ACTA THERIOLOGICA

VOL. XIII, 1: 1—30. BIAŁOWIEŻA 15.III.1968

STUDIES ON THE EUROPEAN HARE XV.

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Some Ecological Aspects of Introduction of the European Hare

[With 8 Figs. & 11 Tables]

Large groups of European hares (from 400 to 1400 individuals in number, depending on the size of the area), were introduced into three areas differing as to the density of the local hare population and quality of the habitat. The hares introduced were marked so that they could be distinguished from individuals belonging to the local population. Observations made by means of the assessment belt method and captures of the animals for checking showed that the introduced hares disappear from the settled areas to a greater degree than would appear to be the case with normal interchange of individuals in a population. The intensity and rate of this process is greater where the local population is more numerous, but it does not seem to depend on habitat conditions. The hares introduced occupy a relatively smaller percentage of the crops preferred by the local population. The distribution in space of the hares takes the form of concentrations. It was not found that the numbers of the populations examined were increased as a result of the introduction of other hares.

I. INTRODUCTION

Ecological studies on game animals possess that particular aspect which usually characterises studies on objects of use to man, that is, the dual character of such studies, theoretical and practical. The purpose of the present studies was similar —

on one hand they were aimed at comparing, under natural conditions, some of the results obtained by laboratory experiments, and on the other they were intended as a preliminary attempt at scientific assessment of the method in general use in game management of increasing the hare population by introducing new individuals.

The introduction of new individuals into populations living in a given area is not in itself an artificial phenomenon from the nature point of view, since the continuity of any population is only possible by means of the constant addition to it of new individuals of the same species. This is effected primarily by the entry of young individuals born from individuals of the local population. It is also known, however, that interchange of adult individuals takes place in vertebrate populations by means of migration and therefore processes of entry and settlement also exist (Rall, 1936; Naumov, 1956, 1961; Allee *et al.*, 1958; Andrzejewski & Wierzbowska, 1961; Andrzejewski & Wrocławek, 1962; Andrzejewski, 1963; Odum, 1963; Petrusewicz, 1965, and others. If therefore the phenomenon of natural introduction of new individuals takes place in nature, experimental introduction should make it possible to define the factors governing the course of this phenomenon and its effect on the population. It would therefore appear useful to present some of the opinions held on this subject.

The entry of new individuals evokes the reaction of resistance on the part of the population, which may prove disadvantageous to them not only directly in the physical sense, *e.g.* as the result of intensive fighting in which the newcomers lose (Andrzejewski *et al.*, 1963) but also on account of the fact that these animals may be subjected to more powerful and lasting effects of stress (Christian, 1960). Soldatova (1962) draws attention to the results of resistance from the population towards newcomers in her discussion of the way in which *Citellus pygmaeus* (Pallas, 1778) occupies an area in cases of high population density of this species. Adamczyk & Ryszkowski (1965) also demonstrated that a greater percentage of individuals introduced into an empty area settle there than those introduced into an area occupied by a population of the same species. They also showed that individuals introduced into an occupied area disappear from it more quickly than from an empty area, and also that in the first case they disappear earlier than local individuals. It must however be added that it is difficult to say whether such a situation is typical. Andrzejewski (1963) in examining the processes of incoming, settlement and disappearance of small rodents, found that the number of animals entering and settling is in proportion to the number of resident animals.

This situation of course involves further consequences to the individuals introduced. Andrzejewski *et al.* (1963) draw attention to the high mortality rate of introduced individuals, as did Adamczyk & Ryszkowski (1965) who also showed that introduced animals are characterised by smaller reproductivity, considerable activity and a lesser degree of attachment to a given place. This latter characteristic points to the tendency of introduced animals to migration and in this connection it must be remembered that the generally unfavourable situation of a migrant and its reduced chances of survival as the result of poorer knowledge of the area, greater exposure to predators etc. are well known (Andrzejewski & Wrocławek, 1961; Pielowski, 1962; Petrusewicz, 1965). Andrzejewski *et al.* (1963) showed that introduced individuals which succeeded in integrating themselves with the local population occupy the lowest places in the social hierarchy of the population. All this of course applies for as long as the

individual continues to retain the character of an introduced individual. After a certain time the introduced individual becomes integrated with the population and it is then that its advance within the social structure of the population becomes possible (W a l k o w a, 1964).

Attention must next be drawn to the directions in which introduction may affect a population into which it takes place. This problem is directly connected with a question of considerable economic importance to game management, that is, increase in population numbers forming the result of man's intentional efforts.

In populations in which changes in the composition of individuals are of defined intensity and thus in which there is a certain constant or only slightly variable level of interchange between individuals, it would seem that the ecological organisation is also of a relative stable character. This stability may be disturbed by a change in intensity of interchange between individuals in the population, causing as a result reconstruction of the population organisation and in consequence, variations in population numbers. A change in the intensity of individual interchange may also evoke in the population the phenomenon of conservative counteraction to the changes in the existing organisation.

When considering introduction problems from this aspect it must be emphasised that the effect of introduction on a local population may be expressed not only by an immediate increase in the numbers of this population to the extent of the number of individuals introduced or by their reproduction during the period directly subsequent to introduction. This latter, in the light of the studies made by A d a m c z y k & R y s z k o w s k i (1965) would in fact appear to be of very little importance in certain cases, particularly when introduction takes place into areas already occupied by a population of the same species. Introduction may also have an inducing effect on variations in numbers of the local population as the result of disturbing its population structure (P e t r u s e w i c z, 1963). It would not appear, however, that such disturbance is lasting in character, since as shown by the investigation made by A n d r z e j e w s k i *et al.* (1963) after a certain time the introduced individuals occupy the lowest places in the hierarchic structure of the population while the basic system of relations between local individuals determining that structure, remains unchanged. It is possible however that the introduction of a sufficiently large group of individuals is capable of causing the threshold of the population's resistance to a change in its organisation to be crossed. In such cases this organisation may undergo far-reaching reconstruction or dissolution, which as a result leads to the creation of a new model of organisation. Support for this hypothesis is provided by the fact that A n d r z e j e w s k i *et al.* (1963) found a decrease in the number of fights per one introduced individual with an increase in the ratio of introduced to local individuals in favour of the former. It is possible that with the introduction of so large a group of individuals, in this case also their lot may be different from that presented previously.

The choice made of time of introduction is also of importance to the course taken by introduction. P e t r u s e w i c z (1963) found that intensity of increase caused by introduction may vary depending on the phase of the population's life and its general predisposition to growth at the time of introduction. A n d r z e j e w s k i (1963), on the other hand, showed that intensity of settlement in relation to the numbers of resident individuals is, in the case of small forest rodents, low during the winter months, then increases to attain a peak in the autumn months.

In game management practice introduction of fresh animals has long since been used as a breeding practice. The first records on this subject refer to pheasants

introduced for game purposes by Charlemagne about 800 A.D. In the 16th and 17th century resettlement of game was relatively often carried out, although this applied only to the »noble« species — European bison, elk, fallow deer, wild goat, bear, wild cat, beaver (Bieger, 1941; Niethammer, 1963). This method became common practice in the 19th century, particularly in relation to red deer, pheasants and hares (Thungen, 1911; Bieger, 1941; Niethammer, 1963), and what is more it is still held to be highly effective. Many authors express their conviction as to its effectiveness in relation to the hare (Thungen, 1911; Bieger, 1941; Berger, 1944; Kokeš, 1948; Szczepkowski, 1951; Budzyński, 1953; Tilgner, 1954a; Szederjei, 1958 and others). It is perhaps worthy of note that this conviction generally shared by practical sportmen has resulted in several hundred thousand hares being introduced in Europe every year, at great expense, but the scientific basis of these operations is very shaky.

