A C T A T H E R I O L O G I C A

VOL. X, 5: 79—91. BIAŁOWIEŻA 15.VIII.1965

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Studies on the European Hare. X. Results so far Obtained from Research in Poland and Trends in Continued Studies

[With 2 Tables]

The authors presented a general discussion of certain results contained in nine studies dealing with the morphological variations in the skull and pelvis, dimensions and weight of the body, the moult, reproduction, estimation of age, degree of infestation by parasites and certain structural elements of the populations of the European hare. In order to permit of general application of the results obtained over one yearly cycle further investigations are essential, particularly of the reproduction potential, extent of embryonic mortality and death of young hares and means of counteracting these, and of the effect of parasites on the basic life processes of the hare. Reliable estimation of age forms a basic problem in the correct control of the development of the hare population. Further research is required on the elaboration of age indices based on animals of known absolute age. If the main intensity of shoots is shifted to December and the first half of January the hares shot will have the highest mean weight and fur of the greatest industrial value.

The role of the hare in the agrocenosis is as yet little known, but it would seem that this species, even when density is great, does not reduce to any appreciable extent the productivity of cultivated crops. The data given by Kolosov & Bakeev (1947), Korneev (1960) and others show that the hare's food is formed by those elements of the plant biomass which are not directly utilized by man, or which return to the circulation of matter in the agrocenosis before the crop is harvested (e.g. the leaves of corn near the ground, young leaves of root crops etc.). It would therefore be a considerable advantage from the economic aspect to maintain the hare population on a level which would guarantee high net production together with its maximum exploitation.

Taking as a basis data only approximately estimated for the whole of Poland and the few assessments made for defined areas (Jezierski, 1959; Pielowski, 1962; Andrzejewski & Jezierski, in preparation) it is found that the present population density of the hare in different parts of Poland varies within limits of 0.04 to 0.6 per hectare, with productivity of shot hares from about 10 to 25% a year. The wide range of the limits given here is due to a great degree to the absence of appropriate data based on an objective method of assessing density and productivity of the European hare population. There is, however no doubt that the density and productivity of the hare in Poland are very low, particularly in comparison with similar data for our shooting areas obtained about twenty to thirty years ago. Data encountered on this subject in literature (e.g. Szederjei, 1959) point to the possible existence under natural conditions of densities of the European hare population up to 2.0 hares per hectare. Bearing in mind that one hare supplies about 1.4 kg of actual meat of high value, in demand in both Polish and foreign markets (Tilgner, 1949, Budzyński, 1953) we reach the conclusion that even with the productivity of the hare population on its present level very real advantages, not only sporting but primarily economic, are obtained. As mentioned above this production is based chiefly on the utilization of the useless part of plant biomass in fields, and therefore its costs are negligible.

A series of investigations with the eventual aim of increasing density and ensuring the proper control of development of the European hare population were initiated in 1956/57 by the Institute of Ecology, Polish Academy of Sciences. In planning the research programme at that time it was clearly understood that the key to the solution of this problem was a knowledge of such questions as the general regularities of population dynamics, interdependences between the habitat situation of a population and its structure, reproduction, mortality etc. — and therefore ecological examinations or investigations in other fields of biology should be carried out against a wide ecological background (Andrzejewski & Pielowski, 1957). The initiation of such research depends to a great degree, however, on the general state of knowledge of the biology of the given species and should be preceded by all-round basic studies.

Despite the fact that the European hare has a wide geographical range and its importance as a game animal has been and still is very great in many countries, yet it has not so far formed the object of thorough investigation. Literature on the morphology, biology, physiology or pathology of this species is relatively meagre and does not permit of undertaking ecological and game studies on a wide scale. It is true that references may be made to about 100 titles of original studies and notes on the European

hare, published during the last 30 years, but in relation to other game mammals this material is far from abundant. It is not our task here to give an exhaustive review of studies on the hare, we desire only to mention certain of the more basic publications of recent years, which in our opinion are important on account of the questions they deal with.

The most important question, on account of its effects, of the biology of the hare, that is, reproduction, has been examined by many research workers such as Kolosov & Bakeev (1947), Hediger (1948), Stieve (1952), Bloch *et al.* (1954; 1958; 1963), Rieck (1956b). The results of reproduction and the natural increase in the population of the European hare have been investigated by, among others, Rieck (1956a; 1956b; 1962), Valentincic (1956), Szederjei (1959), Jezierski (1959), Pielowski (1962), Hell (1964). Certain of the population problems, in particular those of variations in numbers, and age and sex structure, were analysed by Naumov (1947), Siivonen (1956), Jezierski (1959), Pielowski (1962).

