DANISH REVIEW OF GAME BIOLOGY Vol. 8 no. 2

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HANS JØRGEN DEGN

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Резюме на русском языке

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COMMUNICATION NO. 105 FROM VILDTBIOLOGISK STATION
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CONTENTS




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## Introduction

In spite of the fact that the squirrel *(Sciurus vulgaris* LINNAEUS 1758) is widespread and fairly common over most of Denmark, and is furthermore the only Danish mammal which is exclusively active in daytime, there are still large gaps in our knowledge about this species. In order to determine distribution and colour variation, an investigation covering the whole country was carried out during 1970 and 1971 (DEGN, in preparation). At the same time, specimens were collected for examination. In particular, the purpose of the study was to investigate the questions of systematic position and reproduction in Danish squirrels, as the information available on these matters was either extremely insufficient or totally lacking altogether. In order to evaluate the data correctly, it was necessary to know the age of the animals. This was determined by independent methods, and as these were applied to the same animal it was possible in most cases to compare them. The reliability of the different methods was also evaluated.

The author would like in particular to thank FINN KRISTOFFERSEN, assistant at the Game Biology Station, P. KJELGAARD, gamekeeper on Mejlgård estate, and MOGENS FOG, forest proprietor, Gudbjerg, who have provided the greater part of the material. In addition, thanks are due to cand. mag. P. VALENTIN JENSEN for passing on records and for allowing access to the collections of the Zoological Museum in Copenhagen. Particular thanks are due to mag. scient. BIRGER JENSEN for much informative discussion.

## Material

The material collected comprises 407 animals from the period August 1968 to January 1972. Since 1968 there has been a close season for squirrels from March 1 until June 15, and thus only two animals (both killed by vehicles) originate from this period. As the collection of specimens extended over some years, most of the specimens have been kept in a deep-freezer for shorter or longer periods. For most purposes, this has no practical importance, but one exception is the use of

| Locality<br>*Lokalitet* | Period<br>*Periode* | Nos.<br>*Antal* |
|---|---|---|
| Kalø | Nov. 1969–Jan. 1972 | 306 |
| Mejlgård | Jan. 1970–Feb. 1971 | 66 |
| Gudbjerg | Aug. 1970–Jan. 1971 | 14 |
| 11 different localities<br>*11 forskellige lokaliteter* | Aug. 1968–Aug. 1971 | 21 |
| Charlottenlund | May 1939–Mar. 1956 | 50 |
| Bornholm | Feb. 1942–Feb. 1943 | 58 |

Table 1. The distribution of the material with regard to locality and period of collection. The material from the first four localities is to be found at the Game Biology Station, while that from the last two is from the Zoological Museum, Copenhagen.

*Tabel 1. Fordeling af materialet med hensyn til lokalitet og indsamlingsperiode. Materialet fra de første 4 lokaliteter er samlet på Vildtbiologisk Station, mens materialet fra de 2 sidste er fra Zoologisk Museum, København.*

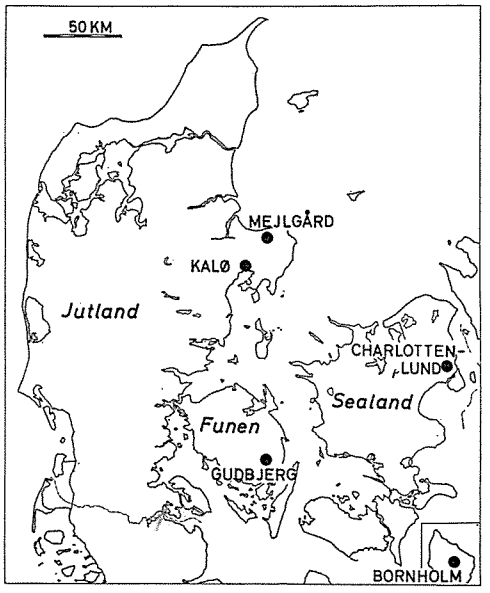


Fig. 1. Localities of origin of the material given in Table 1, together with place names used.

