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STUDIES ON THE EUROPEAN HARE. XXIX.

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Home Range and Degree of Residence of the European Hare

[With 3 Tables & 1 Fig.]

Data on the size of the home range were obtained by means of repeat captures of individually marked hares. With a density of 50 hares to 100 ha the home range extends over an area of approx. 330 ha. The degree of residence of the hare was also investigated and it was found that this depends on, *inter alia*, whether the given population lives in an undisturbed state of whether it is subject to serious disturbance of its numbers and structure due to shoots. Settled residence is greater in the first case than in the second. Hares transferred ot other districts exhibit a greater tendency to migrate, but only a relatively small number return to the place in which they previously lived even when this is only a few or several km away. The effect of introduction is increased when transferred hares are kept in an acclimatization enclosure.

I. INTRODUCTION

There is a lack of information on the different aspects of the spatial structure of populations in what we know today about the hare. Apart from the studies by Pielowski (1966) and Jezierski (1968), which in any case discuss only certain aspects of the problem of spatial organization, there are practically no comprehensive publications on this subject. This deficiency is particularly marked when considered in the light of the comprehensive studies which have been made of other species of mammals, especially of small rodents.

The Research Station of the Polish Hunting Association at Czempiń has carried out individual marking of hares for several years in connection with the complex studies made of the hare. These studies have resulted *inter alia* in providing data on the size of the hare's home range and the degree to which it is resident.

Use of hare populations for game purposes can form a factor seriously disturbing intrapopulation relations, and particularly spatial structure (Andrzejewski & Pielowski, 1957). Investigation of the effect of shooting on different elements of the population structure is thus a question of prime practical importance. Shooting not only affects numbers directly by reducing them but also indirectly by causing disturbances in the population structure.

II. STUDY AREA AND METHODS

Individual marking of large numbers of hares was carried out over the area of a field shoot 15000 ha in size situated in the west of Poland, in the Poznan voivodship (a detailed description of the area is given by Pielowski, 1968) Density of the hare population studied has varied of recent years around 50 individuals per 100 ha in the late autumn period. Hares were obtained only by catching them in nets. The average amount of hares obtained annually formed about 30% of the total numbers.

The capture method has been described by Pielowski (1969) and consists in enclosing an area of about 100 ha with nets and catching the hares inside this area. Definition of the distance between different captures of given individuals is accurate up to 1 km, which is equal to the average diameter of the area surrounded by nets. Spatial planning of catches provides a sufficient guarantee that the great majority of hares in a given population will have been included in the studies within a few years.

Every year about 35% of the individuals in a population pass through the researcher's hands and 5% of these animals return to the area. These are hares which had been marked in previous years or newly-tagged individuals (N=300—400 animals annually). Hares intended for release again, together with these caught for the first time, are given ear-tags with consecutive numbers. All data on dates and places of successive captures are entered on the ear-tagging cards of the individuals marked.

Studies on the degree of residence of the hare were carried out in three different variants of the experiment, corresponding to the system of hare management currently in force in Poland: (1) in an area covered by shooting operations, (2) in an area not shot over in a given year and (3) in an area not shot over and where hares were introduced. In the first variant the marked hares were released on the capture site, on which as the result of captures the density of the hare population was reduced by about 50%. In the second variant all the hares caught were given ear-tags and released again on the same site. In the third variant hares caught in different peripheral places in the experimental capture area were released on a central site situated at a distance of 4 to 12 km from the capture site. The hares were released in an enclosed area 21 ha in size. Although the wire-netting fencing 150 cm high did not form an insurmountable obstacle, yet it made it difficult for the hares to escape. In all cases the hares were released on the day following capture.

In order to obtain data on the way in which hares disperse over the area numerous direct observations were made at different times of the year, including all visually marked individuals. Two kinds of observations were made: (1) ob-

servations of the behaviour of undisturbed hares, recording the distances they covered and paying attention to the size of the area over which they moved. In all during a total period of 200 hours of observation at different times of the day and year data were obtained relating to about 350 individuals. (2) hares started up by humans or dogs were observed and the distance they covered in escaping estimated. Of the numerous observations of this type made it proved possible to trace the whole escape route only in 85 cases.

