the animals of prey may play a certain role in this connection.

Storage of Food

The way in which the wolverine stores its food varies according to the social position of the animal. In family territories utilization is naturally very heavy. The females have to keep very busy. When wolverines appear in winter districts of reindeer herds outside the normal area of distribution, the habit to store food seems to be less prominent. During tracking, a total of 23 different stores of varying contents were observed (Table 17 on page 216). The wolverine's commonest method of storing food is to dig it down into the snow. Sometimes it is dug down rather carelessly, other times very carefully, deep into the snow. Suitable places are also crevices or heaps of rocks. A very particular type of storage place is that of a well. In water meat lasts even longer than in snow. Finally, the females of the wolverine collect big caches of meat close to the propagation den. Never did the trackers observe that meat of reindeer or any other food had been stored in a tree.

Meat is often carried long distances to storage places. Distances up to ten km or even more were noticed by the trackers. A female carried a piece of meat to her young in the propagation den a distance of eight km. The job was so exhausting that she had to put down the meat on the ground many times and rest.

Very often, the wolverine takes the head off the reindeer and carries it away. This is not the general rule, however.

A place where four reindeer had been killed by wolverines and two by lynxes was subjected to close investigation. In ten days towards the end of March, the wolverine visited the place at least five times, two of which in the middle of the day. All the time the wolverine collected and dug down pieces of meat. A month later, one of the reindeer was still almost untouched, whereas the four others had been almost

destroyed. The wolverine had been in the place at least twice, probably more.

On three occasions, trackers observed a female walking with her young. Very evident signs of mucous vomits were observed. In no other cases were such traces reported. Very likely, the female wolverine might under certain circumstances carry pieces of meat in her stomach in order to later vomite for feeding her young. Chrisler (1958) observed the same thing in wolves.

Killing Technique of the Wolverine

The wolverine attacks by jumping up on the back of the reindeer and then aims a powerful bite into the back of the neck. However, sometimes it might be unable to strike this point. In that case it will try to bite its victim in the back or the withers wherever possible. The table on page 213 shows some reports of the injuries caused to some thirty reindeer killed by wolverines. The last column gives an account of three reindeer injured but left alive by the predator. From reports made by reindeer shepherds or mountain hunters, it is well known that this sometimes happens. One of the above-mentioned cases was very accurately described by the observer. A three-year-old reindeer buck had been attacked. At first, however, it was able to through off the wolverine. The wolverine made new attacks and after a while the buck stood still tramping on the same spot and finally fell over. After that the wolverine left the reindeer. Examination at the National Veterinary Institute proved that this three-year-old reindeer buck had been in good health. It had been badly bitten in the withers. When the trackers arrived at the place a day after the incidence, the reindeer was able to get up on its feet, but soon fell over again. This and similar cases might be explained by the particular killing technique practiced by this beast of prey. Its bites into the back of the victim injure muscles and nerves around the spinal cord. This might cause a temporary paralysis lasting long enough to give the predator the impression that its hunt has been successful.

Sociable Disposition of the Wolverine

As a rule, the wolverine is a lonely walker. Krott (1959) stated that tracks from adult wolverines walking together could be noticed only

in April. Furthermore, he believed that the male did not have any contact with his family. He was not even present within the territory surrounding the propagation den.

Nevertheless, the present tracking reports contain information about contact between male and female:

January 26, 1962. Two individuals. Judging from the size of the tracks, a male and a female had accompanied each other for six km.

March 16, 1961. The male had made his bed on a stone about two km from the propagation den. The day before, the trackers had passed the den at a close distance. As a consequence of this disturbance, the female had moved the young about 500 metres to a new den in rocky ground.

March 25, 1961. The same male and female had walked almost simultaneously in the same track.

March 20, 1962. Three different individuals, probably two large males and one female, were tracked within a distance of 15 km.

March 18, 1961. A female went from the propagation den to the place where three reindeer had been killed. The male was already there and had dug three deep tunnel beds in the snow. The two animals met and followed each other for a while.