*Fig. 1. Lokaliteter hvorfra materialet i tabel 1 stammer, samt anvendte stednavne.*

the eye lens for age determination, which is discussed on p. 12.

A summary of the origin of the material is given in Table 1. The first part of the table comprises animals collected in connection with this study, while the last part comprises specimens from the Zoological Museum of Copenhagen which were only used for systematic studies. The geographical position of the localities is indicated in Fig. 1.

## Systematic position

In spite of the existence of several works on squirrel systematics, only little is known of the systematic position of Danish squirrels. DEGERBØL (1950) reports that *Sciurus vulgaris vulgaris* L. 1758 occurs throughout the country. However SIDOROWICZ (1958) indicates on a map that *Sciurus vulgaris fuscoater* ALTUM 1876 occurs in Jutland, but no information is given for the larger islands to the east. No studies on the systematics in Denmark exist, and the reason for indicating the presence of the last mentioned subspecies may be that it is found in northern Germany, and that there apparently are no geographical barriers between the two countries. However, the case is that in southern Jutland squirrels are almost non-existent in spite of many forests in the region, and there may be an as yet unknown natural barrier (DEGN, in preparation). Furthermore, squirrels of unknown origin have been released at many places in the country, and it is thus no longer possible to expect to find that the original conditions still prevail. For these reasons it is of interest to discover which subspecies is present, not only from purely systematic interest but also to allow evaluation of the results with regard to age determination and reproduction in other subspecies.

## CRANIAL MEASUREMENTS

Over most of its area of distribution, the squirrel is polymorphic, that is to say, it occurs in several different colour variants. Due to the great amount of variation in colour, it must be considered too unreliable to base the systematics of subspecies on the colour of the fur alone. The author agrees with SIDOROWICZ (1958,

1961) that identification should mainly be based on morphological characters and especially on cranial measurements.

Four sets of measurements were made with an accuracy of 0.1 mm. on the crania available. These were of condylobasal length, zygomatic breadth, interorbital constriction, and length of the diastema. In that which follows only the condylobasal length has been used, as the other characters were associated with much greater uncertainty of measurement and variation. For example, in the upper margin of the orbit (formed by the frontal bone), the supraorbital notch which varies in size occurs just at that point where the interorbital breadth is measured.

Several geographically separate squirrel populations exist in Denmark (DEGN, in preparation), and it was only possible to obtain a sufficient number of specimens for analysis from some of them. These were the squirrel populations of Bornholm (released about 1886), North Sealand (released), and Jutland (origin unknown). Although the material of the Funen population can hardly be considered fully satisfactory, it has been included as it is the only material from an original population and therefore of special interest. Naturally the results from this last material must be considered with some caution.

The distribution of the condylobasal length of the five population samples is illustrated in Fig. 2. The average values for the Scandinavian *Sciurus vulgaris vulgaris* L. 1758 and the Mid-European *Sciurus vulgaris fuscoater* ALTUM 1876, given by SIDOROWICZ (1961) are also shown on the figure. These two subspecies are the only ones relevant in this case. It is evident that the measurements of the Bornholm population sample are in agreement with those of the Scandinavian subspecies, while the others are much more similar to those of *Sciurus vulgaris fuscoater* ALTUM 1876. Although the average values may be affected by unknown factors in the sample (e.g. the age distribution), the difference is still very clear.