III. ATTEMPTS AT ESTIMATING THE SIZE OF THE HOME RANGE

Direct observations show that the area actively occupied by a hare is relatively small and extends over less than 20 hectares. In this area there are one or more currently occupied forms and a feeding ground. An undisturbed hare emerges in the evening and makes its way to the feeding ground and remains there until the early morning. It then moves to one of its forms and remains lying there for the rest of the day. An

Table 1

Length of escape routes of hares started up from hollows (distance from hollow to furthest point of route — measured in straight line).

N	Distance in km					
	0.5	1.0	1.5	2.0	2.5	$\bar{x} \pm SD$
85	15	54	8	2	6	1.09±0.02

area defined in this way also contains the place where the young are born and reared. During the oestrus the hares' activity is greater than at any other time in the year. Groups of males usually race about over a small area, probably the area occupied by the female in oestrus.

The area over which the hare moves is, however, far larger, this being primarily connected with the fact that the hare seeks safety in escape when in danger. Observations established the fact that during the period when the fields are almost bare of vegetation (October-April) the distance from starting point to the furthest point in its line of escape does not on an average exceed 1 km (Table 1). These lines of escape are usually loop-shaped. When alarmed the hare usually runs off in an almost straight line, then changes direction to describe a loop and finally returns to the area from which it was started up. Such escape routes are not completely devoid of direction, as each hare has its own preferred route. Nevertheless they run in different directions depending on the lie of the land, the direction from which danger approaches *etc.* Such escape routes define, as it were, the boundaries of the home range

covered by each individual. If we assume that the home range is circular in shape, then with a radius of average length of 1090 m we obtain an area about 350 ha in size.

Data on the sites of capture of hares repeatedly caught during the study period were used to estimate the size of the home range. Calculation was made of the size of a circular area covering in all successive movements of the hare for 45 such individuals. This value was established by noting the various places on which a given hare was caught on

Table 2

Size of the hare's home range (defined on basis of several repeat captures).

Sex	N	Radius of circle embracing different capture sites, km						Home range,
		0.5	1.0	1.5	2.0	2.5	$\bar{x} \pm SD$	ha
♂♂	17	7	7	1	1	1	0.97±0.48	295
♀♀	28	9	13	1	3	2	1.07±0.35	360
Total	45	16	20	2	4	3	1.03±0.28	333

a map scale of 1 : 25000 and then drawing a circle on it, taking in all the sites. The length of the radius of this circle was used for calculating πr^2. Length of radius only was established for certain individuals. Average area was calculated on the basis of average length of radius of all the cases examined. The average value of the hare's home range assessed in this way was 333 ha. The fact is remarkable here that the home range of males is smaller that than of females (Table 2).

Thus very similar results on the size of the home range were obtained by two different means.

IV. DEGREE OF RESIDENCE

It might be assumed that, depending on the kind of quantitative situation created by man, the spatial structure of the population, and consequently the degree of residence of different hares, must undergo certain changes. In the first variant of the experiment marked hares were released on the capture size in an area in which the density of hares had been abruptly reduced by about 50%. Hares released in this situation exhibited a far greater tendency to settle in the new place and abandon the place in which they had hitherto lived. Only 54% remained on the spot, 19% moved 1 km away, which in the light of the discussion on the home range can be considered as migration within the limits of this

range. The remaining individuals settled in new placed from 2 to 7 km away (Fig. 1). It is permissible to speak of settling in a new place here, as the animals were not again investigated until the following netting season. The actual number of individuals which emigrated to a distance

