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THE SEASONAL MIGRATIONS OF A SIBERIAN ROE DEER POPULATION

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Nearly all populations of European Roe deer (*Capreolus capreolus* L.) are sedentary, some individuals migrating seasonally only in deep-snow areas (Cederlund, 1982 ; Danilkin & Minayev, 1988). On the other hand, numerous populations of the Siberian roe (*Capreolus pygargus* Pall.) are migratory and travel each year between their wintering and breeding ranges in spring, and back in autumn. These migrations are known since a long time, but the available information still remains anecdotal, if not conflicting, and the ecology of the migrant populations has never been studied in detail, largely owing to tracking difficulties. Modern biotelemetric techniques allow us to fill this gap in our knowledge of the biology of the Siberian roe.

The observations reported in this paper were made in the Amur Region and Selemdja River Basin in 1986-1991. From 1988 to 1990, numbered collars were put on 14 roe, and radio transmitters fitted on 17 other individuals, at river crossings. Radio tracking from an AN 2 airplane was performed every 1 to 5 days during migration, and 2 or 3 times per month in winter and summer. Visual observations of animals on migration were carried out each year along a 2 km section of the Nora River, 5 km from its month. Use was then made of high amplification and night vision devices, when necessary. Counts were made from an airplane or an helicopter, and from the ground. The authors express their gratitude to fellow zoologists, game specialists, hunters, engineers and pilots, who participated in the work, and helped in many ways.

TIMING AND INITIATION OF THE SEASONAL MIGRATION

The initiation of the autumn roe migration is usually ascribed to a heavy snowfall, and a shortage of food. However, our observations show that most animals in the population under study start migrating each year in September, i.e.

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1 to 1.5 months before the formation of a stable snow cover, when the day temperatures still remain above freezing, and when forage is still abundant in their summer habitat (Table I and II).

The first frost is the most probable « starting signal » for the autumn migration. The first solitary migrants usually appeared at our Nora River observation point in the days following the first frost, mass arrival being observed only 1 or 2 weeks later (Fig. 1), as many roe living east of our observation point have to travel 30 to 100 km to reach it, which takes them 8 to 15 days. Radio tracking shows that some roe leave their summer territories only after the second frost (or a series of frosts), thus generating true « migration waves » (Fig. 1).

TABLE I

Meteorological conditions of the area under study.

Roe zones	Snow cover				Total annual precipitation, mm
	Date formed	Depth (cm)		Date disappears	
		average	max.		
Northern limit of range	Oct. 25	54	69	May 4	781
Summer range	Oct. 25	38 to 43	64 to 67	April 27-29	695 to 707
Limit of winter range	Oct. 31	36 to 38	47 to 48	April 22-25	581 to 606
Winter concentration area	Nov. 1	23 to 29	32 to 35	April 20	502 to 558

Nevertheless, not all the population members migrate in September, before heavy snowfalls. Some individuals begin to migrate only in November, after the formation of a continuous snow cover ; solitary migrants can even be seen till December. Furthermore, several dozen roe remain during the whole of the winter on the southern slopes of some foothills, nearly at the northern limit of the species' range.

Having reached their winter quarters, migrants usually stay there until spring. However, in December 1990-January 1991, 5 roe fitted with transmitters left the winter quarters where they had spent about 2 months to move further West (Table II, Fig. 2). Their migrations coincided with heavy snowfalls, which leads us to infer some cause-and-effect relationship.

The bulk of the spring migration of Siberian roe takes place in late March-early April. Some individuals (N° 1 and 2 on Table II) started moving towards their summer quarters as early as December and January, but most of them, however, do not return to their summer range before April or May.