March 26, 1961. The same animals met at the same place of kill. The male followed the female to the propagation den after a short while. Both animals were checked within a circle of one km in diameter.

March 20, 1961. Two wolverines judged to be a male and a female had walked together for about 15 km in a high mountain plateau. Three unsuccessful attacks by the animals on reindeer were noticed.

May 8, 1960. Two wolverines (male and female) were observed together on the high mountains (900 m above the sea). They separated and then the male disappeared down into a deep cache of meat. He came up between the skis of a tracker.

The Rutting Season

Wright and Rausch (1955) studied the sexual organs of the wolverine. From their studies they drew the conclusion that the rutting season of the American wolverine falls between April and August (same as for European species). The present trackings gave no information about sexual activity, except for one single case. Two wolverines were noticed once in April running together and playing very long and intensely.

Most probably, however, the female in question had recently lost her young (killed by the Lapps) which might explain the behaviour in this case possibly as an early rut. The tracking operations covered seven mounths of the year. Within that time no other signs of sexual activity could be noticed. Very likely, the rutting season of the European wolverine is the same as that of the American.

Birth and Development of the Litters

Birth of the young is considered to take place in February and March (Zetterberg 1945 and Krott 1959). Early births might not be unusual. A couple of young were heard whimpering in a propagation den on the 3rd of March. According to Krott no such sounds are produced until the age of three or four weeks. There is also a wide range of the birth dates.

Females wandering on the snow with their young were observed once the 19th of April, once the 7th and once on the 8th of May.

Material collected from different authors revealed a mean of 2.4 young per litter. One litter with four young is found. Seventy-three litters were checked.

Territorial Marking

The wolverine marks its territories in several different ways. The marks are those of urine or excrements. Biting into small coniferous trees is also practiced. As mentioned by Krott the wolverine also marks by means of secretion from anal glands. Such things can not, however, be observed by trackers.

The caches of meat were often noticed to be marked by urin or excrements. A more unusual sign was once noticed. An individual had bitten off a twig of a spruce, and placed it over a place where a fox had been dug down.

The signs of bites into coniferous trees are often very marked. They prove that repeated visits are made to trees selected for marking. Pine, spruce, and juniper are the trees usually subjected to marking. Once a mark in a birch tree was observed. The present author is of the opinion that coniferous trees are bitten into in order to bring out the smell of the ethereal oils of these trees.

The wolverine often climbs in trees. It is probable that some sort of marking then takes place on the basis of smell.

Marking seems to be commoner within the propagation areas than down in the coniferous forest where the wolverine wanders around on its long strolls.

Measurements of Wolverine Tracks

The table on page 226 contains a number of track measurements. Some of the measurements which derive from the propagation territories from cases in which adult wolverines have walked in couples, can be fixed to age group and sex. As a rule the same wolverine is not represented more than once for a certain year. Most of the measurements concern different individuals.

IV. The Effect of the Lynx' and the Wolverine's Selection in Reindeer Hunting

The effect that predatory animals' selection has on their prey is often discussed; however, often without arriving at any definite conclusions. In the United States and in Canada, investigations have been made concerning the wolf and different species of deer or wild sheep. Borg (1962) also discusses this problem concerning the lynx and the roe deer. Nor have these investigations resulted in any final conclusions. The primary reason for selection is that the predator has difficulties in caching a prey in its best age and state of health. Especially during the winter, weather conditions might render a hunt more or less difficult. In Sweden and everywhere in the northern hemisphere, the climatic variations have a great influence on a predator's hunting possibilities. When, e.g., cold weather follows upon strong thaw, hunting conditions change very quickly from good to hopeless and back to extraordinarily favourable. When the snow is still soft and wet, the predator is able to sneak up to the reindeer. The reindeer, on the other hand, sinks down deep into the snow and has difficulties in escaping. When a weak crust has frozen on the snow, the beast of prey becomes absolutely unable to hunt since the prey can then hear every step that the predator takes even at a long distance. A common observation is that both the wolverine and the lynx under such circumstances pass through a herd of reindeer or roe deer without even attempting to catch a prey. If it gets colder, the crust becomes stronger and in due time the predator will again be