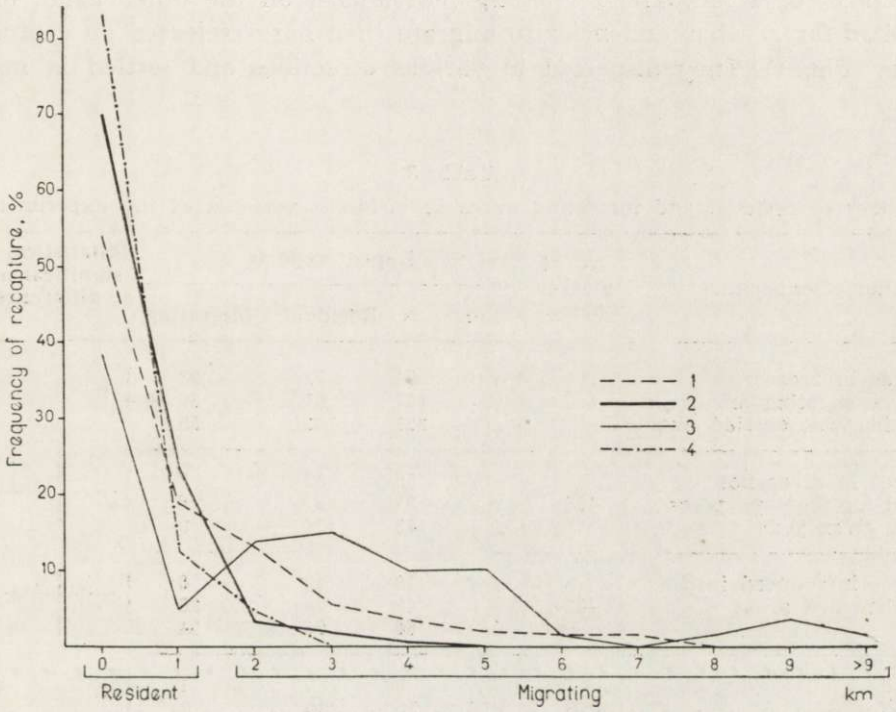

Fig. 1. Degree of residence of hares, established on basis of repeat captures of marked individuals — in per cents.
1 — in areas where shooting or netting was carried out, 2 — in areas not used for these purposes in a given year, 3 — hares introduced into undisturbed area, 4 — hares in first year of life.

of several kilometres was perhaps even larger, since some of them most certainly went beyond the boundary of the study area, which was almost rectangular, with sides 17×9 km, and consequently these animals evaded further investigations.

In the second variant hares were marked in an area not used for shooting purposes in the given year, and consequently the disturbances of population numbers usually caused by shooting did not occur and disturbances in the spatial structure were lesser than in the first variant. The degree of residence proved to be far greater under these conditions. 70% of repeat captures originate from the same place and a further

24% from distances less than 2 km. Only 6% of the hares dispersed over distances up to 4 km (Fig. 1).

The third variant of the experiment was the counterpart of introduction of hares. Only 38% of the transferred individuals settled in the place on which they were released. A further 5% remained within distances of 1 km. The remaining individuals, on the other hand, exhibited far greater tendencies to migrate than hares released on capture sites (Fig. 1). They dispersed in various directions and settled in new

Table 3

Number of resident and migrating hares in different variants of the experiment.

Kind of experiment	No of marked hares	Repeat reports				Statistical significance of differences	
		Sex	N	Resident	Migrating		
Hares in areas where shooting or netting was carried out	615	♂♂	94	71	23	+	
		♀♀	127	91	36		
		Σ	221	162	59		
Hares in areas not used for these purposes in a given year	408	♂♂	56	53	3	+	++
		♀♀	87	81	6		
		Σ	143	134	9		
Hares introduced into undisturbed areas	182	♂♂	18	12	6	++	++
		♀♀	42	14	28		
		Σ	60	26	34		
Hares in first year of life	948	♂♂	8	7	1	+	
		♀♀	16	16	0		
		Σ	24	23	1		

+ — differences statistically non-significant, ++ — differences statistically significant with confidence interval of 0.01.

places from 2 to 14 km away. While in the other variants of the experiment dispersal of the hares took place according to a regular gradient — the further from the site of release the fewer the reports of captures, in the case of transfers up to a distance of 5 km the number of migrants was maintained on a more or less uniform level. Only 6 individuals were found to return to the first capture site.

A certain amount of data were obtained on the degree of residence of young hares marked during the first few day of life and then caught as adults during the winter capture period (P i e l o w s k i, 1971). It was established that as many as 83% of these hares remain in the place of their birth up to the winter period and the others did not move

more than 1 km away (Fig. 1). The relevant data are unfortunately few in number, although more than 900 young hares were marked. With the enormous natural reduction in this age class (Petrusewicz, 1970) only a relatively small number of young hares have any chance of surviving until their first winter, and only a certain percentage of these is caught.