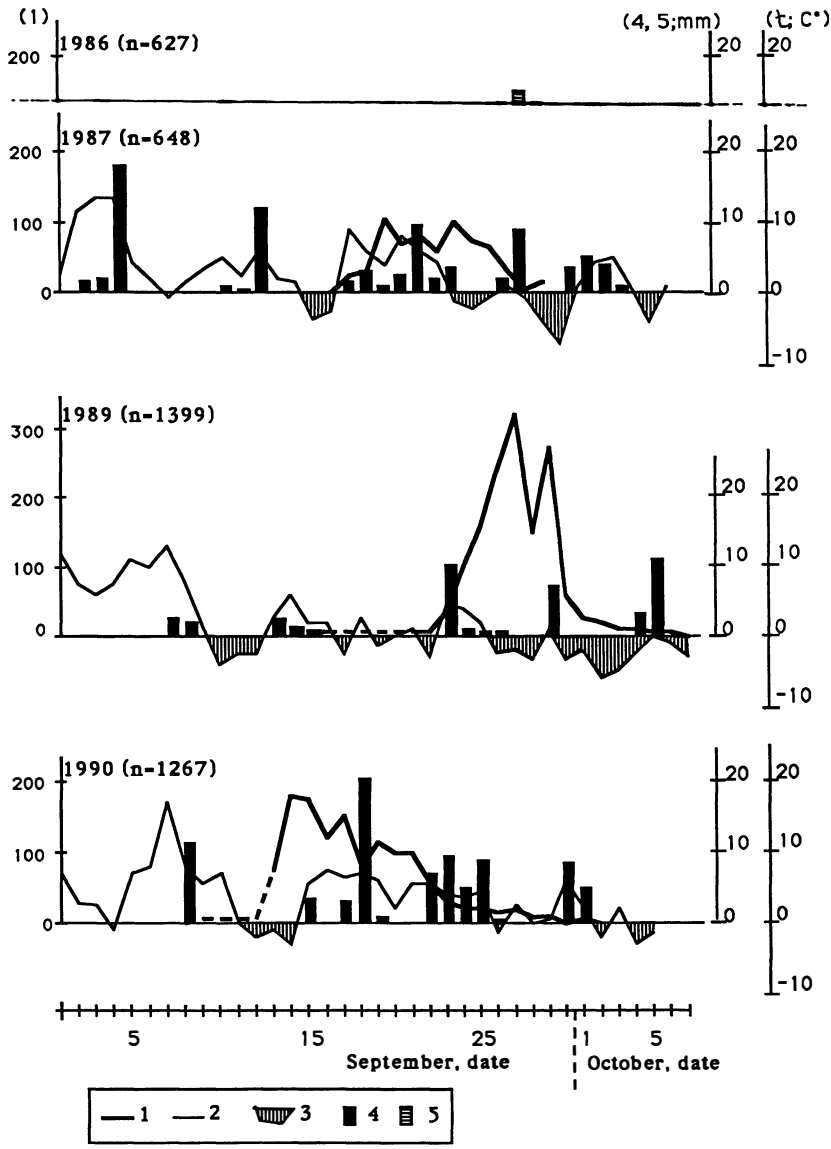

Figure 1. — Siberian roe deer population in different years : Migratory activity and weather conditions : 1, number of migrating roe deer crossing « 2 km river section per day » ; 2, minimum air temperature (°C) ; 3, frost periods ; 4, rain (mm) ; 5, sleet (mm).