II. DESCRIPTION OF THE STUDY AREA

Three areas with different habitat conditions and different density of the local population were chosen for the purposes of these studies. The principle observed was that poorer habitat conditions occurred together with a decrease in population density. Population numbers and habitat conditions were arranged in this gradient in order to facilitate analysis of the effect of these two factors on the course of introduction.

The areas chosen were three game areas: (1) »Brody«, in the Nowy Tomyśl district of the Poznań province, 6.947 ha in area, (2) »Lutom«, in the Międzychód district of the Poznań province, 7.535 ha in area, (3) »Sokółka«, in the Sokółka district of the Białystok province, 28.960 ha in area (Fig. 1—3).

Details of the soil conditions of these areas were given in the studies by Lencewicz & Kondracki (1952), Krygowski (1961) and the Institute of Soil Science, Cultivation and Fertilization (1961). The basic agricultural characteristics can be summed up as follows:

Cultivated soils of II—IV bonitation class predominate in the Brody area, belonging mainly to large farms, intensively cultivated and on a relatively high level of agro-technical operations. Crops of the wheat-beet type.

Soils of the III—IV bonitation class predominate in the Lutom district, the great majority being private farms of medium size. A small part of the area consists of waste land and degraded pasture (about 2%). The area is moderately intensively cultivated, the agrotechnical operations on the whole thorough. Crops of the rye-potato type.

Soils of the III—IV bonitation class predominate in the Sokółka area, which consists almost entirely of small private farms. Waste land and degraded pasture occupies a considerable part (about 23%) of the area. Cultivation is not very intensive, agrotechnical operations somewhat primitive. Crops of the rye-potato type.

III. METHODS AND MATERIAL

The studies consisted of three main stages: (1) pre-experimental inspection, (2) introduction and (3) inspection after introduction.

(1) Routes were marked out (Fig. 1—3) in the first stage, along which an estimate was twice made of local population numbers, using the assessment belt

method, during the last 70 days before introduction. Certain modifications were made to the assessment belt method (Jezierski & Pielowski, 1958; Pielowski, 1966), as the result of experience gained over the period of several years of making studies, and also the methodical requirements of the studies described.

Belt assessment was carried out in the following way. Four people (an assessor + 3 assistants) walked along a belt 50 m wide in such a way that the two people on the outside marked out the breadth of the belt and the other two walked

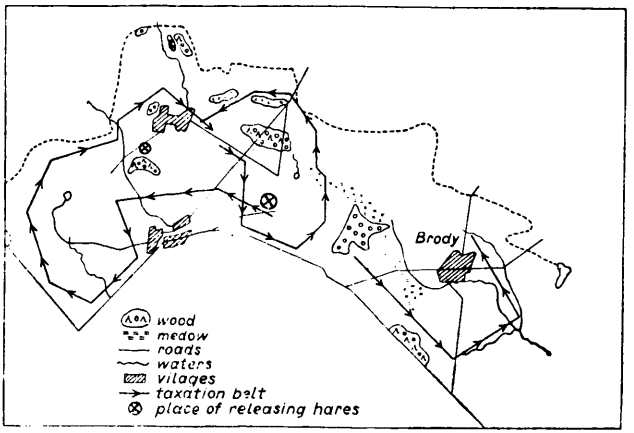

Fig. 1. Plan of the Brody experimental area.

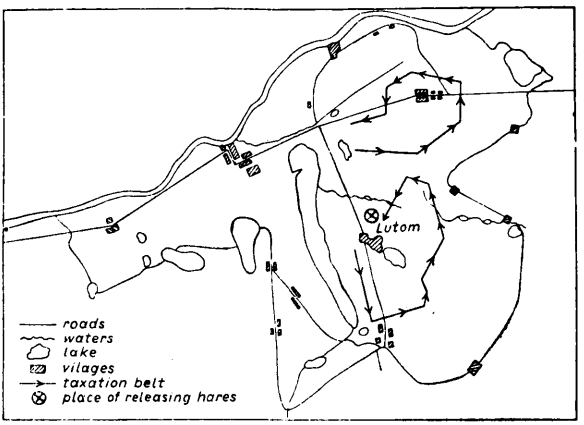

Fig. 2. Plan of the Lutom experimental area.

between them at even intervals of about 16.5 m. The assessor recorded in his report all the hares started up, keeping those starting up from the belt and those from outside the belt separate. The following details were noted for each hare: exact time at which it started up, distance from the line of assessors and kind of crop from which it started up. By multiplying the length of the belt by its breadth an area is obtained to which the hares observed in the belt can be related and the density per unit of area calculated. Belt assessment was used only from

September to April, as during the remaining months the crops make it impossible to use this method.

It was shown in the studies by Pielowski (1966) and Jezierski (in preparation) that belt assessment exhibits a tendency to registering a larger number of hares during the winter months, December, January, February and sometimes

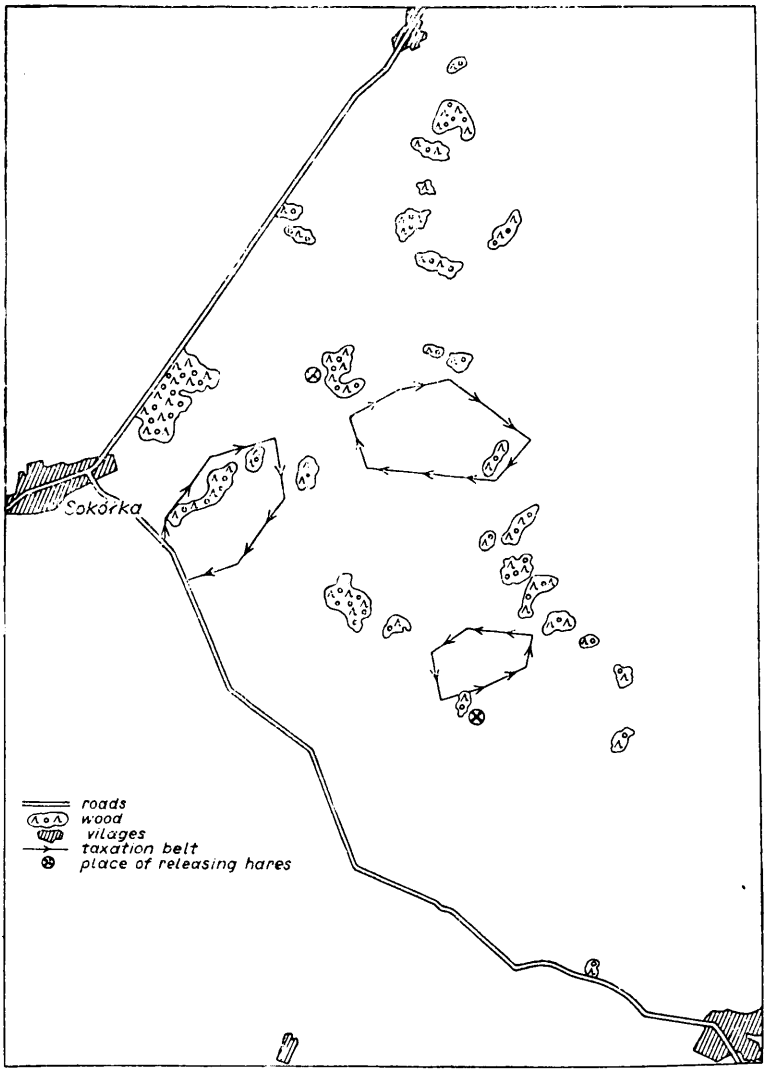

Fig. 3. Plan of the Sokółka experimental area.