No exhaustive study has yet been made of many problems concerned with the morphology and biology of the hare. The series of studies published in "Acta Theriologica" fills this gap to a certain extent. Using representative material collected over the whole year's cycle certain debatable questions have been solved and a good basis provided for the continued research planned for the immediate future. The majority of the studies published in this series refer to the same material, obtained from a relatively small area and elaborated from many aspects, and for this reason it would seem both possible and desirable to summarise the results obtained.

We do not intend to discuss all the results contained in the various studies, since this has already been done by the respective authors. We are rather concerned with laying emphasis on problems of a more general character, the collection of studies having made it possible to take a more critical view of them and to establish correct methods and the questions to be dealt with in further studies.

I. ESTIMATE OF THE YEARLY INCREASE IN THE POPULATION OF THE EUROPEAN HARE

The fundamental problem in increasing the productivity of the hare population (increasing the number of animals shot) is the effectiveness of reproduction and survival of the young hares. The greater reproduction and survival, the greater the yield of shot hares, while simultaneously ensuring that the numbers of the basic population are maintained. Methods for investigating the biology of reproduction have been carefully

elaborated and in the case of the hare there is a certain number of publications analysing this question more or less thoroughly in different populations over almost the whole of the geographical range of this species.

The estimate of the hare's reproduction potential as 7—10, and even 11 young from one female during the year, given by different authors for different years and areas (Kolosov, 1941; Rieck, 1956; Reynolds & Stinson, 1959; Scarlatescu *et al.*, 1963), would seem to be too high, at least as far as Poland is concerned. Not all these authors take into consideration in their calculations such factors as embryonic mortality and the percentage of reproducing females. According to the data given by Raczyński (1964) the number of young produced by one female

Table 1.

Percentage of young hares (groups A and B) and old hares (group C) the age of which was determined by different methods. Figures and indentification of age groups after Table 1, p. 4, from the study by Bujalska, Caboń-Raczyńska & Raczyński, 1965 — altered.

Age group	Method of determining age:														
	I Stroh, field		II Stroh, visual			III Skull sutures			IV Pelvis sutures			Lens weight I/Stroh/		V /Lens/		
	n	%	n	%	Diff. I/II	n	%	Diff. I/III	n	%	Diff. I/IV	n	%	n	%	Diff. I/V
Young /A+B/	100	67	70	47	20	82	55	12	86	59	8	58	71	41	50	21
Adult /C/	50	33	80	53	-	68	45	-	59	41	-	24	29	41	50	-
Total	150	100	150	100		150	100		145	100		82	100	82	100	

during 1959, was 7,4. It is necessary to add that 1959 was a favourable year as regards the number of hares obtained (Jezierski, 1965; statistics of hares shot in Poland — unpublished data). This increase in young means that if no losses had taken place in the head of young hares up to the start of the shooting season, then in the autumn we should have about 79% of animals born that year (with a sex ratio for adult animals of 1:1). The difference between this theoretical percentage and the percentage of young hares under one year old among the hares shot defines the extent of mortality among young hares in the population. Thus the percentage of young hares in the population is a good measure of population increase in a given year and can be used as a basis for regulating the permissible amount of hares to be shot.

The percentage of hares under one year old in the Poznań province over the period from 1957—1961 was, according to Jezierski (1965), about 50% (exceptionally 56% in 1959). This expresses an increase of 2.2—2.4 young from one female over the course of the year (in 1959 — 2.9). Jezierski (l.c.) defined the hares' age by Stroh's method, consisting in palpating the epiphysal thickening of the ulna. This method, however, produces significant differences in comparison with other ways of defining age (Bujalska *et al.*, 1965). Taking the figures of the authors referred to above as a basis, we compared the percentage of young and old hares in a series of 150 specimens distinguished by different methods (epiphysal thickening, the degree of obliteration of the skull and pelvis sutures, the weight of the eye lens). The data contained in table 1 show that differences in the percentage of young defined by Stroh's field method and the other methods referred to vary within limits of 8—21%, the mean being about 15%.

In view of these differences the figure given by Jezierski (1965) should be reduced by about 15%. Thus the increase in young from one female in 1959 should be not 2.9, but 2.5 animals.