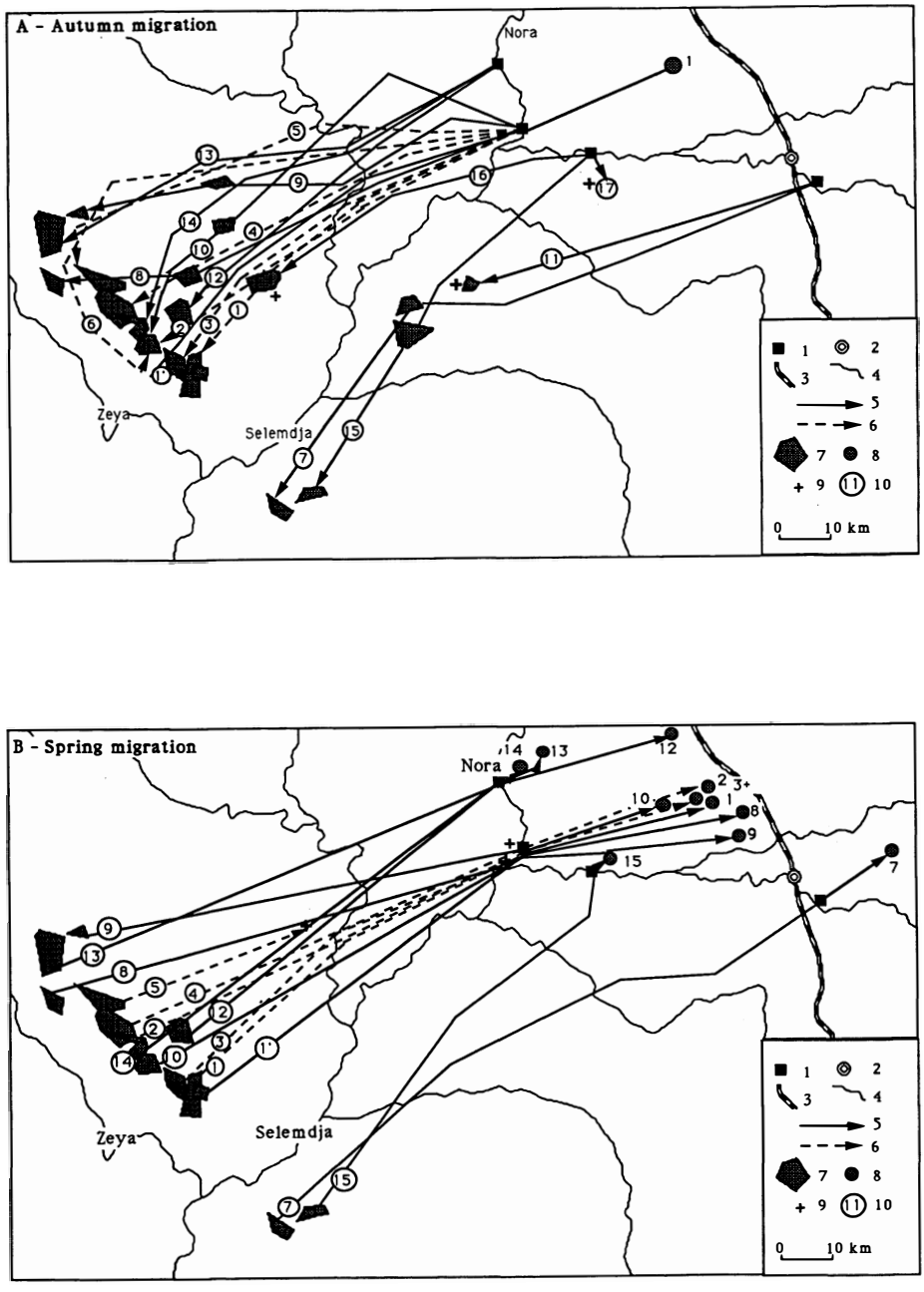

Figure 2. — Seasonal migration routes and home ranges of roe deer equipped with radio transmitters. A, autumn migration ; B, spring migration ; 1, capture and tagging points ; 2, town ; 3, railway ; 4, river ; 5, migration routes of roe deer tagged in September 1990 ; 6, migration routes of roe deer tagged in September 1989 ; 7, winter home ranges ; 8, summer home ranges ; 9, places where mortality was observed ; 10, identification number of roe deer.

ROUTES AND SPEED OF MIGRATION

The migration routes and seasonal ranges of 17 roe fitted with transmitters are shown on figure 2. The adult female 1 (1′) was tracked for 2 years, whereas roe 17 was killed by poachers only 6 days after being radiotagged.

It is obvious that the Siberian roe population summering in the Selemdja River Basin migrates southwestward every autumn, to reach its winter quarters on the left bank of the Zeya River. The width of the migration route is of ca. 100 km. Roe migrate individually, and they travel in the same directions year after year. They cross rivers at the same places, thus displaying strong « social traditions ». For example, we saw roe n° 1 cross the same section of the Nora River on three successive years (September 22, 1989 ; September 14, 1990 ; September 18, 1991), and we also observed at the same place 8 other roe which had been fitted here with radio transmitters or numbered collars in the previous years. In spring, the roe move back, following their autumn routes in the reverse direction.

The length of the migratory routes of radiotagged roe deers is of 108 to 178 km, but individuals living east of the Baikal-Amur railway cover more than 200 km. The average speed of migrating animals during the autumn migration is 6.5 km per day (maximum : 26 km/day) ; in spring the speed is much lower and averages 3.8 km per day. The estimated duration of the autumn migration ranges from 17 to 27 days, and that of the spring migration from 30 to 47 days.

BEHAVIOUR DURING MIGRATION

The number of migrants varies from year to year and depends largely on the size of the population, and on the weather conditions. During the autumn, migration is usually stimulated by the frost and inhibited by warm temperatures. Rain does not stop migration, but snow does ; no migrants were seen during the single snowfall which took place in September 1986 (Fig. 1).

Roe travel at any time of the day, but mostly in the morning. At our observation point, the proportion of individuals crossing the river by night ranged from 11 to 79 % (average : 34 %, Fig. 3). The maximum number of roe crossing the 2 km long river section every day was 318 (Fig. 4), and the total amounted to 1 399 for 16 days, in autumn 1989 (Fig. 1). According to our estimates, from 25 000 to 30 000 roe altogether travel along this migration route. The whole population might even have reached 35 000 to 40 000 head.