March — than in the autumn and spring months (cf. also Fig. 4). These authors attempted to evaluate this phenomenon, pointing out the possibility that the imperfection of the method itself may exert some influence — as may also the fact that hares are less shy when occurring in fields of some crops, the seasonal

migrations within the population's home-range to places which of necessity were not included in the assessment belt (lower head in autumn) — and the winter mortality of the basic stock of the population (lower head in spring). Without entering into very detailed analysis of the value of this method for the purpose of estimating the actual hare population numbers, it would appear that this method is sufficiently reliable for comparing the levels of population numbers. There are unfortunately no other methods by means of which information on variations in hare population numbers can be obtained under field conditions.

In the case of the Brody and Lutom areas data on age and sex structure of the population were collected immediately before introduction on the basis of the hares shot during shoots, in order to compare them with similar data obtained after introduction. Some researchers use analysis of this kind, despite the various objections which can be made to it (Tilgner, 1954b, 1957a, 1957b; Rieck, 1955, 1956; Andrzejewski & Pielowski, 1957; Jezierski & Pielowski, 1958; Szederjei, 1958; Jezierski, 1959, 1965; Hell, 1960; Pielowski, 1961; Petrov & Dragoev, 1962 and others).

Table 1.

Comparison of material obtained before introduction.

Place of introduction	Assessment belts		Number of assessments before introduction	Total number of hares in belt	Number of hares shot immediately before introduction				
	Length, km	Area ha			Total	♂♂	♀♀	Young	Over 1 year old
Brody	30	150	2	172	276	135	141	105	171
Lutom	20	100	2	33	278	106	172	131	147
Sokółka	35	175	1	22	—	—	—	—	—

(2) The second stage covered the release of hares into the various areas. The hares intended for introduction were obtained by ordinary captures made in other areas. Before their introduction they were examined to ascertain age and sex structure and marked by docking one third of the right ear and ringing the ear with a consecutive number. The sex of the hares was established by examining the external genitalia, and the age by the classic Stroh method (1931). Recently this method has been somewhat criticised (Bujalska, Caboń-Raczyńska & Raczyński, 1965), but there is at present no other more reliable method by means of which large numbers of live hares can be examined under field conditions.

(3) The third stage began on the 5th day after introduction, by carrying out belt assessment every 14 days on the same belts as before introduction and by using the same method. A 10× magnifying field-glass was used to ascertain whether the hares belonged to the local population or was one of the introduced animals. It was found that this glass was sufficient to distinguish marked from unmarked hares at distance up to 400 m.

In order to establish the percentage of different crops covering the study areas we also carried out chronometry of the crops. One of the assessors recorded each change in the kind of crop through which the assessing group passed, with exact timing (with accuracy up to 1/4 of a minute).

During the two-year period following introduction data on age and sex structure were collected in each study area from the hares shot in them, and data were collected up to the time of elaborating material, from those taking part in shoots on the number of marked hares (introduced) shot.

A summarised presentation of the material collected is given in tables 1—3.

Table 2.

Numbers and sex and age ratios in the introduced groups of hares.

Place of introduction	Date of introduction	Place of origin	N	♂♂	♀♀	Young	Over 1 year old
Brody	Jan. 21, 1960	Czempiń	473	213	260	129	344
Lutom	Jan. 28, 1961	Czempiń	398	156	242	42	356
Sokółka	Febr. 13, 1962	Olszyny Gierłoż	1.376	491	885	467	909

Table 3.

Comparison of material obtained after introduction.

Place of introduction	Assessment belts		No. of assessments	No. of hares observed				
	Length, km	Area, ha		Total	In belt		Beside belt	
					Local	Introduced	Local	Introduced
Brody	41	205	8	2.392	702	40	1.595	55
Lutom	20	100	7	436	147	54	181	54
Sokółka	35	175	7	352	129	80	78	65

	Number of hares shot over period of 2 years after introduction					No. of recoveries
	Total	♂♂	♀♀	Young	Over 1 year old	
Brody	490	259	231	78	412	7
Lutom	227	105	122	73	154	49
Sokółka	274	120	154	93	181	24

Differences in the length and area of assessment belts in the Brody area due to the fact that the initial estimate of numbers was made using two belts, but observations were made on three belts after introduction.

IV. RESULTS

1. Numbers of the Local Population

The relative density of local populations was defined by averages for the whole study period. The density of hares in the Lutom area — 23

hares per 100 ha — was approximately twice, and in the Brody area — 48 hares per 100 ha — four times greater than in the Sokółka area — 11 hares per 100 ha. These differences are statistically significant. This was checked by the *t* Student test for significance of differences in two independent means.

The hare populations in the study area did not exhibit marked differences in numbers over the whole period during which material was collected, which would seem to form evidence of their considerable stability, which even the introduction carried out was incapable of

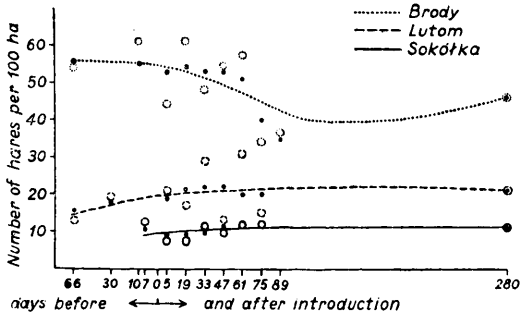

Fig. 4. Curves of local population numbers (using movable means).

disturbing (Fig. 4). The absence of variations in numbers observed 280 days after introduction, that is, after the reproduction period of the resident populations, is particularly noteworthy.

2. Settlement of Introduced Hares

The percentage of marked hares in the total number of hares encountered during assessment was determined, taking into consideration jointly the hares encountered within the assessment belt and outside it. Despite the fact that the hares' reaction to general assessment conditions may differ on different days (Fig. 4) it was assumed that the reaction of introduced and local hares should be the same on the same day. This was checked by comparing the shyness of introduced and local hares statistically (χ^2). No statistically significant differences were found in this respect between Brody and Sokółka, but at Lutom the introduced hares proved shyer than the local ones (the ratio of all encountered hares to those starting up at a distance of less than 50 m was 2.9 for the local hares and 4.2 for the introduced). This makes it possible for assessment to register a slightly larger number of introduced hares than was in fact really the case in the area. At a distance of about 100 m, however, these relations are balanced. For practical purposes this can be ignored, assuming that the chances of starting up introduced and local hares are

particularly in view of the absence of variations in the density identical. In this connection the ratio of introduced to local hares expressed in percentages should define sufficiently accurately the changes observed in the number of introduced hares (Fig. 5), of the populations examined, and thus invariability of the basis for calculating the relations in question.