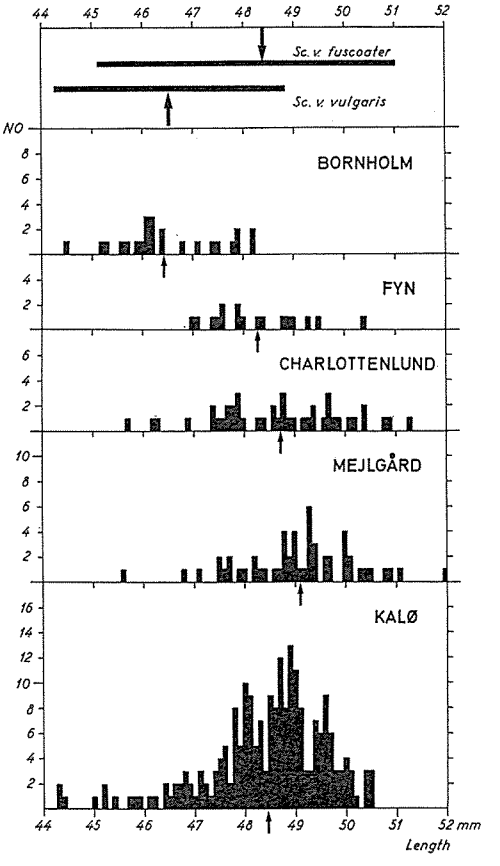


Fig. 2. The distribution of condylobasal length values from 5 samples of squirrels from Denmark. For each population, the average is indicated by an arrow under the x-axis. For comparison, the average and range of values for the two subspecies occurring in neighbouring countries is given.

*Fig. 2. Fordelingen af condylobasallængden i 5 prøver af danske egern. For hver bestand er gennemsnittet angivet med en pil under x-aksen. Til sammenligning er anført gennemsnit og variationsbredde for de to underarter, der forekommer i nabolandene.*

*Importance of age composition*

As the age of the animals from Kalø was known (see p. 15), it was possible to separate the young animals from the adults. Then it is possible to determine how large the difference is between a randomly composed sample consisting of young and older animals and one consisting entirely of sexually mature, i.e. adult, animals. The condylobasal length of juvenile and adult animals from Kalø is indicated in Fig. 3. The average value of this parameter for the 132 adult animals was 48.94 mm., which is a small increase in relation to the value of 48.41 mm. for the total sample of 216 individuals. The average condylobasal length for the 84 juveniles in the present sample was 47.59 mm. This value is rather a chance one however, as the specimens were collected while they were still rapidly growing. Thus the time of collection of specimens will have some influence on the average value of this parameter.

A consequence of the above information is that caution must be taken in employing samples of unknown age composition in systematic studies. The average for a given sample will vary in relation to the time of year, as a result of variation in the proportion of young and the growth of these juveniles. The use of randomly composed samples, which has almost exclusively been the case until now, may perhaps prove to be less than completely reliable. The comparison of adult animals of the same age class would probably provide more reliable results, but this would require stricter conditions for the size of the sample.

*Difference in size between sexes*

In many animals there is a difference in size between the sexes, and the data from the material available is sufficient to investigate this factor. The condylobasal length of adult animals of each sex from Kalø is shown in Fig. 4. The value for females is on average a little larger than that for males, being 49.08 mm. (n = 61) as opposed to 48.81 mm. (n = 71). This difference is statistically significant, but the difference of 0.27 mm. must however be considered as little in relation to the range of values.

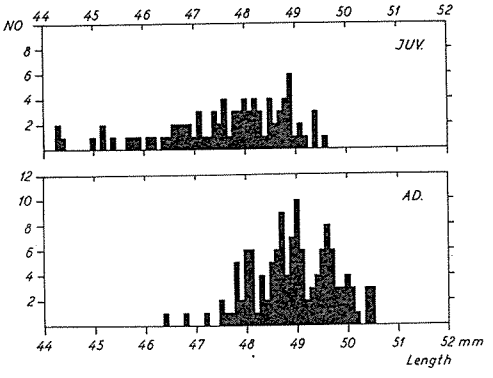


Fig. 3. Condylobasal length values for juvenile and adult animals from Kalø, Djursland.