As a rule, groups of migrating animals are led by adult females. Most adult males migrate alone or in small groups which originate at river crossings as follows : a number of bucks hesitate to enter water, and stay on the bank for a time, older animals pushing weaker yearlings into water. Others wait for others to enter water first, before darting out of the bushes to join those already swimming. Attempts by « male groups » to cross rivers are not always successful : after swimming for several metres, the leading buck sometimes looks ahead, stops, and lets the following deer overtake him ; then the second buck gives way to the third, etc... Roe can even circle in water for a long time, before returning to the bank.

Mothers often lose their offspring at river crossings, despite numerous vocal contacts. Fawns which drop behind their mothers give loud squeaks and try to join other roe on the bank, but they are driven away. The mother usually waits for

TABLE II. *Individual characteristics of the radio-tagged Siberian roe deer*

Years of tagging	1989	1989	1989	1989	1989	1989	1990	1990	1990	1990	1990	1990	1990	1990	1990	1990	1990
Number, sex and age of radio-tagged roe deer	1 ♀ ad	2 ♂ ad	3 ♂ ad	4 ♀ ad	5 ♀ ad	6 ♂ sad	1′ ♀ ad	7 ♂ ad	8 ♂ ad	9 ♂ ad	10 ♂ sad	11 ♀ sad	12 ♀ sad	13 ♀ ad	14 ♂ sad	15 ♂ ad	16 ♀ ad
Date of tagging	22.09	23.09	23.09	23.09	24.09	25.09	14.09*	15.09	18.09	18.09	19.09	19.09	20.09	20.09	21.09	22.09	22.09
Date of first observation on the winter home range	03.10	12.10	12.10	03.10	03.11	20.10	29.09	29.09	01.10	01.10	03.10	18.10	11.10	11.10	11.10	11.10	03.10
Length of the route from place of tagging (km)	108	122	121	108	140	119	118	106	91	78	124	93	102	129	107	74	87
Average speed (km/day)	9.8	6.4	7.1	10.8	3.5	4.8	7.9	7.6	7.0	6.0	8.9	3.2	4.9	6.1	5.4	3.9	7.9
Maximum speed (km/day)	16	26	12	14	12	6	12	14	12	14	15	13	7	19	11	14	13
Date of first observation on the new winter home range	-	-	-	-	-	-	-	28.12	22.01	28.12	22.01	-	-	-	-	28.12	-
Distance covered to reach the new winter home range	-	-	-	-	-	-	-	57	34	53	41	-	-	-	-	40	-
Area of the winter home range, old and new (ha)	7 500	1 900	6 300	14 400	10 600	-	1 800	2 500 2 500	3 100 2 500	2 500 1 300	3 100 2 500	-	4 400	10 000	3 800	7 500 2 500	5 600
Date of first observation of the return migration	26.01	14.12** 27.03	27.03	27.03	27.03	-	13.04	29.03- 13.04	29.03- 13.04	29.03- 13.04	29.03- 13.04	-	29.03- 13.04	29.03- 13.04	29.03- 13.04	29.03- 13.04	-
Date of first observation at the summer home range	05.05	07.04	05.05	-	-	-	19.04	25.05	30.04	24.04	24.04	-	30.04	06.05	19.04	25.05	-
Distance covered during spring migration (km)	137	138	138	-	-	-	132	178	163	154	126	-	130	128	113	108	-
Average speed (km/day)	1.4	1.7	2.6	4.3	3.5	-	6.3	3.1	5.1	5.9	4.8	-	4.1	3.4	5.4	1.9	-
Maximum speed (km/day)	2.3	4.4	5.1	8.3	-	-	7.0	4.9	7.0	6.5	6.0	-	6.0	5.4	-	3.9	-

* Date of detection at the tagging place ; the migration of roe deer 1′ started on 11.09.1990.

** A two-stage migration was recorded : from 14.12.1989 to 26.01.1990, and from 27.03.1990 to 07.04.1990.

Roe deer 3, 4, 5, 11 and 17 were killed by hunters and roe 16 was killed by a Lynx. Transmitters 2 and 6 were probably damaged.