Analysis of the material collected (Tab. 4) was divided into two parts. The first of these covered the period from the time the hares were

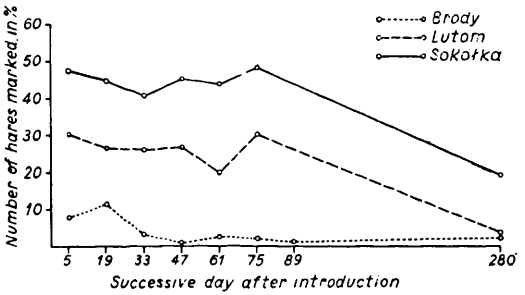

Fig. 5. Curves of percentages of marked hares in total number observed.

Table 4.

Variations in number of introduced hares (I%) defined in percentages of total number of hares observed (N) on successive days of assessment.

Day following introduction	Brody		Lutom		Sokółka	
	N	I%	N	I%	N	I%
5	291	7.9	69	30.4	46	47.8
19	253	11.6	64	26.6	47	44.7
33	373	3.5	88	26.1	32	40.6
47	448	1.1	52	26.9	51	45.1
61	438	2.7	91	19.8	57	43.9
75	251	2.4	46	30.4	62	48.4
89	205	1.5	—	—	—	—
280	128	2.3	26	3.8	57	19.3

introduced up to the end of April (89th day at Brody and 75th at Lutom and Sokółka), the second — from May to the end of November (280 days after introduction). It was anticipated that during the initial period after introduction the population situation of the introduced hares might be specific and different from that of the local hares.

The material collected indicates that the phenomenon under discussion takes a markedly different course in the Brody area on one hand and at Lutom and Sokółka on the other. Differences were examined to see whether they were statistically significant by means of the χ^2 statistics. The phenomenon of disappearance from the area of introduced hares

was observed on the 33rd day after introduction at Brody. Continued decrease of these hares was found on the 47th day also. The remaining days did not reveal significant differences in the numbers of introduced hares. At Lutom and Sokółka significant differences were found in the percentage of introduced hares during the first 75 days. It was found by means of the simple regression test that the difference in the course of this phenomenon is statistically significant.

The above findings lead to the assumption that the hares introduced at Brody encountered conditions decidedly different from those in the Lutom and Sokółka area. It is a characteristic fact there that material obtained from these last two areas does not even exhibit changes in numbers (losses) due to natural mortality, which at this period should be expected to be at least 6—10% (Andrzejewski & Jezierski, 1966).

The second part of the material was treated somewhat differently on account of the long interval (about 200 days). As there were no significant differences in the number of hares introduced at Lutom and Sokółka on successive days, calculation was made of the mean density per 100 ha for the first 75 days after introduction, next comparing it with the density on the 280th day after releasing the animals, which gave the decrease in the number of introduced hares during the study period. This was 89% for Lutom and 68% for Sokółka.

The material presented above shows that hares introduced into populations with different degrees of density disappear from these populations at different rates. An attempt was made at analysing this question in yet another way. The number of hares intended for introduction was divided by the size of the settled area and multiplied by 100. The mean number of introduced hares per 100 ha on the day of introduction was obtained in this way. It was assumed that these hares cover the area allocated for introduction evenly. The index obtained was termed »introduction measure«. Using the formula in which: x — mean number of hares per 100 ha, p — percentage of introduced hares encountered on the assessment belts, calculation was next made of the mean numbers of introduced hares per 100 ha observed on the different days of assessment (Table 5). Comparison of the introduction measure with the mean densities of introduced hares on different assessment days permits of concluding that the disappearance of introduced hares took place very quickly at Brody, whereas such hares remained for a long time in the settled area at Lutom and Sokółka. At Brody the introduced hares appear to occupy, immediately after introduction, an area greater than that allocated for settlement (the introduction measure is throughout greater than the means from the different assessment days).

In the Lutom and Sokółka districts the introduced hares do not spread over the whole area for the first 75 days. In the case of these last two areas it is not until the 280th day after introduction that the data show the inrtoduced hares to have gone beyond the limits of the settled area, and that to differing degrees. This analysis of course only points to tendencies in this process. Many factors influencing occupation of the area by hares such as, for instance, mortality or evenness of dispersal, have not been taken into account in it.

Table 5.

Introduction measure (I. M.) and density of introduced hares per 100 ha, calculated for different days of assessment.

Day following introduction	Brody	Lutom	Sokółka
I. M.	6.9	5.3	4.8
5	3.7	6.9	6.2
19	5.4	7.2	5.8
33	1.7	6.0	5.3
47	0.5	6.6	5.8
61	1.3	4.5	6.2
75	1.4	7.4	6.3
89	0.5	—	—
280	1.2	0.9	2.1

Table 6.

Percentage of marked hares in total number of hares shot during control shoots.

Year after introduction	Brody	Lutom	Sokółke
1st	5.1	9.7	6.0
2nd	0.3	9.0	2.0
3rd	0.0	0.0	2.4

Control shoots were also made in which the percentage of introduced hares was defined in relation to the total number of hares shot (Table 6). Attention must be drawn to two things here. In the first place there is the absence of any significant difference between the above data and material collected at approximately the same time by means of belt assessment. In the second there is the absence of introduced hares in the material shot at Brody and Lutom in the third year after introduction, although a certain percentage of such hares remained at Sokółka. It would appear that the general characteristics of this picture form a logical continuity of the results obtained during the first year of belt assessment.

The methods used did not permit of evaluating the disappearance of introduced hares during the period from May to August. As there were no significant differences between the numbers of introduced hares at Lutom and Sokółka estimated for the first 75 days after introduction, it is impossible to determine accurately the rate at which hares disappeared from these areas. As the latter are, however, characterised by unevenness of the disappearance rate of introduced hares an attempt was made at calculating what part of these individuals remained in each of the study areas.

At Brody the introduced hares began disappearing about one month after they were released there, and this continued for approximately the following month. After this the situation became relatively stable

Table 7.

Number of introduced hares remaining in study area 280 days after date of introduction (N).

Area	$N = \frac{\bar{x} \times p \times P}{100 \times 100}$	No. of introduced	Ratio of remainder to those released
Brody	$N = \frac{48 \times 6900 \times 2.3}{100 \times 100} = 76 \approx 80$	473	$\frac{1}{6}$
Lutom	$N = \frac{23 \times 7500 \times 3.8}{100 \times 100} = 66 \approx 70$	398	$\frac{1}{5}$
Sokółka	$N = \frac{13 \times 28900 \times 19.8}{100 \times 100} = 744 \approx 750$	1376	$\frac{1}{2}$

$\bar{x}$ — Mean number of hares per 100 ha, p — Area in hectares, P — Percentage of introduced hares remaining in belts 280 days after introduction.

and was subject to slight variations only. During this period about $^2/_3$ of the introduced hares disappeared (assuming that the maximum value established on the 19th day after introduction illustrates the stay there of 100% of introduced hares). Later there is a change of about $^1/_6$ only of the numbers introduced (Table 4).