Bearing the above in mind, and also the results of the investigations made by Raczyński (1964) and Jezierski (1965) we reach the conclusion that about 34% of the young hares born survived to the start of the shooting season (a reduction from 7.4 to 2.5 young from one sexually active female).

It must be added here that in order to establish correctly on this basis the amount of animals which can be shot without reducing the head of the basis stock it is essential, in addition to an exact knowledge of the abundance of this stock, to estimate the mortality (losses) among the population during the period from the shooting season to the end of the reproduction season the following year. These losses can also be estimated on the basis of the percentage of each of the older age groups in the population.

The balance made here between the potential reproduction and the actual increase in the shooting season is undoubtedly burdened with a certain degree of error, due in part at least to the fact that the increase in young hares was estimated with a different degree of accuracy by Raczyński (1964) on the basis of the developing embryos, and by Jezierski (1965) on the basis of the percentage of young hares in the population, their age being defined by Stroh's method. The investigations were made over the course of one year and, in addition, in a so-called "good hare year". The figure of 7.4 given by Raczyński (l.c.) as the increase in young hares should therefore be treated as a guide only. The questions as to how intensivity of reproduction and in particular

the mortality of young hares varies from year to year remains an open one. Judging by Jezierski's data (1965), the differences in the increase in young from one female in the majority of the study years (1957—1961) were not very great, but could be as much as 0.7 animals.

In estimating the increase in young hares the number of litters over the course of the year, understood by us as the number of litters of a defined percentage of females, is an important factor. Raczyński's (l.c.) examinations show that under our climatic conditions it is theoretically possible for one female to have 3—4 litters during the year, but the differences found by certain authors in the date at which the reproduction season starts, depending on the climatic conditions in a given year (Naumov, 1937; Wight & Conway, 1961; Raczyński l.c.) and the high embryonic mortality rate in early pregnancies (Raczyński, l.c.) permit of assuming that at least one of these litters never occurs. It is also possible that the litters born and reared under unfavourable biometeorological conditions may be subject to practically complete wastage. Population increase from such litters may therefore vary greatly in different years. It is a question here of the weather conditions during the period when the first oestrus occurs (start of the reproduction season — second half of December, January) and also the conditions during the period in which the first litters are born (second half of February, March). These factors should be taken into consideration when forecasting the numbers of hares and when estimating population increase.

Embryonic mortality is an important factor limiting the increase in young. During the study year 1959 maximum mortality occurred in January and February (over 80%) and during the period May—June included over 50% of all implanted embryos — Raczyński (l.c.). This phenomenon is the more interesting in that in the latter case it occurred in what would seem to be a favourable period for the development of young hares. The decrease in the mortality of embryos towards the end of the reproduction season additionally complicates the possibility of explaining spring mortality. If the causes of this kind of mortality could be found (food conditions, climatic conditions?) it would be of considerable assistance in endeavouring to reduce its extent and as a result to increase reproduction. Studies made over one year only cannot of course make it possible to establish the dimensions and periods of mortality in different yearly cycles.

II. ESTIMATION OF THE AGE STRUCTURE OF A POPULATION

The obvious conclusion is reached from the above reasonings that the fundamental data for proper regulation of the way in which use is made

of populations of the European hare (maximum utilisation without reducing the basic stock) are: 1) accurate estimate of the age structure of population, split into classes of one year, two years and over two years old, and 2) density and variations in numbers, especially over the yearly cycle. The problem is therefore reduced, to a great extent, to choice of the appropriate criteria for assessing age.

The studies known to us on determination of age in different representatives of *Lagomorpha* are limited to an analysis of the degree of ossification of different elements of the skeleton (Stroh, 1931; Petrides, 1951; Watson & Tyndal-Biscoe, 1953; Taylor, 1959; Wight & Conaway, 1962) and of the weight of the eye lens (Lord, 1959; Dudziński & Mykytowicz, 1961; Rieck, 1962; Edwards, 1962). Other criteria, especially those given by hunters, cannot be accepted as they are not based on reliable material.

The studies by Caboń-Raczyńska (1964b) and Bujalska (1964), give a description of additional criteria for relative assessment of the age of hares, based on ossification of the skull and pelvis and of the sacral bone. Comparison made of the different methods of estimating age known up to the present (Bujalska *et al.*, 1965), however, reveals their inadequacy. The fundamental defect is the absence of a key based on material of known absolute age. Only in the case of the Stroh (1931) method generally used by hunters are there the approximate data given by Andersen (cited after Rieck, 1956b) and by Rieck (1956b) indicating that the epiphysal cartilage of the ulna disappears about the age of 8 months. The elaboration of a key of this kind for free-living hares is one of the chief postulates resulting from the studies referred to above.