*Fig. 3. Fordelingen af condylobasallængden hos juvenile og adulte dyr fra Kalø, Djursland.*

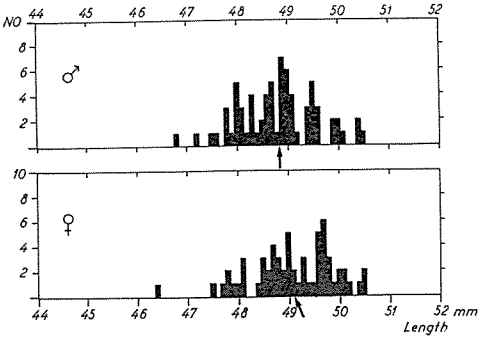


Fig. 4. The distribution of condylobasal length values in the sexes; only adult animals from Kalø are included. The average value is indicated by an arrow under the x-axis.

*Fig. 4. Fordelingen af condylobasallængden hos de to køn. Kun adulte dyr fra Kalø er medtaget. Gennemsnittet er angivet med en pil under x-aksen.*

## SIZE AND WEIGHT

Cranial measurements are often used as an indicator of size, as they have several advantages over body weight. For instance, they do not depend on the immediate state of nutrition, stomach contents, gravidity and other physiological changes, and in relation to body measurements they can be taken more accurately. As a result the variation is reduced. Nevertheless, it is of interest to consider the size and weight of whole animals. Consequently, the specimens collected were weighed to the nearest gram, and body length, tail length and total length measured with an accuracy of 1 mm. The corresponding information for the populations of northern Sealand and Bornholm was obtained from the records of the Zoological Museum, Copenhagen. This information is presented in Table 2. It is quite evident that the squirrels of Bornholm are again clearly different from the others as they are much lighter, being only 274 g. in weight. The remaining populations are the same in weight, just a little over 350 g. Although squirrels from Bornholm are only 3/4 of the weight of the other squirrels, the body length is about the same size as that of squirrels from eastern Jutland (Kalø and Mejlgård districts), and only a little less than those of northern Sealand. However, the tail length of the Bornholm squirrels is clearly less, 164 mm. as compared to 180 mm. The lesser weight and tail length of the Bornholm squirrels clearly supports the view stated previously on their systematic position, based on cranial measurements. The weight differences among the remaining populations are very little, and as they may be due to current physiological differences, they therefore give no further grounds for discussion. Nor is the difference in body length necessarily of any consequence; it is only the animals from northern Sealand which differ from the rest, and this may be due to a difference in methods of measurement.

### *Size and weight in adult animals*

For the samples described above, no mention was made of the age composition, which naturally can affect the average values obtained. As in the case of cranial measurements, the age determined material from Kalø will also be used here

| | Weight (g.) *Vægt* | n | Body length (mm.) *Krops-længde* | n | Tail length (mm.) *Hale-længde* | n | Total length (mm.) *Total-længde* | n |
|---|---|---|---|---|---|---|---|---|
| Bornholm | 274 | 58 | 215 | 60 | 164 | 50 | | |
| Charlottenlund | 362 | 50 | 227 | 83 | 181 | 85 | | |
| Kalø | 356 | 299 | 212 | 292 | 181 | 294 | 397 | 232 |
| Mejlgård | 357 | 66 | 213 | 65 | 178 | 65 | 390 | 45 |

Table 2. The average values of length and weight of four squirrel populations in Denmark. No allowance was made for age or sex.

*Tabel 2. De gennemsnitlige mål og vægte for 4 danske egernbestande, uden hensyntagen til alder og køn.*

for a closer study of the difference between the values for adult animals and for a randomly composed sample.

These values are given in Table 3 for juvenile and adult animals and for the total sample. Comparing the data for adult animals with that for the total sample, it is surprising that the measurements for body and tail do not show a greater difference. The difference in weight of 17 g. is also rather small, especially in consideration of the large individual variation. It must, however, be emphasized that in stating size, it is most correct to use data from a sample of known age composition, even though in practice the difference is not particularly large.