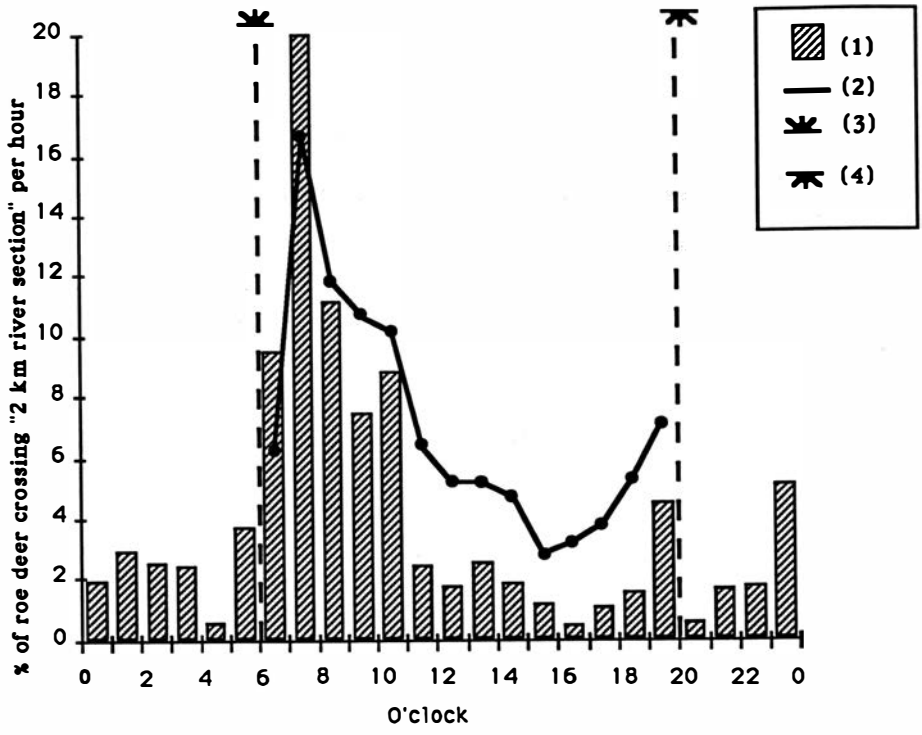

Figure 3. — Daily activity of migrating roe deer. 1, from 5 round-the-clock observations made from September 16 to September 25, 1991 (n = 671) ; 2, from daytime observations in September and October, 1987-1991 (n = 4 580) ; 3, sunrise ; 4, sunset.

her offspring on the opposite bank, answering their squeaks, and sometimes swims back to retreive them. In case of danger, fawns may cross the river on their own. If they do not meet their mother on the opposite side, they swim back, exhausting themselves.

These squeaking, lost fawns, together with the lame and crippled roe closing the migration wave, fall readily prey to predators. As a matter of fact, wolves visited our observation point every year, and, by the end of the mass migration, they even tried to catch the roe waiting on the bank or entering water before our very eyes. The cries of dying victims bore witness to the success of their hunt.

During the autumn migration we often observed roe deer on heat. Bucks chased and tried to mount not only adult and yearling does, but also young females of the year. Such a concentration of migrant animals might well contribute to increase the number of fertilized females, thereby contributing to the reproductive success of the population.

SEX AND AGE STRUCTURE OF THE MIGRATORY POPULATION

Migration is usually initiated by females with fawns, but at the peak of the migration the sex and age ratios of migrant animals every day remain approximately the same as those of the population as a whole (Table III, Fig. 5).