The second question is the practical application of the most widely used method, "the Stroh method". The discrepancies revealed in identifications of age made by an experienced assessor, by palpation of the epiphysal thickening through the skin and inspection of the thickening on the skeleton of the forearm or on fresh material after the skin had been split are as much as 38%, even when the material is divided into two groups only, animals under one year old and animals over a year old (Bujalska *et al.*, 1965). The error increases in different groups to 50 or 70%, when three age groups are distinguished. Estimates of age based on inspection of the skeleton of the forearm and ossification of other parts of the hares' skeleton, and also on the weight of the eye lens exhibit a much higher, although far from perfect, percentage of agreement (74—88%). It must be added that serious differences may arise in estimating the age composition of a hare population by Stroh's "field" method at the beginning and towards the end of the shooting season. The

error increases as the epiphysal thickening gradually disappears. In the transitional group with the disappearing thickening there was 70% of incorrect identifications (Bujalska *et al.*, 1965). Similar results were also obtained by Wight & Conaway (1962) for *S. floridanus*. We must therefore treat certain studies, giving indices of the percentages of hares under one year old in a population, with a considerable dose of scepticism (cf. also tab. 1). Data of this type, such as are included in the study by Jezierski (1965) or Czaplińska *et al.* (1965) may therefore be burdened with considerable error.

From the above it can be seen that the problem of the age structure of a population is still unsolved, and great care should be exercised in taking as a basis indices of age so far available, when establishing the numbers of hares to be obtained.

III. DEGREE OF PARASITISATION

The highest indices of extensiveness of parasitisation, for both parasites of the alimentary tract and for mites, were obtained from the spring period (March—June), the peak in the case of mites occurring slightly later (Czaplińska *et al.*, 1965; Wasylik, 1965). This would therefore constitute one more critical period in the life of the hare over the course of the year. The question next arises as to what effect extensiveness and intensiveness of parasitisation have on the population, and whether the high degree of infestation may exert an unfavourable influence on the life processes, which in turn might produce serious biological consequences (for instance decrease in the number of young born as the result of resorption of embryos in intensively infested females).

The preliminary investigations referred to above do not make it possible to form an opinion on problems of this kind, on account of the fact that the material was somewhat scanty and also that it related to one year only.

IV. SHOOTING SEASON

The period of utilisation of the hare population should take place at the time of maximum development of the young hares and when the adult individuals are completely inactive sexually. This is obvious from the purely economical calculation aimed at obtaining the greatest mass of meat, and most valuable fur (winter), while leaving the basic stock undisturbed.

With regard to the hare's reproduction we must put on record that pregnant females were not found to occur from October to December. The

first pregnancies were observed in 1959 as early as mid-January, in a fairly large percentage of females (about 20%) — R a c z y ń s k i (l.c.). If monthly fluctuations at the beginning and possibly at the end of the reproduction period are taken into account, absence of sexual activity would occur only in November and December.

In November over 20% of the hares still have summer coats, of far less value as industrial raw material. In December only a small percentage of the population (chiefly individuals less than one year old) is still in moult. From December to February inclusive almost all the hares have winter coats (B o r o w s k i, 1964).

The data given by C a b o ń - R a c z y ń s k a (1964a) on increase in body weight in young hares indicate that during the late autumn period and even in the winter (December, January) a large percentage of the young

Table 2.

Body weights and percentages of individuals weighing less than 3.0 kg in age classes I—III (up to one year old). Calculated after data given by C a b o ń - R a c z y ń s k a, 1964a, p. 236.

Month	Min.	Max.	Avg.	n	% of individuals with body weight of 3 kg.
X	1.75	4.25	3.17	18	37
XI	2.50	4.00	3.25	12	
XII	2.25	4.25	3.13	29	59
I	3.00	4.50	3.72	31	13
II	2.75	4.50	3.70	29	7

hares in age classes I and II (up to about 8 months) increase their body weight and have not yet reached 3.0 kg. From October to December the percentage of such individuals varies from 37 to 59 (Table 2).