*Comparison of the sexes*

It was mentioned previously (p. 6) that on average the crania of female squirrels were a little longer than those of males. This prompts the question of whether there is a corresponding difference in body weight and size. The average values and ranges of the weight and size of the sexes is illustrated in Table 4. It is evident that the averages of weight and size in females are slightly larger than in males. This is in agreement with their greater cranial size. The difference in tail length is however exceptionally large, that of females being on average 10 mm. greater. On examination of the distribution of the results, it is seen that tail length in females follows a normal distribution, whereas in males many tails lie outwith the normal as they are too short. In preparation of the skins it was noticed that some of the tails (especially those of males) were shortened or broken. This excludes the possibility of there being an inherited difference in tail length; the reason for the

| | Adult & juvenile | | Adult | | Juvenile | |
|---|---|---|---|---|---|---|
| | | n | | n | | n |
| Weight (g.) *Vægt* | 356 | 299 | 373 | 173 | 331 | 126 |
| Body length (mm.) *Kropslængde* | 212 | 292 | 216 | 167 | 206 | 125 |
| Tail length (mm.) *Halelængde* | 181 | 294 | 179 | 170 | 182 | 124 |
| Total length (mm.) *Totallængde* | 397 | 232 | 400 | 132 | 393 | 100 |

Table 3. Comparison of weight and length of adults and juveniles, separately and together, from Kalø estate.

*Tabel 3. Sammenligning af mål og vægt for juvenile og adulte dyr fra Kalø, hver for sig og sammen.*

| | Males *(hanner)* | | | Females *(hunner)* | | |
|---|---|---|---|---|---|---|
| | Average | Range | n | Average | Range | n |
| Weight (g.) *Vægt* | 371 | 310–431 | 92 | 376 | 295–450 | 81 |
| Body length (mm.) *Kropslængde* | 215 | 193–243 | 90 | 217 | 202–233 | 77 |
| Tail length (mm.) *Halelængde* | 174 | 110–201 | 92 | 185 | 150–209 | 78 |
| Total length (mm.) *Totallængde* | 395 | 333–432 | 71 | 406 | 370–444 | 58 |

Table 4. Weight and length of adult squirrels from Kalø estate.

*Tabel 4. Vægt og mål for voksne dyr fra Kalø.*

difference may be that the tip of the tail gets bitten off in contests. BROWN & YEAGER (1945) also found that tails of 1/8 of all *Sciurus niger* and *Sciurus carolinensis* were affected, and assumed that this was due to contests and mating chases.

## DISCUSSION AND CONCLUSIONS

In general, cranial measurements in animals are good indicators of size. This is also the case for the squirrel, in which there is a good correlation between cranial measurement and body size. Even the small difference between the cranial lengths of males and females is reflected by a similar difference in body size.

All the data indicate that the Bornholm squirrel is considerably smaller than specimens from the other populations. The size of the former is the same as that of a Scandinavian squirrel, whereas the remainder are of the same size as the German subspecies.

Although coat colour cannot be used as an independent criterion, it may be taken into consideration in identification work. Bornholm squirrels also resemble Scandinavian ones in appearance, as the tail and ears appear dark, due to the black colour of the outer end of the hairs. In winter, the sides of the body become more grey than in the other populations, and where the coloured side of the body meets the white underside there is a rust-red transition zone.

In other parts of the country than Bornholm one of these characteristics may occasionally be found, but never all of them in conjunction. The occurrence may be a result of one of the numerous releases of an introduced squirrel. It is difficult to describe the appearance of squirrels in the rest of Denmark as there is such great variation. Generally, it is however true to say that the extreme colour differences occurring in an individual of the Bornholm population are seldom found elsewhere. The population of northern Sealand is very much dominated by light-coloured reddish animals, while the remaining populations are polymorphic, where either black or very dark individuals are occurring (DEGN, in preparation). On the basis of the above information, it is presumed that the Bornholm squirrel belongs to the subspecies *Sciurus vulgaris vulgaris* L. 1758, whereas squirrels from northern Sealand, Funen and Djursland (eastern Jutland) are presumed to belong to the subspecies *Sciurus vulgaris fuscoater* ALTUM 1876.