able to sneak on the surface of the snow while the deer are still caught in the deep snow. A wolverine, e.g., with its broad paws can then easily master its prey. Finally, if the crust has frozen very hard, both types of animals have the same possibilities of moving on the snow. This again means difficulties for the predator. On the other hand, such a hard crust of snow will make it difficult for the deer to get food and cause starvation which facilitates the kills. A predator's hunting technique is also of importance as far as selection is concerned. The quick attacks of the lynx result in very few failures. Sneaking up however means selection with regard to the physical qualities of the deer. On the other hand, the clumsy hunts by the wolverines with its attempts to chase and overcome the prey, ought to result in a high proportion of prey in bad state of health.

An estimation of the problems mentioned above was made possible by studying the remains of slain animals. The state of nutrition was judged on the basis of the fat content of the bone marrow. Macroscopic and in some cases microscopic examinations as well as chemical analyses were carried out. The findings were divided into three classes, viz., Nothing remarkable (Class 1), Less good condition (Class 2) and Inanition (Class 3). The latter condition must be considered a pathological condition from which the animals had no possibilities of recovery. Class 3 also includes the presence of parasites (Elaphostrongylus rangiferi) which causes cerebrospinal nematodiasis accompanied by locomotor disturbances. However, it is necessary to have a material referring to a normal state of health in the reindeer herds. Such a material was accessible since a number of reindeer killed by the train along the railways during the same years and months as the investigation, were made available for studies according to the same technique as used concerning reindeer killed by predators. This material was placed at my disposal by Dr. Magnus Nordkvist at the National Veterinary Institute in Stockholm. In this material the frequency of classes 2 and 3 together is not more than 13.6%. This proves that the classification is very sharply defined. According to Nordkvist (1964) "Less good condition" means beginning serous atrophy and, consequently, has to be designated as a fairly advanced stage of malnutrition.

Tables 20 and 21 demonstrate the studied specimens with regard to estimated condition and predatory animal species. In Table 22 the material is also divided into different districts and years (page 234, 236, and 238).

Table 21 has a special column for cases of cerebrospinal nematodiasis. This condition is not unusual. The cause of it is considered to be the above-mentioned parasite (Elaphostrongylus). Among 45 reindeer collected during tracking and studied in this respect, seven had the disease, i.e., 16%. If some specimens not killed by predatory animals are disregarded, five of 40 reindeer remain. This gives a percentage of 12.5. For comparison may be mentioned that among 137 reindeer killed by the train or slaughtered by the Lapps and studied by Nordkvist, only two cases of cerebrospinal nematodiasis have been recorded or 1.5%. This really indicates selection. As has been mentioned, animals with this disease have a reduced ability of movement.

Finally, the figures demonstrate a pronounced difference between different years. After a certain reduction in the numbers due to the fact that the early material had not been studied with regard to cerebrospinal nematodiasis the relative number of healthy animals preyed during the winter, 1960/61 and 1961/62 will be 70% and 45%, respectively.

The age distribution among the killed animals as well as in the comprehensive material of data collected in connection with the payment of compensations for animals killed by predatory animals (Table 23) demonstrates a marked difference between the hunts by the lynx and those by the wolverine. The lynx kills mainly younger animals while the wolverine catches middle-aged animals or older (page 238).

However, there is no safe material available for comparison. Thus it is difficult to decide which of the two types of prey is closest to what is normal in reindeer herds. Most likely, the age ratio in a reindeer herd normally falls somewhere between the different age ratios of the groups preferred by the two predators. The fact that the wolverine catches bigger animals may seem surprising since the animal is a poor killer. However, adult reindeer are also heavier. The probable explanation is found above, in the statement that the wolverine more often hunts animals in deep snow where a heavy animal more easily gets stuck than a lighter one.

The figures in Table 23 demonstrate that the lynx as well as the wolverine kills about 75% females and 25% males. It seems probable that these figures are in accordance with the normal sex ratio within the herds. This is a consequence of the slaughter of reindeer carried out by the Lapps.