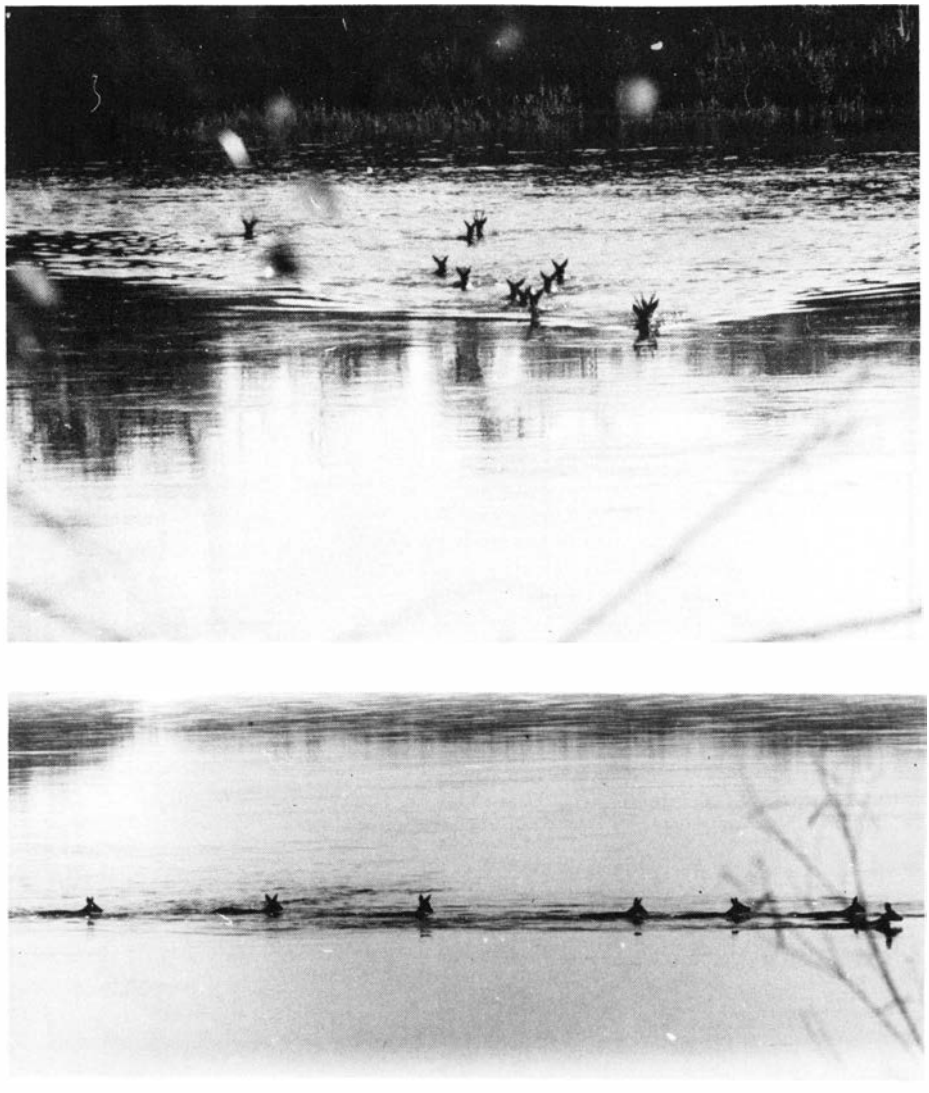

Figure 4a and b. — Migrating Siberian roe deer crossing river.

The bulk of the migratory roe deer population consists of family groups (a mother with one or two, seldom three, fawns) and solitary individuals (mainly adult males and yearling females). Other groups are also observed, made up of one or two family groups, and a few other animals which joined them. It should be noted that some of these groups are composed mostly of adult males which were solitary before the start of the migration, and were then living on small territories actively marked and defended against other males. On September 27, 1989, one of these male groups was composed of 12 adult and 3 yearling males.

TABLE III

Sex and age structure of the population studied.

Years	Males						Females over one year of age		Calves		Total roe
	Adults		Yearlings		Total						
	n	%	n	%	n	%	n	%	n	%	n
1987*	no data				164	25.3	231	35.7	253	39.0	648
1988	no data				69	22.4	118	38.3	121	39.8	308
1989	218	18.7	108	9.3	326	28.0	365	31.4	472	40.6	1 163
1990	197	17.5	129	11.4	326	28.9	398	35.2	405	35.9	1 129
1991	186	18.7	75	7.5	261	26.3	357	36.0	374	37.7	992
Total	601	18.3	312	9.5	1 146	27.0	1 469	34.7	1 625	38.3	4 240

* As reported by V.M. Sapayev and V.A. Voronov

The largest social groups encountered during the autumn migration was made of 17 individuals. Larger herds comprising hundreds of animals can probably be seen in the winter concentration areas, when roe move « en masse » after heavy snowfalls.

In September, 36.9 % to 40.6 % of the population consisted of fawns. Females over one year of age averaged 34.7 %, and males 27.0 % (adult and yearling bucks respectively accounting for 18.3 % and 9.5 %, Table III). The sex ratio of roe over one year of age was on average of 1 male for 1.28 female (1 : 1.41, 1987 ; 1 : 1.71, 1988 ; 1 : 1.12, 1989 ; 1 : 1.22, 1990, and 1 : 1.37, 1991). The sex ratio of fawns was very similar : 1 : 1.3 in 1989 (108 males and 140 females sexed), 1 : 1.24 in 1990 (89 males and 110 females), and 1 : 1.09 in 1991 (112 males and 122 females).

The breeding success of females can be estimated on the basis of the preceding September figures : a female over one year of age raised 1.10 fawn in 1987, 1.03 in 1988, 1.29 in 1989, 1.02 in 1990, and 1.05 in 1991. On average, the adult does (more than 2 years old) raised 1.65 fawns in our population.