## Age determination

In discussing reproduction in the individual and turnover in the population, it is necessary to employ certain criteria for separation into sexes and age classes. In the squirrel, no problems arise in distinguishing between the sexes, even in very young animals. It is however not possible to separate the different age classes offhand, and no studies of the European squirrel exist in which suitable methods are described. In the present study, the only differentiation made is between juvenile and adult animals. The age distribution of the material available was unknown, and therefore it was found necessary to use more than one method to ob-

tain a better degree of accuracy. Therefore in this study three criteria were employed; those of epiphyseal cartilage, baculum weight, and eye lens weight. Initially each criterion is treated independently of the others, and then they are compared to examine their applicability in age determination.

## THE EPIPHYSEAL LINE

In the long bones of the limb, growth occurs in two areas a few millimetres from the ends. These zones are two cartilaginous plates between the long shaft of the bone, or diaphysis, and the two shorter end regions or epiphysis, and are known as epiphyseal cartilage. This cartilage is altered towards the termination of growth and is replaced by bone; ossification often takes place at different times in the various limb bones. The sequence of ossification in the squirrel has not been studied in detail, but in most work the distal end of the radius and ulna has been used.

In the squirrel, two different methods have been used to examine the extent of ossification; radiography (PETRIDES 1951, CARSON 1961, BEALE 1962 and FISHER & PERRY 1970), and manual examination of the surface structure of the cleaned bones (KIRKPATRICK & BARNETT 1957). In the present study, the cleaned bones of the forelimb were examined visually and manually. It was found that the distal end of the radius was the most suitable for study, as it generally closed together a little later than that of the ulna. The bones were placed into monthly groups to determine how late in the year the criterion could be used, that is to say, at what time so many of the epiphyseal cartilages were ossified that the uncertainty became too great. In each month, specimens were divided into juveniles and adults and occasional indeterminate cases. Juveniles could be separated into two further groups, depending on whether the epiphysis and diaphysis separated on skeletisation. The treatment was fairly gentle (see p. 12), and thus when the parts separated it indicated that ossification was far from complete. The results from July

| Month<br>*Måned* | Juveniles without epiphyseal knob<br>*Juvenile uden epifyseknop* | Juveniles with epiphyseal knob<br>*Juvenile med epifyseknop* | Adults<br>*Adulte* | Doubtful<br>*Tvivlsomme* | Total<br>*I alt* |
|---|---|---|---|---|---|
| July | 5 | 0 | 16 | 0 | 21 |
| Aug. | 11 | 0 | 24 | 0 | 35 |
| Sep. | 25 | 3 | 55 | 2 | 85 |
| Oct. | 37 | 12 | 49 | 1 | 99 |
| Nov. | 13 | 4 | 20 | 2 | 39 |
| Dec. | 6 | 11 | 11 | 0 | 28 |
| Jan. | 1 | 8 | 14 | 0 | 23 |

Table 5. The distribution during the months of July to January of different age groups determined by visual and manual examination of cleaned radii.

*Tabel 5. Fordelingen i månederne juli til januar i forskellige aldersklasser ved hjælp af visuel og manuel undersøgelse af rensede radii.*

up to and including January are given in Table 5.

Even towards the end of February, bones with decidedly juvenile characteristics may be found. At this time the youngest animals must be at the latest. They thus have the same age as that of the oldest juveniles in September, and although a certain degree of variation may perhaps occur, it is presumed that animals which mature during the summer also show juvenile characteristics at the age of six months. In fact, in September 98 % of the bones collected can be determined without difficulty, and 89 % of the juvenile bones do not have a permanently fixed epiphysis. If the epiphysis of animals born in early spring grew together so soon that these animals were classified as adults towards the end of the year, then the percentage of juveniles in the population would fall during the autumn. This in fact it does not do. This evidence would appear to support the view that this criterion can be used with a fair degree of accuracy up to and including the month of September. Later in this paper the method will be taken in conjunction with others, thereby obtaining a greater degree of accuracy.