Both regarding the state of nutrition and the presence of cerebrospinal nematodiasis, the material of slain reindeer shows an incidence

which must be considered much higher than normal in reindeer herds. It is difficult to judge whether this difference is the consequence of a selection during the hunts or whether the predatory animals more often hunt in areas where reindeer are in particularly poor condition (single animals or groups of animals left behind in poor feeding areas during winter migrations).

The strong variations between different years and also between different districts indicate that the last-mentioned opinion could be correct, at least in certain cases. Nevertheless, it is also true that poor health among the reindeer is not a prerequisite for successful hunting. More than 50% of the studied reindeer killed by predators are animals in which nothing remarkable has been noticed.

However, the material of this study distinctly indicates that the lynx as well as the wolverine feeds to considerable extent on prey animals or carcasses of animals of a comparatively low quality. It seems that wolverines in several respects hunt more selectively than do the lynxes.

The fairly limited material of examined roe deer killed by lynxes gives no reason for drawing conclusions concerning selection of the prey. On the other hand the figures indicate difficult feeding conditions for roe deer in North Sweden during the winter. Material for studying selection among small game has not been available.

V. LITTERATURFÖRTECKNING — REFERENCES

Allen, D. R. och Mech, D. 1963. Wolves versus moose on Isle Royal. National Geographic 123: 2, s. 200–219.

Amon, R. 1956. Zur Ausrottungsgeschichte der grossen Raubtiere in den Ostalpen. Zeitschrift für Jagdwissenschaft h. 1 s. 214–15

Anonymus, 1949. Dalajägaren, s. 84.

Borg, K. 1960. Svensk Jakt, h. 11, s. 515–519.

— 1962. Predation on roe deer in Sweden, The journal of wildlife management vol 26, No 2, s. 133–136.

— 1965. Svensk Jakt, h. 5, s. 225–226.

Bourlière, Fr. 1959. Seder och skick i djurvärlden, s. 88, 92 (övers.). Stockholm.

Burkholder, B. L. 1959. Managements of a wolfpack in Alaska. The journal of wildlife management 23: s. 1–11.

Bäck, P. 1867. Sv. Jägarförbundets tidskrift, s. 45.

Chrisler, C. L. 1956. Observations of wolves hunting caribou. Journal of mammalogy, s. 337–346.

— 1960. Vargar (Artic Wild, övers.). Stockholm.