THE DETERMINANTS OF MIGRATION IN SIBERIAN ROE DEER

Siberian roe deer follow the same migration routes between their winter and summer quarters year after year. Furthermore they appear to be as « conservative » in their migratory behaviour as in their territorial behaviour. Each year in summer they occupy territories ranging in size from several dozen to several hundred hectares in the same area, and they assemble in winter in one or two areas whose size varies from 1 800 to 14 400 hectares (Table II). During the winters of 1989 and 1990, the density of the population under study reached 70 roe per 1 000 ha in these concentration areas, while it was lower by nearly an order of magnitude outside them.

What attracts roe to their wintering areas, and what distinguishes these areas from their summer territories during the winter ? First of all, it is the thickness of

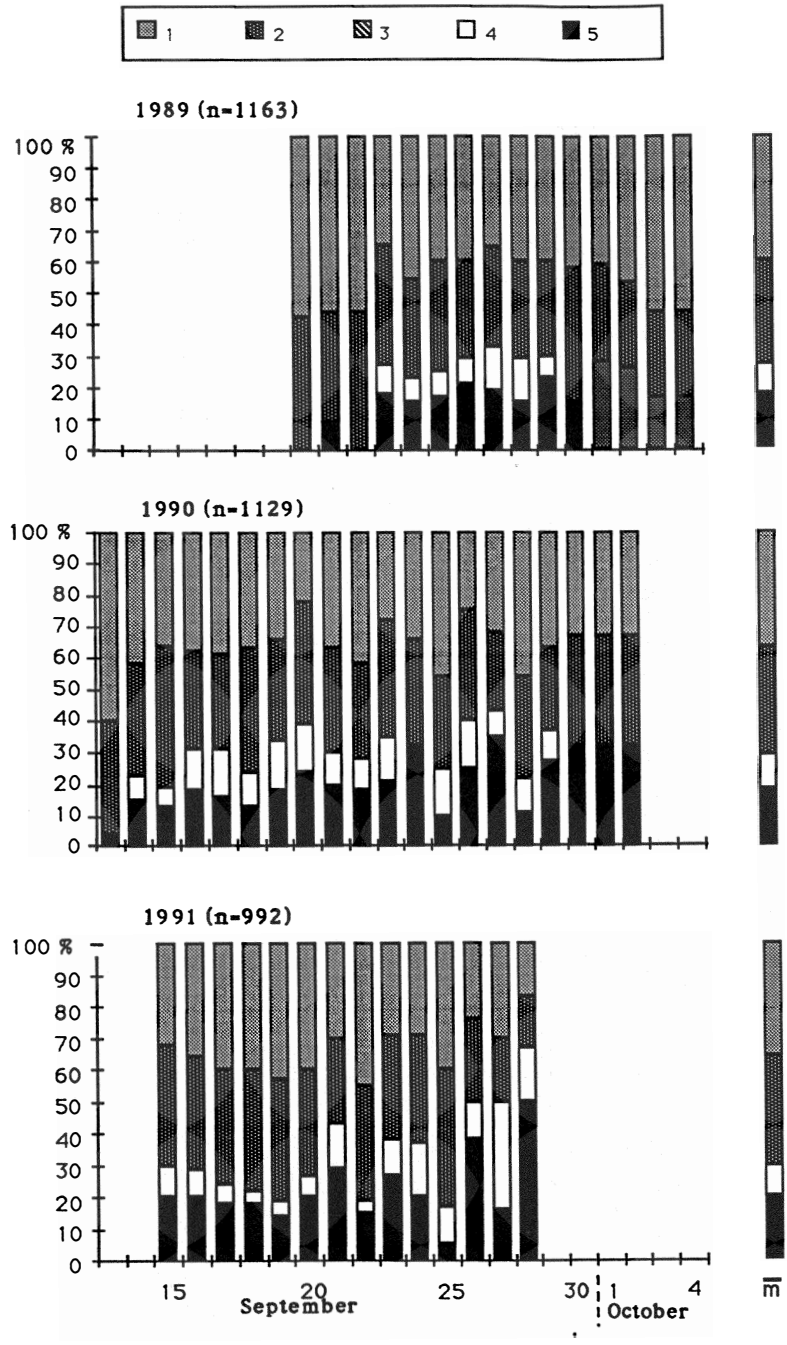

Figure 5. — Sex-age structure of Siberian roe deer population during autumnal migration. 1, juvenile males or females ; 2, subadult or adult females ; 3, subadult or adult males ; 4, subadult males ; 5, adult males.

the snow cover which averages ca. 30 cm in the winter concentration areas, whereas it reaches 40 to 60 cm in the summer ranges, and even more in some years (Table I). Such a deep snow cover would hinder roe locomotion and foraging ; it might even prevent them altogether.