In all the variants of the experiment females exhibited a greater tendency to migration, but it was only when hares were introduced that the differences between females and males proved to be significant (Table 3).

V. DISCUSSION

It must be emphasised that the reports obtained on the size of the hare's home range form the first, and as yet very far from exact, material on this subject. Neither the quality and quantity of the data available on different individuals would appear to be sufficient for carrying out a detailed analysis or for applying the various ways known in literature of elaborating this question. The results obtained, however, serve to define more accurately the only mention encountered in scientific literature of the size of the hare's home range, namely Rieck (1963) considers that this home range (Wohnbezirk) does not as a rule exceed 500 ha. The author bases his opinion on the fact that 85% of the hares marked by him were caught later at distances of up to 3 km from the site on which they were marked.

A significant new addition to our knowledge of the hare, contributed by the present study, would seem to be the finding that the home range occupied by a given individual during the lifetime is divided into the large area covered by its movements and several clearly defined areas, far smaller in size and occupied periodically, situated within the boundaries of the whole home range. The specific properties of the biology of the species sets the pattern for this form of spatial utilization of its home range, a very large part of which serves solely for safety purposes.

It may be assumed that the size of the hare's home range — as in the case of many animals — depends on density. In the study population the density of hares living in the area was considerable, but with a greater degree of dispersal home ranges are probably larger. The mechanism regulating the size of the hare's home range, which is the resultant of the length of effective escape routes, may be as follows: the greater the hares' density, the better the safety conditions for the various individuals. A hare escaping from a pursuing dog seizes the advantages offered by the fact that new hares are continually started up and so

distract the pursuer's attention, cause it to mistake trails and thus draw off the dog to chase after them. The escape routes of different individuals do not therefore have to be very long. When, however, there are few hares the predator persistently chases the same prey, obliging it to run greater distances to escape and therefore the area covered by the hare will under such circumstances be very large.

The data obtained on the size of the home range and its specific properties made it possible to consider the question of the degree of a hare s settled residence in greater detail. They formed grounds for accepting the assumption that movements over a distance of less then 2 km are not migrations but a change in the place of residence within the boundaries of the home range. In the first and second variant of the experiment significantly differing results were obtained. When the spatial system oi a population is greatly disturbed by man hares exhibit a greater tendency to change their place of stay. The objection may be made here that hares caught in nets suffered in additional a serious shock (stress) which might have affected their later behaviour. All the marked hares in an area, however, where there had been no reduction in numbers, were subjected to the same manipulations, yet great majority of them remained in the original place. The significance of the difference confirmed statistically between the two distributions (see Tab. 3) permits of stating that disturbances in the spatial system of a population caused by its being used for shooting form the cause of the intensified tendency for the hares to move away permanently to another place several kilometers distant. The conclusion can be drawn from this fact that it is primarily population relations which determine the degree of residence of a hare, and not environment conditions or attachment to a given place.

Migrations of hares caused by their transfer away form a completely different phenomenon from the qualitative aspect. J e z i e r s k i (1967) considers that in this case the »homing instinct« is aroused in hares, expressed in a tendency to migration in a particular direction to a given destination, appearing as a return to the place in which it had previously lived. The studies made by J e z i e r s k i (1968) led him to state that one of the basic factors conditioning the effectiveness of introducing hares is the density of the population into which the hares are released. In that author's opinion density above which introduction has little chance of being successful is approx. 15 hares per 100 ha. With greater density, after one year only a negligible percentage of the transferred hares remain in the place to which they were introduced. J e z i e r s k i (1968) explains this phenomenon convinicingly by, *inter alia,* the difficulties in fitting the introduced individuals into the spatial structure of the local population.

Transfer of hares from one place to another, which forms the subject of the present study, however, produced a result of 43% of settled introduced individuals near the place in which they had been released, despite the fact that the local hare population was very numerous there — after captures there were about 35 hares per 100 ha. Successful introduction may have depended on the transfer technique (cf. Jezierski's recommendations, 1969). After transporting the hares to the new place they were not directly released on to the open shoot, but placed in an acclimatization enclosure which they gradually left over a period of several weeks. In the meantime they recovered from any possible shock caused by their being caught and kept in transport cages. Presumably their »homing instinct« was also upset, which facilitated their settlement in a new place. About 28% of the transferred hares exhibited marked migratory tendencies and settled again at distances over 3 km.