This situation is completely different in the Sokółka area. No disappearance of introduced hares was recorded for the first 75 days, and it is not until assessment is made on the 280th day after introduction that data are obtained showing considerable disappearance of introduced hares (extent of disappearance about $^2/_3$).

Lutom occupies an intermediate position between the areas described above. Disappearance of the hares starts at about the same time as at Sokółka, that is, after the first 75-day period. Minimum level was in

this case also found on the 280th day after introduction (disappearance — $^3/_5$).

The extent described of disappearance of introduced hares of course only forms an attempt at describing this phenomenon and does not pretend to be exact. One more attempt at quantitative assessment of disappearance was, however, made in order to verify them. The mean density of hares per 100 ha, extent of the study areas and established percentage of introduced hares, all on the 280th day after introduction, were taken as the basis for calculation (Table 7). The results obtained are very close to, and in the case of Brody the same as, those obtained previously. It would also seem that they give an illustration of the course taken by introduction of hares over the course of nearly a year from the start of introduction which is very close to reality. This period completely covers the reproduction period of the resident population taking place soonest after introduction, which in particular is worthy of emphasis in view of the absence found of increase in numbers of these populations.

Table 8.

Density of introduced hares per 100 ha acc. to data obtained by control shoots and assessments made 280 days after introduction.

Area	Density		Introduction measure
	Assessment	Shoots	
Brody	1.2	1.0	6.9
Lutom	0.9	1.5	5.3
Sokółka	2.1	0.5	4.3

Calculation of the density of introduced hares was made from the material obtained by assessment on the 280th day after introduction and from the results of control captures (Table 8). The same number of about 1 introduced hare per 100 ha of settled area was found after about one year from the time of introduction, on each of the study areas. There are no significant differences between the data obtained by assessment and by control captures. It is worthy of emphasis here that data from captures come from a relatively large area covering about 10—15% of the study areas. Comparison of these data with the introduction measure confirms the previous arguments as to the total extent of disappearance of introduced hares.

As it was found that the introduced hares disappear from settled areas at different rates, the authors searched for an answer to the question as to whether there are differences in the population situation of introduced hares disappearing from, or remaining in the area and local hares. Two aspects of this question were analysed — the first was

whether the spatial structure of the hare population takes the form of concentrations and if so, whether the introduced hares »installed« in concentrations have a different chance of remaining in the area than hares living outside the concentrations. The second was whether there is a difference between introduced and local hares as regards occupation of different kinds of crops, taking this last as the exponent of habitat attraction.

3. Tendency to Form Concentrations

Analysis of tendencies to form concentrations in hare populations was made by comparing the distribution of observed frequencies of hares per unit of area with the Poisson distribution (W h i t a k e r, 1914). It was assumed here that the size of unit of area characteristic of the population examined at a defined time, depends on the current density of the population (T a r w i d, 1960).

The length of the assessment belt with a constant and known breadth is the counterpart of its area. It was therefore divided by the number of hares encountered on the belt and the size of the section of assessment belt corresponding to the unit of area proper to the given density was

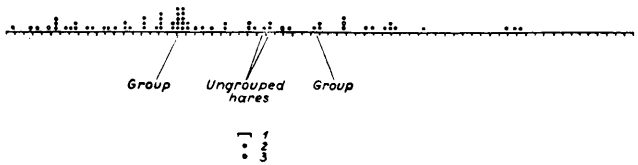

Fig. 6. Example of graph used for analysing the concentrations in the spatial structure of hares.

obtained. Sections calculated in the way described above were laid off on a chart corresponding to the length of the belt, and points corresponding to the places in which hares were observed on the belt were marked on it (Fig. 6). The number of hares present in different units of area were read from this chart and the distribution of observed frequency compared. Distributions for each day of assessment and jointly for each study area were compared by means of the χ^2 test with the Poisson theoretical distribution. Statistically significant differences were found between these distributions, which means that the distribution in space of the hares takes the form of concentrations (Fig. 7, a—c). The basic size of the concentration is the number of three hares per unit of area. It is not however impossible that with very low population density this value may be reduced to two (Fig. 7c).

As the spatial distribution of hares was found to take the form of concentrations, consideration was next given as to whether the »instal-

ment« of introduced hares into concentrations causes these individuals to remain in the settled area. Analysis of the material collected shown in Fig. 8 indicates that with the passage of time an increasingly small

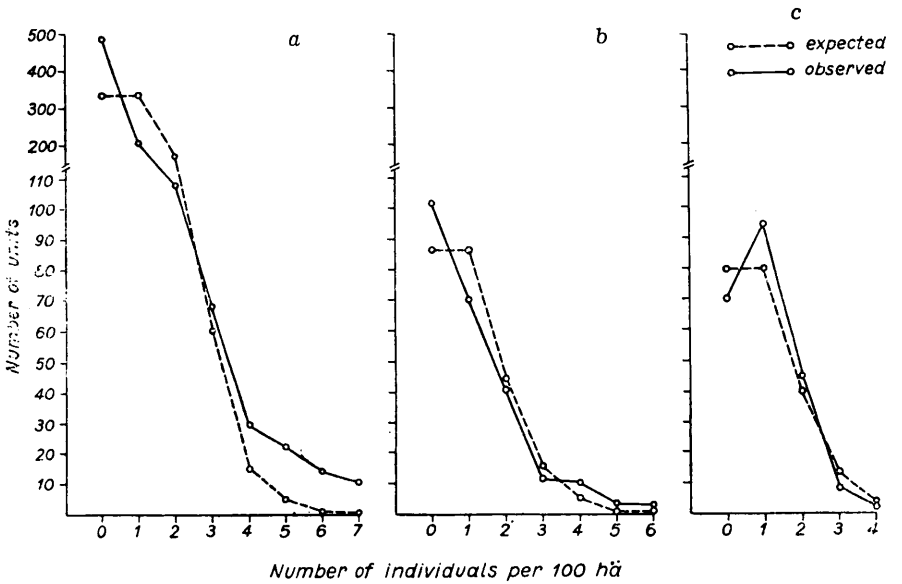

Fig. 7. Poisson's distribution for distribution of hares in experimental areas. a — Brody, b — Lutom, c — Sokółka.

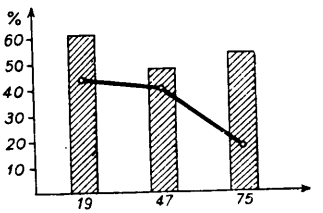

Fig. 8. Curve of percentage of introduced hares »installed« into a concentration compared with the total number of introduced hares encountered on assessment belts (bars).

number of the introduced hares which had remained in the settled area remain in the concentrations. The differences were statistically significant (test t).

4. Habitat — Its Attractiveness and Influence on Settlement

The problem of occupation by introduced hares of more or less attractive places was analysed. For this purpose the percentage of different crops in total area of the study area was grouped into four

categories: arable land, winter corn, waste land together with degraded pastures and others. The participation of introduced and local hares for each of the crops was next determirned. Table 9 shows that different crops are occupied to a different extent by these two categories of hares. At Brody the distribution of local hares in crops was more or less proportionate to the percentage of these groups in the total area of the study area, with perhaps a slight preference for crops defined as »others«. At Lutom and Sokółka, on the other hand, local hares clearly prefer the »other« category od crops and avoid waste land and degraded pastures (particularly at Sokółka). The fact that introduced hares occupy the »other« group of crops in all three areas to a markedly lower percentage than local hares indicates that the former are in a less favourable situation.