Unfortunately we have no adequate data on intensified mortality among hares in different months of the year. R i e c k (156b) theoretically estimates the lose in young hares during the autumn as over 50%. Only if original factual data were obtained would it be possible finally to establish the advantages which we might secure as the result of the individual development of young hares, by planning the most intensive shoots for December up to mid-January. It is a question here of the differences which arise in relation to losses in the hare stock as the result of natural mortality in October and November. It would, however, seem that shifting intensive shoots to December and the first half of January (January pregnancies do not promise great increase in the population)

would make it possible to obtain hares with the maximum mean body weight and fur of the highest industrial value, but it must be emphasised that these data are based on investigations made only over a one-year cycle and therefore can serve only as a pointer. If, however, these factors are born in mind, and their variations determined over the space of several years with different biometeorological conditions, it will probably be possible so to regulate the shooting season as to ensure the greatest possible productivity from the shooting areas.

V. CONCLUSIONS

1. The series of studies carried out as a basis for large scale research on control of density and productivity of the European hare provide a very important supplement to our knowledge of the biology of this species and form a good starting point for the ecological research planned for the immediate future in Poland.

2. The material elaborated by Raczyński (1964), defining the reproduction potential of the hare as 7.4 young from one sexually active female and 3—4 litters yearly — relates to one year's cycle only. As it may form a basis for assessing the effectiveness of counteracting mortality among young hares in shooting areas it is essential to find out how much these values may fluctuate over the period of several years.

3. Discovery of the high rate of embryonic mortality, particularly during the spring period, should be followed by determination of the regularity of this phenomenon over a period of several years. It is also necessary to investigate its causes and means of counteracting mortality among young hares during the autumn period.

4. The problem of estimating age, one of the fundamental points making correct control of the development of the hare population possible, still remains an open one. Continued research is essential on methods of establishing the absolute age of the individuals, at least in one-year divisions of accuracy, based on material consisting of animals of known absolute age and living under natural conditions.

5. One of the open questions is that of the dynamics of parasitisation of the hare population and effect of parasites on mortality and the basic life processes.

6. Shoots from the beginning of December to mid-January guarantee the maximum mean weight of the hares during the shooting season, and the highest industrial value of the fur. The lack of determination of mortality over the yearly cycle makes completely rational regulation of the hare shooting season impossible.

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BADANIA NAD ZAJĄCEM SZARAKIEM. X. DOTYCHCZASOWE WYNIKI BADAŃ W POLSCE I KIERUNKI DALSZYCH PRAC

Streszczenie

1. Wykonana jako podstawa do szerokich badań nad kierowaniem zagęszczeniem i produkcyjnością populacji zająca szaraka seria prac, szeroko uzupełnia wiadomości z zakresu biologii tego gatunku i jest dobrą bazą do prowadzonych i planowanych na najbliższą przyszłość badań ekologicznych w Polsce.

2. Materiały Raczyńskiego (1964) określając potencjalny rozród zająca na 7,4 młodych od samicy płciowo aktywnej i 3—4 miotów rocznie — dotyczą tylko jednego cyklu rocznego. Ponieważ mogą być one podstawą do oceny efektywności przeciwdziałania śmiertelności młodzieży w łowiskach, należałoby stwierdzić jakie wahania mają te wartości w cyklu wieloletnim.

3. Stwierdzenie wysokiej śmiertelności zarodkowej, szczególnie w okresie wiosennym, powinno pociągnąć za sobą ustalenie prawidłowości tego zjawiska w okresie wieloletnim. Konieczne jest również podjęcie badań nad jego przyczynami i sposobami przeciwdziałania śmiertelności w okresie jesiennym.

4. Problem oceny wieku, jeden z podstawowych dla możliwości prawidłowego kierowania rozwojem populacji zająca, pozostaje nadal otwarty. Konieczne są dalsze badania nad metodyką ustalania bezwzględnego wieku osobnika, przynajmniej w jednorocznych przedziałach dokładności, w oparciu o materiał zwierząt o znanym wieku absolutnym i żyjących w warunkach naturalnych.

5. Jednym z otwartych problemów pozostaje kwestia dynamiki zapasożycenia populacji zajęczych i wpływu pasożytów na śmiertelność i przebieg podstawowych procesów życiowych.

6. Polowania w grudniu do połowy stycznia gwarantują największą średnią wagę bitych zajęcy, w dopuszczalnym okresie polowań oraz najwyższą przemysłową wartość futra. Brak określenia śmiertelności w cyklu rocznym nie pozwala na zupełnie racjonalne regulowanie okresu polowań na zające.