These data correspond closely with the results of studies by Szederjei (1959), who in his introductions of hares obtained 24% of repeat reports at distances of over 3 km from the place of release. This author does not, however, give the density of the local populations into which the transferred individuals were transferred, neither does he describe the study methods used. Szederjei (1959) also marked small hares and then collected data on the individuals shot during shoots. On these grounds he reached the conclusion that these hares exhibit the greatest degree of residence, and this view is fully confirmed by the results of the present study.

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AREAŁ OSOBNICZY I STOPIEŃ OSIADŁOŚCI ZAJĄCA

Streszczenie

Drogą powtórnych złowień zajęcy znakowanych indywidualnie uzyskano dane dotyczące wielkości areału osobniczego i stopnia osiadłości u tego gatunku. Każdej zimy, przy intensywnych odłowach w sieci podlegało kontroli ca 35% osobników badanej populacji, przy czym 5% wypuszczano z powrotem do łowiska. Były to zające już znakowane w latach ubiegłych lub też świeżo zakolczykowane (N = 300—400 sztuk rocznie). Zającom tym zakładano numerowe kolczyki. Stosowana metoda odłowów pozwala określić odległości ewentualnych przemieszczeń zajęcy w odcinkach nie mniejszych niż 1 km.

Dzięki wielokrotnemu złowieniu zajęcy w ciągu kilku lat oraz na podstawie licznych obserwacji terenowych spróbowano ocenić wielkość areału osobniczego zająca. Stwierdzono, że obszar terenu aktywnie zajmowanego przez zająca wynosi tylko kilkanaście hektarów. Znacznie większy natomiast jest areał penetracji każdego osobnika. Wielkość jego oszacowanego dwiema metodami — długością tras ucieczek przed niebezpieczeństwem (Tab. 1) oraz miejscami powtórnych złowień pewnej liczby zajęcy (Tab. 2). Wielkość areału osobniczego oceniono na ca 350 ha.

Wyniki badań pozwalają również wysunąć przypuszczenie, że areał osobniczy zająca składa się z dużego areału penetracji i kilku znacznie mniejszych, zajmowano okresowo ścisłych rewirów, znajdujących się w jego obrębie. Specyfika biologii gatunku uwarunkowuje taką formę przestrzennego wykorzystania areału osobniczego. Ogromna jego część służy wyłącznie sprawom bezpieczeństwa.

Stopień osiadłości badano w trzech różnych wariantach eksperymentalnych, odpowiadających aktualnemu w Polsce systemowi gospodarowania pogłowiem zajęcy. W pierwszym wariancie znakowane zające wypuszczano w miejscu złowienia z tym, że liczebność i struktura populacji była tam naruszona zabieraniem drogą odłowów 50% osobników. Stwierdzono, że pozostałe po odłowach zające wykazują znaczną skłonność przemieszczenia się i 27% osiedliło się na nowo w odległości od 2 do 7 km (Tab. 3).

W wariancie drugim znakowano zające na terenie nie objętym w danym roku użytkowaniem łowieckim. Nie było tam więc zaburzeń w układzie przestrzennym populacji a stopień osiadłości okazał się znacznie większy. Tylko 6% zajęcy rozeszło się na odległość powyżej 2 km.

W trzecim wariancie przesiedlono zajęcy na odległość kilku do kilkunastu km. Przez stosowanie zagrody aklimatyzacyjnej uzyskano lepszy efekt tego zabiegu bowiem 43% introdukowanych zajęcy osiedliło się w pobliżu miejsca wypuszczenia. Pozostałe natomiast wykazały znacznie większą tendencję migracyjną niż zające nieprzesiedlone.

Najbardziej osiadłe okazały się zające w pierwszym roku życia. Aż 83% zajęcy znakowanych w pierwszych dniach życia, pozostało do okresu zimowego w pobliżu miejsca urodzenia, a pozostałe oddaliły się nie dalej niż 1 km (Fig. 1).