## THE BACULUM

In the males of many different mammalian species, a special bone known as the baculum occurs in the penis. In young animals it is little developed, but during sexual maturation it grows fairly rapidly, reaching dimensions characteristic of that of the adult male. This rapid growth from one stage to another enables the division of a collection of bacula into two separate groups, sexually mature and sexually immature animals.

As yet, this method has not been used with European squirrels; the only detailed study is that of KIRKPATRICK & BARNETT (1957) on the grey squirrel *(Sciurus carolinensis)*. They reported that both the weight and length of the baculum were acceptable criteria, weight being the better of the two.

The appearance of a macerated baculum is shown in Fig. 5. The terms dorsal and ventral refer to the orientation of the bone when the tip, or plate, points forwards towards the skull. In live animals the end of the penis points backwards and downwards. The baculum in the Danish material differs from that described by WADE & GILBERT (1940), who consider that a ridge passing in a curve over the dorsal side of the shaft is also part of the baculum. In the bacula of *Sciurus vulgaris* examined by the author, the ridge was not found to be ossified, and it disappeared entirely during maceration. This is in agreement with KRÖLLING (1921), who performed a histological study of the same species, and found that even in mature males this ridge was cartilaginous in nature. Nor do HOWELL (1938) or KIRKPATRICK & BARNETT (1957) in their studies

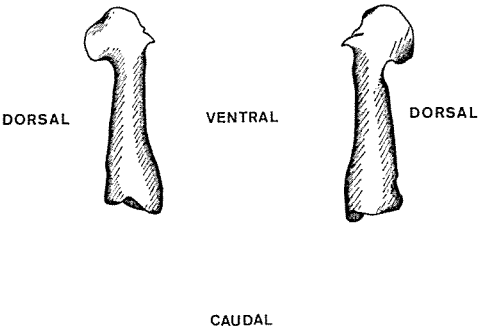


Fig. 5. The appearance of the skeletized penis bone (baculum) of *Sciurus vulgaris* L.

*Fig. 5. Udseende af den rensede penisknogle hos* Sciurus vulgaris *L.*

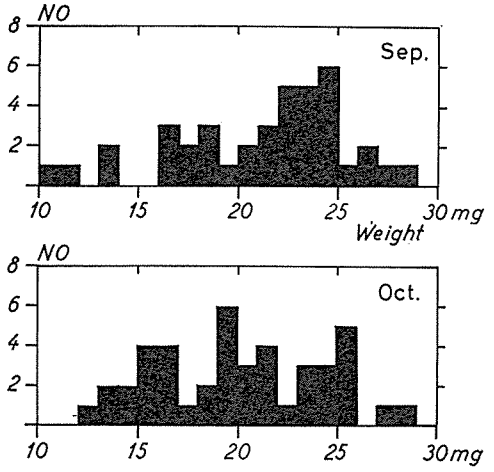


Fig. 6. The distribution of values of the baculum weight of squirrels from Kalø collected in September and October.

*Fig. 6. Fordelingen af baculumvægte hos egern fra Kalø fra september og oktober måned.*

produce any evidence that the ridge in the grey squirrel is a part of the baculum. The difference of opinion on this point may be due to the methods used for the removal of flesh; in this study material was kept in water in plastic bags for 1–2 months at 30° C, after which time the skeletons could easily be rinsed clean.

When the bacula were quite dry, they were weighed with an accuracy of 0.1 mg., and the length was measured with an accuracy of 0.1 mm. On examining the relationship between the two sets of figures it was found that the length varied more than the weight. This is due to the fact that much of the increase in weight follows a thickening of the shaft of the bone, without a corresponding increase in length. Subsequently therefore, only the weight of the baculum is used.