Another feature of the wintering quarters of the roe deer is the abundance of Erman's birches (*Betula ermanii*) in hummocky meadows. The autumn biomass of roe forage (branches and twigs) here reaches 163 kg/ha (wet weight), whereas these shrubs are scarce or lacking in the summer range of the roe deer.

In our opinion, it is the combination of these two factors — a shallow snow cover and the abundance of birch forage — that makes roe concentrate for winter on the left bank of the Zeya River. Another factor contributing to their aggregation is that does are then far less aggressive than normally, since most of them have already borne their offspring at the time of their autumn migration. It is therefore quite likely that autumn migration results from the roes' inability to survive long in deep snow.

The winter concentration areas also harbour resident roe during the summer, at densities quite similar to those of the migrant roe on their summer range (23 and 28 roe per 1 000 ha of foraging range, respectively). Why then do most of the roe leave such areas able to support them the year round, to move for dozens and even hundreds of kilometres, and suffer the hardships of such long journeys ?

As there are no major differences in summer foraging conditions and other environmental parameters, between the winter and summer ranges of our roe deer, their spring return migration can only be explained by the attraction of their traditional breeding grounds.

THE ORIGIN OF ROE DEER MIGRATIONS

On the basis of our findings, one may hypothesize on the origin of seasonal migrations of roe deer. The starting point of our speculations is the sedentary life style and territoriality of roe inhabiting areas enjoying mild winter conditions (Sokolov & Danilkin, 1981 ; Darman, 1986). Such areas could be located in sheltered areas between glaciers, steppes and foothills with shallow snow cover. In such conditions roe populations thrived, leading to strong competition for territories. This, in turn, may have led the younger animals to emigrate during the breeding season. In autumn, some of these emigrants probably came back to their natal territories, to leave them again next spring (Danilkin & Minayev, 1988). Those which returned with their offspring survived, whereas those which tried to settle permanently in their new summer range died out after heavy snowfalls. The information about the best routes to follow was probably transmitted through learning by the offspring, and more and more population members gradually learned to migrate from their summer range to suitable winter quarters and back.

Most probably, it is how migrants were selected, and still are, in Siberian roe deer populations. What is more, selection also favours early autumn migrants, insomuch as late migrants inhabiting deep snow areas are isolated from those with shallower snow cover ; such late migrants are doomed to death when snow falls early in the season.

As seasonal migration is an individual attribute in *Capreolus pygargus,* its pathways are not unidirectional, as in many other migratory species. On the contrary, roe tend to radiate out of their breeding grounds, in different

directions, to converge in autumn towards areas with shallow snow cover, returning to their breeding quarters next spring (Danilkin, 1989).

SUMMARY

The results of long-term studies on the ecology of a migratory population of Siberian roe deer (*Capreolus pygargus* Pall.) inhabiting the Amur Region are presented. In September, at the first frosts and 1 to 1.5 months before permanent snow cover forms, most individuals migrate 100-200 km from their summer territories to winter quarters. They spend the winter within one or two small areas measuring 1 800 to 14 000 ha. For many animals, the return (spring) migration begins in late April and early May. The average speed of this migration is 6.5 km per day in autumn, and 3.8 in spring. The autumn and spring migration routes remain the same year after year. Details are given on the sex and age structure of the population, and on the behaviour of the animals during migration. The possible origin of this behaviour is briefly discussed.

RÉSUMÉ

Les auteurs rapportent les résultats d'une étude à long terme de l'écologie d'une population migratrice de Chevreuil sibérien (*Capreolus pygargus* Pall.) de la région de l'Amur. Dès les premiers froids en septembre, et de 1 à 1,5 mois avant la formation du tapis neigeux, ces chevreuils quittent leurs territoires estivaux pour gagner des quartiers d'hiver situés à 100-200 km de distance. Ils y occupent une ou deux zones d'une superficie allant de 1 800 à 14 000 hectares. Pour la plupart des individus, la migration de printemps ne débute pas avant la fin avril ou le début mai. La vitesse de migration est en moyenne de 6,5 km/jour en automne, et de 3,8 km/jour au printemps. Les trajets migratoires restent les mêmes d'une année sur l'autre. Des détails sont donnés sur la composition par sexes et par âges de la population. Les causes probables de ce comportement migratoire sont brièvement discutées.

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