Elsey, C. A. 1954. Journal of mammalogy, 34: 129.
Elton, Ch. och M. Nicholson 1942. The ten year cycle in numbers of the lynx in Canada. The journal of animal ecology, vol. 11, 1942, s. 213–244.
Enoksson, J. W. 1945. Svensk Jakt, h. 2, s. 48.
Espmark, Y. 1966. Tågdöden bland ren, Zool. Revy, h. I, s. 20–31.
Frisendahl, E. 1925. Sv. Jägareförbundets tidskrift, s. 343.
Gashwiler, J. S. 1961. Journal of mammalogy, s. 76–84.
Gavrin, F. W. och Donaurow, S. S. 1954. Vargen i Bialowiezer parken (på ryska), Zoolog. Zhurnal 33 (4) s. 905–924.
Hainard, R. 1948–49. Mammifères sauvages d'Europe, Paris.
Hoppe, St. von 1959. Grossraubwild in polnischer Wildbahn. Wild und Hund s. 147–148.
Klein, D. R., Dufresne och Williams 1959. Track differentiation for censuring bear populations. The journal of wildlife management 23, s. 361–363.
Krott, P. R. 1959. Der Vielfrass. Monographien der Wildsäugetiere XIII, Göttingen.
Laestadius, L. 1832–34. Tidskrift för jägare och naturforskare, s. 146.
Leopold, A. 1943. Wis Conservation Bulletin 8: 1–11.
— 1947 (tills. m L. K. Sowla och D. L. Spencer). A survey of over-populated deer ranges in the United States The journal of wildlife management vol. 11: 2, s. 162–177.
Lindeman, W. 1950. Beobachtungen an wilden und gezähmten Luchsen. Zeitschrift für Tierpsychologie 7, s. 217–240, Berlin.
— 1952. Über den Karpaterluchs. Der Anblick 7, s. 52–53.
— 1955. Jugendentwicklung beim Luchs. Behaviour VIII: 1.
— 1956. Der Luchs und seine Bedeutung im Haushalt der Natur. Kosmos Stuttgart, s. 187–193.
Lingonblad, B. 1952. Något om vargen, lon etc. Arkiv för Svenska Österbotten 10, s. 215–236.
Lönnberg, E. 1930. Lodjurets förekomst i Sverige de sista hundra åren. K. Vetenskapsak. skrifter i natursk. ärenden, nr 14.
— 1931. En järv skjuten i Uppland, Fauna och Flora 26, s. 269.
Munsterhjelm, L. 1931. Några biologiska rön om järven. Från skog och sjö, s. 121.
Murie, A. 1944. The wolves of Mount McKinley U. S. Dep. of the interior, National Park Service, Fauna Series N:o 5.
Mäki, T. 1954. På tal om järven. Finlands Jakt och Fisketidskrift, s. 16.
Naumow, N. P. 1955. Djurvärldens ekologi (på ryska), s. 185.
Nordkvist, M. 1964–66. Personl. medd. (Personl. comm.)
Nordkvist, M., O. Ronéus och O. Nilsson. 1962. Fortsatta undersökningar över cerebrospinal nematodiasis hos ren orsakad av Elaphostrongylus rangiferi. 9th Nordic vet. congress, Copenhagen. Sect. B. n:o 4.
Novikov, G. A. 1956. Lodjur och järv. Mammals of the Fauna of USSR (translated Jerusalem 1962).
Ognew, S. T. 1935. Lodjur och järv. Mammals of USSR and adjacent countries, Moskva (translated Jerusalem 1962).

Palmgren, R. 1920. Högholmens zool. trädgård 1888–1918. Acta Soc., F. Fl., Fenn, 47.

Parowoschtschikow, W. Ja. 1960. Om järvens biologi. Zoolog. Zhurnal 29, s. 1111.

Ronéus O. och M. Nordkvist 1962. Cerebrospinal and muscular nematodiasis (Elaphostrongylus rangiferi) in Swedish reindeer. Acta vet. scand. vol 3, s. 201–225.

Saunders, J. K. 1963. Food habits and movements of the lynx in Newfoundland. The journal of wildlife management vol. 27, n:r 3, s. 384–400.

Siivonen, L. 1948. Structure of short-cyclic fluctuations in numbers of mammals and birds. Papers on game research. Helsingfors.

Teplow, W. P. Zur Ökologie des Vielfrasses im Winter-Bjul. Moscow obsc. Ispyt Prir NS Otdel (enl. Krott).

Valverde J. A. 1957. Notes ecologiques sur le lynx d'espagne. La terre et la vie. Paris, s. 51–67

Vasiliu, G. D. 1964. Über den Luchs der rumänischen Karpaten. Säugetierkundliche Mitteilungen. XII: 4, s. 155–183.

Werner, K. F. 1951. Luchs, Wildkatze und Wiesel. Der Anblick VI: 9.

— 1953. Beiträge zur Freilandsbiologie des südosteuropäischen Luchses. Säugetierkundliche Mitteilungen 1: 3, s. 104–110.

Widahl, S. 1963 (i brev, in letter).

Wright, P. L. och Rauch 1955. Reproduction in the wolverine. Journal of mammalogy vol. 36, s. 348.

Zetterberg, H. 1945. Två fredlösa. Uppsala.

— 1948. Järven. Svenska Djur, Däggdjuren, s. 233–247.

— 1948. Lodjuret. Svenska Djur, Däggdjuren, s. 313–326.

Zuckerman, S. 1952. Proceedings of the Zool. Society of London, vol 122, s. 827.

Author's address: Box 830, Norrtälje, Sweden

Printed August 1966