Table 9.

Percentage of different kinds of crops in study areas (1), distribution of local (2) and introduced hares (3).

Area		Ploughland	Winter corn	Wasteland and degraded pastures	Others
Brody	1	49	29	—	22
	2	47	28	—	25
	3	42	37	—	21
Lutom	1	47	40	2	11
	2	39	36	1	24
	3	51	42	—	7
Sokółka	1	36	32	23	9
	2	33	22	4	41
	3	41	26	—	33

The problem was also considered as to how great an effect habitat conditions exert on the disappearance rate of introduced hares. By effect of habitat conditions their direct and not indirect effect on hare populations is meant. For the purposes of the present study habitat conditions were examined only from the aspect of the soil, plant cover, water relations and level of agricultural culture.

There has so far been little documentation on the question of the hare's habitat requirements, nevertheless many authors (Thungen, 1911; Hegendorf, 1933; Kokeš, 1948; Szczepkowski, 1951; Budzyński, 1953; Koenen, 1956; Boback, 1957; Szederjei, 1958; Szederjei & Studinka, 1959; Müller - Using, 1962; Rieck, 1963 and others) express the opinion that the hare prefers

fertile, permeable and warm soils, with intensive cultivation, and varied vegetation. The study areas have been described from this aspect in the description of study areas and in table 9.

In the Brody district soils prepared for spring cultures and »other crops« which consisted chiefly of perennial green crops (alfalfa), formed a large percentage of the total area, whereas at Sokółka the percentage of ploughland is lowest, and the percentage of wasteland and degraded pastures high. The most faourable habitat conditions for hares were therefore those at Brody and the least favourable at Sokółka. Lutom occupied an intermediate position in this respect. It may therefore be concluded that the influence of the habitat on the process of the introduced hare's settlement is subordinate to the influence exercised by the local hare populations on this phenomenon. The possibility that the habitat modifies the effect of the local population on introduced individuals cannot of course be excluded, but it was impossible to examine this question on the basis of the material available.

5. Effect of Introduction on the Age and Sex Structure of the Population

In order to examine the effect of introduced hares on the local population the variations in sex ratio and age structure were investigated (Table 10). The percentage of females in the hare populations at Brody and Lutom exhibit a decreasing trend, although statistically significant deviations from the 1:1 ratio in all three areas were only found for the 1960/61 and 1961/62 periods in the Lutom area. The significance of this deviation was examined by comparing the numbers of females and males obtained in different years with the anticipated numbers obtained from formula $np \pm 3s$, where n — total number of hares examined, p — anticipated proportion, s — standard deviation. On the basis of the above material it may be stated that the introduction of large goups of hares did not affect the sex structure of the population in the three study areas. Some researchers draw attention to the existence of connections between variations in sex structure and the phase of the population's life and its density (P e t r u s e w i c z, 1960) and the increase due to the birth of young animals (H e l l, 1964).

The data given on the percentage of young hares (increase per population) and effective increase (increase per each sexually mature female) show that introduction did not contribute to restriction of the drop of effective increase of young animals. This increase is increasingly smaller in each successive year, and differences are statistically significant. This is not of course equivalent to saying that the decrease described is due to introduction, especially as the picture obtained

(particularly at Brody) is similar to the population structure for the whole of the Poznań province (J e z i e r s k i, 1965). Material collected in the Sokółka area, on the other hand, points to a marked rise in the effective increase in the two consecutive years after introduction. Unfortunately the lack of material from the pre-introduction period makes it impossible to make a proper analysis of this phenomenon.

To sum up it may be said that the introduction of large groups of hares in the Brody and Lutom districts did not cause additional changes

Table 10.

Age and sex structure of local hare population before (0) and after introduction (I, II).

Area	Season	Year	N	Females		Young		Effective increase
				%	Student test	%	Student test	
Brody	0	1959/60	276	51	0.4166	38	3.4965	1.2
	I	1960/61	179	49		23		0.7
	II	1961/62	311	46	0.6410	12	3.0218	0.3
Lutom	0	1960/61	278	62	1.1881	47	2.6315	1.3
	I	1961/62	145	56		34		1.1
	II	1962/63	82	50	0.9615	29	0.8880	0.9
Sokółka	0	1961/62	—	—	—	—	—	—
	I	1962/63	174	55		27		0.7
	II	1963/64	100	59	0.6451	46	2.8780	1.3

in the age and sex structures of the local population during the two years following introduction. It would, however, appear that the age structure of the population at Sokółka underwent a favourable change.

6. Return Information on Introduced Individuals

A certain numebr of the ear-tags were returned from shot hares or those which had died and been found (Table 11), but the number of recoveries was negligible (3.5% from a total number of 2.247 released hares). It is of course possible that no return information was obtained in respect of a certain number of hares, but in view of the fact that the reward for their return was high, their number cannot have been very large. A relatively large number of recoveries come from the Lutom district, due to a certain extent to the very intensive shoots carried out in this area. It would seem nevertheless that here also other causes must have been involved, especially that the range of returns was less extensive in this area than in others.

One further calculation was made in order to form a theoretical picture of the distance from which possible returns of ear-tags might be expected. It was assumed that the hares disperse evenly in all directions from the place of release (K a l a b u k h o v & R a j e v s k i, 1935). It was also assumed that about $^1/_3$ of the basic stock die over the course of the year (A n d r z e j e w s k i & J e z i e r s k i, 1966). Assuming that mortality among the introduced hares is the same after 280 days as in the local population over the period of a year (on account

Table 11.
Number recoveries on introduced hares obtained by ear-tags.

Recovery after	Distance in km. from place of release																								
	0—	1.1—	2.1—	3.1—	4.1—	5.1—	10.1—	20.1—	0—	1.1—	2.1—	3.1—	4.1—	5.1—	10.1—	20.1—	0—	1.1—	2.1—	3.1—	4.1—	5.1—	10.1—	20.1—
	Brody								Lutom								Sokółka							
1 year	2	2	1	—	1	—	—	1	13	1	2	3	2	—	—	—	—	1	3	—	—	—	1	1
2 years	—	—	—	—	—	—	—	—	—	4	1	7	16	—	—	—	—	—	4	—	1	—	7	—
3 years	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	2	—	—

of the poorer population situation of introduced individuals), it is possible to calculate what area these hares would occupy, and therefore the radius of dispersal also. This radius was calculated from the formula:

$$r = \sqrt{\frac{2N}{3M_{280}}}$$

in which: N — number of introduced hares, M_{280} — number of introduced hares per 100 ha (density) established on the 280th day after release. This formula is the appropriately modified formula for calculating the radius of a circle. The area of the circle was calculated from the ratio of total number of introduced hares to their density on the appropriate day of assessment, after subtracting mortality proper to that period. It must be emphasised here that the form of the formula given is correct only for mortality forming $^1/_3$ of the basis stock.

Distances calculated for the study areas were: Brody — about 9 km, Lutom about 10 km and Sokółka — about 12 km. Data contained in table 11 do not greatly diverge from the above theoretical picture.

V. DISCUSSION

Depending on the density of the local population, the chances of the introduced individuals' settling permanently vary, and as a result the rate of their disappearance from the settled area varies. The results obtained are in more or less complete agreement with the views held by the

majority of researches dealing with these problems. They point to the fact that the entry of new individuals evokes a reaction of resistance on the part of the local population (Soldatova, 1962; Andrzejewski *et al.*, 1963). There is a greater degree of settlement in an empty area than in an area settled by a population of the same species (Adamczyk & Ryszkowski, 1965). Reduction of introduced individuals may be due to their increassed mortality (Adamczyk & Ryszkowski, 1965) or reduced chances of survival during migration (Andrzejewski & Wrocławek, 1961; Pielowski, 1962; Petrusewicz, 1965). Finally some researchers draw attention to the fact that the so-called »homing instinct« occurs in many species of animals (Fenjuk & Popova, 1940; Fenjuk, 1941) expressed in the tendency of such animals to return to the habitat which they had previously been obliged to leave. This phenomenon, well-known in birds, has also been described for some species of small rodents. A description has also been given of four cases of introduced hares returning from places at distances of 250—500 km in a straight line from the areas on which they were originally caught (Jezierski, 1967). Koenen (1956) also refers to similar cases. It is obvious that the »home instinct« may be yet another stimulus to the creation in introduced individuals of a tendency to leave a settled area.

Despite the general conviction as to the effectiveness of introducing hares, original studies in this field do not show that this operation produces (with one exception — Szederjei, 1958; 1959) really useful effects (Ullrich, 1940; Pielowski & Wasilewski, 1960; Pielowski, 1962a). This is also emphasised by Ernst (1965) in his review of studies on introductions of hares. It is true that in the investigations described by Pielowski & Wasilewski (1960) and Pielowski (1962a) an increase of about 10 hares/100 ha was observed by means of belt assessment in the year following introduction, but the next year, which was characterised by intensive increase of the hare population all over Poland, no increase in population numbers was observed in the study area. In addition the year following introduction assessment was carried out only during the period from November to February, which in view of the specific properties of the method (Pielowski, 1966) would not appear to supply sufficient material for an accurate estimate of numbers.

The results of the present study differ fundamentally from the material published by Szederjei (1958; 1959) who introduced considerable numbers of hares, then over a period of 5 years obtained 72% of return information from shoots, 55% of such returns coming from places closer than 3 km to the place of release. These results would appear to provide evidence of the very low tendency to migrate on the

part of the hares, the penetration area of which according to some opinions is about 2 km (Thungen, 1911; Ullrich, 1940; Kokeš, 1948; Budzyński, 1953), and according to others as much as 6 km (Szederjei, 1959; Ernst, 1965) in diameter. The results would also appear to point to a very low mortality rate in the basic stock of less than 6% annually. These results also disagree with the opinion held on the occurence of the phenomenon of migration in vertebrate populations (Kalabukhov & Rajevski, 1935; Rall, 1936; Fenjuk & Popova, 1940; Ullrich, 1940; Fenjuk, 1941; Naumov, 1956; 1961; Wilusz, 1956; Allee *et al.*, 1958; Andrzejewski & Wrocławek, 1961; 1962; Andrzejewski, 1963; Odum, 1963; Ernst, 1965; Petrusewicz, 1965 and others) and opinions on the average length of life of hares (Andrzejewski & Jezierski, 1966). It must however be emphasised that Szederjei himself (1959) considers the results of his study as completely specific and expresses the opinion that they were caused by the exceptionally favourable habitat conditions in which he carried out the introduction operation. Ernst (1965) represents a similar point of view.

Both the studies by Szederjei (1958, 1959) and Ullrich (1940) show, on the basis of comparable marked material of local and introduced hares, that the latter exhibit a far greater tendency to migration, which agrees with the results of the present study and is understandable in view of the results of studies on the »home instinct«.

Attention must however be drawn to yet another aspect of the process reflected in the results under discussion. There is constant interchange of the individuals composing it in each animal population. This finds expression in deaths, births, emigrations and immigrations. Hare populations into which introductions were made in connection with studies are of course also subject to this process, as are marked individuals (of course excluding births and immigration) from the moment of integration with the local population, at the normal rate of intensivity. It is essential to point this out clearly, as the phenomenon decribed of rapid disappearance of introduced hares during the first phase after introduction is the result of the same, although more energetic, process. The question therefore arises as to when the disappearance of marked hares ends and the normal disappearance of these individuals integrated in the local population starts, that is, the process of normal interchange of individuals in a population.

At Brody the first phase lasted from one month to six weeks, while the second phase did not appear to occur at all. It is difficult to say why this was so. It is not impossible that individuals which, despite the generally known unfavourable situation of introduced animals, succeed-

ed in settling in during the first phase, have so strong a tendency to settlement that for a long time afer integration they do not take part in the general exchange of individuals. It is also possible that in very dense populations rotation is generally greatly reduced (N a u m o v, 1956) or that migrations of individuals within the scope of such exchange are so restricted in distance that they were not perceived by means of belt assessment along belts measuring a considerable number of kilometers in length.

It unfortunately proved impossible to trace this question in material from Lutom and Sokólka. The whole process of disappearance of introduced individuals occurred in these areas during a period in which it was impossible to carry out observations. It would however appear that in these two areas the second phase of the process may play a fairly important part. It is difficult to assume on the one hand that after a long 75 day period of stagnation, disappearance began to take place very rapidly, and on the other, that over a period of approximately 280 days the introduced hares did not integrate with the local population, but retained their original character of newcomers.

The mechanism of the disappearance process of introduced hares in the present studies proved impossible to trace. An attempt can however be made at drawing conclusions as to the course taken by this process.

A n d r z e j e w s k i & W r o c ł a w e k (1962) showed that settlement by forest rodents of an area emptied by captures (gaps) takes place at the expense of part of the migrating population, by prolonging the time the migrants spend in the capture area. It may therefore be imagined that this process took the following course in a hare population. The introduced hares reach areas with three different degrees of local population density. In each of the areas part of these hares, immediately after release, find themselves in areas occupied by concentrations of individuals from the local population, and part in areas in which there are either no hares or only single individuals. It may be taken that the local population, and especially that part of it which currently forms concentrations, opposes the tendency of introduced individuals to settle. This tendency is in any case probably fairly weak (A d a m c z y k & R y s z k o w s k i, 1965). The general results of the present studies, and the fact shown by A n d r z e j e w s k i & W r o c ł a w e k (1962), that migrants remain longer in an area with a population gap, argue in favour of the corectness of such an assumption. Thus at Brody, where as the result of considerable local population density the introduced hares had little chance of finding themselves in an empty area, disappearance of introduced individuals were very great. The reverse situation occurred at Lutom and Sokółka, where low and very low local

population density created a situation in which considerable areas were completely free of the local population. As a result both migrations of introduced individuals within the population's home range and disappearance of introduced hares from the settled area were incomparably less intensive.

Many researchers attribute very considerable importance to the sex ratio as affecting the life of a population (Tilgner, 1950; Szczepkowski, 1951; Rieck, 1955; Andrzejewski & Pielowski, 1957; Pucek, 1959; Jezierski, 1965; Petrusewicz, 1965 and others). There has however been little investigation of this question, particularly in relation to the hare. Some of the researchers express the opinion that sex ratio is 1:1 (Tilgner, 1950; Rieck, 1955; 1956; Koenen, 1956; Jezierski, 1959, 1965; Pielowski, 1961), and some that it differs from this (Szczepkowski, 1951; Koch, 1954; Hell, 1960, 1964). On the basis of the studies made by Pielowski (1961) and Jezierski (1965) on large amounts of material and comparison of the studies by Pucek (1959) on *Sorex aaneus* Linnaeus, 1758, it seems possible to risk the statement that although in principle sex ratio in the hare is 1:1, it is subject to periodical changes, varying within limits from 2:1 to 1:2. It should also be emphasised here that Petrusewicz (1959) draws attention to the variability of the sex ratio depending on the phase of the population's life, and thus of its density. Pucek (1959) attributes the connection with variations in numbers to variations in sex ratio and treats them as an expression of regulating phenomena in the population.

Some researchers attribute no less importance to the age structure of the population as affecting population life and particularly variations in population numbers (Tilgner, 1954b, 1957a; Rieck, 1956; Andrzejewski & Pielowski, 1957; Alle *et al.*, 1958; Jezierski, 1959, 1965; Pielowski, 1961; Petrov & Dragoev, 1962; Odum, 1963; Hell, 1964; Raczyński, 1964; Bujalska *et al.*, 1965; Petrusewicz, 1965 and others). There can surely be no doubt that these two phenomena are connected in a directly causal way.

In the cases examined introduction did not have a modifying effect on the populations, and therefore did not affect them in a positive sense. If however we assume that the effective increase in young found at Sokółka is the result of introduction, then it must follow that this operation produced a definitely favourable effect, since in consequence an increase in population numbers can be expected. There was, however, no such effect at Brody and Lutom. It may be taken that this is due to the disappearance of introduced hares from settled areas being too rapid. It is not fact impossible that this was also due to introduction coinciding

with an unfavourable phase in the life of the population, as shown by the constant reduction in effective increase of young. In consequence therefore the operation proved abortive (cf. also Petrusewicz, 1963).

No variations in numbers of the populations examined were found in any of the areas. Many researchers have pointed to the connection between variations in the numbers of a population and its organisation and structure (Andrzejewski & Wrocławek, 1961; Petrusewicz & Andrzejewski, 1962; Petrusewicz, 1963, 1965). The maintenance of numbers of the hare populations examined on the same level throughout the whole period (including the time after the reproduction period) indicates that introduction was incapable of disturbing the organisational and structural systems of these populations. The disappearance of introduced hares from concentrations also argues in favour of this conclusion. Only the rise in effective increase of young at Sokółka makes it possible to expect an increase in population numbers.

Despite the fact that introduction has been used for many years now, the results have been little investigated up to the present. It would seem that the results described show that the methods of introduction in use so far do not justify expectations of obtaining real benefits for practical game management. It is the method of introducing hares which should be changed, but it is at present difficult to give directions as to how this should be done. Some indication is formed by the results of Andrzejewski's study (1963), which showed that intensity of settlement by small forest rodents varies depending on the time of the year. It is possible that this also applies to hares, but nevertheless elaboration of the proper method of introducing hares necessitates carrying out appropriate investigations. It is quite certain that only introductions made in areas where the density of local populations is low have any chance of success. It must however be emphasised that the studies described confirm the opinion put forward by Petrusewicz (1965), that increase in population numbers should be effected by acting on the organisation and structure of the population.

Acknowledgments: It is my pleasant duty to take this opportunity of thanking Professor K. Petrusewicz, D. Sc. for his assistance in choice of subject and methods and for his guidance in carrying out the whole of the work. I should also like to thank Dr. R. Andrzejewski for his critical review of the typescript and Dr. eng. W. Dzięciołowski for his critical review of questions relating to soil science. I must also express my gratitude to T. Tarkowski, eng., the then director of the State Stud at Posadowo, for his exceptionally helpful attitude to my work and for making available the help of labourers, teams of horses and accommodation in the Stud buildings, and M. Bartoszewski for his often complete disregard of his own convenience and comfort in assisting me to collect material. I would also like to emphasise that I shall always retain a grateful place in my memory for the help given me by the late director of the State Stallion Stud at Sieraków, J. Kowalski, whose tragically premature death occurred before this study was completed.

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Received, June 29, 1967.

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NIEKTÓRE EKOLOGICZNE ASPEKTY INTRODUKCJI ZAJĘCY

Streszczenie

W latach 1959—1962 na trzech terenach dokonano introdukcji zajęcy metodą stosowaną w łowieckiej praktyce hodowlanej w ilościach: 473 sztuki, 389 sztuk i 1,376 sztuk. Charakterystyka tych terenów przedstawiała się następująco:

1. Brody (Fig. 1) — powierzchnia około 7.000 ha, dobre warunki środowiska i zagęszczenie populacji zajęcy miejscowych na poziomie 48 sztuk/100 ha,
2. Lutom (Fig. 2) — powierzchnia około 6.500 ha, średnie warunki środowiskowe i zagęszczenie populacji miejscowej na poziomie 23 sztuki/100 ha,
3. Sokółka (Fig. 3) — powierzchnia około 29.000 ha, najsłabsze warunki środowiskowe i liczebność populacji zajęcy miejscowych na poziomie 11 sztuk/100 ha.

Wszystkie zające przed introdukcją były oznakowane: indywidualnie kolczykiem usznym z numerem bieżącym i grupowo przez obcięcie $^1/_3$ jednej małżowiny usznej. Następnie przy pomocy taksacji pasowej z użyciem 10-cio krotnej lornety dokonywano obserwacji i liczono zmiany ilości introdukowanych osobników. Przeprowadzono także przed i po zabiegu introdukcji polowania kontrolne dla celów oceny zmian stosunków wiekowych i płciowych w zasiedlanych populacjach a także dla kontrolnego zebrania danych o liczebności osobników introdukowanych. Oceniono wreszcie charakter rozkładu przestrzennego populacji. Zebrany materiał pozwala wyciągnąć następujące wnioski:

1. Zające introdukowane w tereny o rozmaitym zagęszczeniu populacji miejscowej ubywają w większym stopniu niż by to wynikało z normalnej wymiany osobników w populacji. Nasilenie tego procesu i jego tempo jest tym większe im liczniejsza jest populacja miejscowa (Tabela 4, Fig. 5).

2. Warunki środowiska w procesie ubywania zajęcy introdukowanych spełniają mniejszą rolę niż zagęszczenia populacji miejscowej.

3. Introdukcja zajęcy tylko w pewnych warunkach ma wpływ na strukturę wiekową populacji (Tabela 10).

4. Nie stwierdzono aby introdukcja spowodowała wzrost liczebności badanych populacji, które przez cały czas badań utrzymywały się na tym samym poziomie ilościowym (Fig. 4).

5. Zające introdukowane zajmują uprawy preferowane przez populację miejscową w znacznie mniejszym procencie (Tabela 9).

6. Rozkład przestrzenny zajęcy wykazuje charakter skupiskowy, przyczym podstawową wielkością skupiska są trzy osobniki na jednostkę powierzchni (Fig. 7, a—c).

7. W miarę upływu czasu od dnia introdukcji, coraz mniejsza ilość zajęcy introdukowanych, przebywających w terenie zasiedlanym, utrzymuje się w skupiskach (Fig. 8).