The distribution of baculum weights from the months of September and October is illustrated in Fig. 6. It is evident from the figure that if only the baculum weight was used as an age criterion, it would not be possible to make a clear distinction between juvenile and adult animals.

## THE EYE LENS

In the majority of mammals the lens of the eye continues to grow throughout life. LORD (1959) was the first to show that the dry weight of the lens of the cottontail rabbit *(Sylvilagus floridanus)* can be used as an indicator of age. This method was soon applied to many other mammals, including squirrels. The results were not always similar, as in some cases it was found not only possible to distinguish between adult and juvenile animals, but also between spring and summer litters (BEALE 1962). Others even found it possible to estimate age classes in adult animals (PAVLOV & SMYSJLJAJEV 1968, FISHER & PERRY 1970). However, KARPUKHIN & KARPUKHINA (1971) emphasize that in animals of known age in captivity, it was only possible to distinguish between animals of 2–4 and 6–9 months, but not between all other age groups.

The material from Denmark consisted of 78 individuals collected during October–December 1971. The remainder of the material collected (329 animals) was deep-frozen with the eyes in place, and on thawing out the material it was evident from a visual examination that the surface of the lenses was very glazed, and therefore they were not used. The lenses

used were removed as quickly as possible after the death af the animal, and not later than 24 hours afterwards, the body being kept in a cold place. The lenses were then kept in a 10 % solution of formaldehyde for about 2 months, after which they were dried for 48 hours in an oven at 80° C. Subsequently they were weighed with an accuracy of 0.1 mg.

The distribution of the eye lens weight figures for 78 animals is given in Fig. 7. In several cases, either one or both of the lenses were damaged by shotgun pellets. Where only one lens was intact, its weight alone was used. For animals with both lenses intact the average value was taken, as no significant difference between the weights of right and left eye lenses was found.

In the figure, there is an obvious division of the distribution at a weight of about 30 mg. Although no comparison with other methods is to be made as yet, it is presumed on the basis of other knowledge of the applicability of the method that this division is one between juvenile and adult animals.

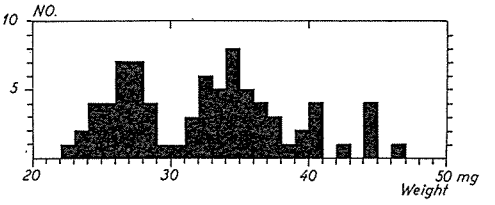


Fig. 7. The distribution of the eye lens weight for 78 squirrels collected from October to December 1971.

*Fig. 7. Fordeling af øjelinsevægten hos 78 egern fra Kalø fra oktober til december 1971.*

## COMPARISON OF THE METHODS

So far, the three methods of age determination have been discussed independently, and only those conclusions have been drawn which would have been possible by using a particular method on its own. In a number of cases, the three methods were applied to the same material, and it is thus relevant to compare the results and gain an estimate of their reliability. In this way it is possible to determine which of the methods, alone or in conjunction with others, is the most reliable.

*Eye lens and epiphysis*

Corresponding values of eye lens weight and epiphyseal closure were obtained from 67 animals collected during October–December 1971. In Fig. 8, these values are illustrated with respect to their distribution in time. There is good agreement between the two methods; all the animals which were classified as juveniles on the basis of epiphyseal cartilage had an eye lens weight of less than 31 mg., whereas those with a greater eye lens weight were classified as adults on the basis of the epiphyseal closure. The material from November and December was far too little to allow conclusions to be made, but that from the latter part of October was numerous and divided into two clearly separate groups. Thus the two methods can be used for age determination until the end of October.

*Baculum and epiphysis*

The eye lens material originated from a short period of time, but fortunately it is possible to compare two criteria which take more account of the influence of time, as the data concerning these criteria originate from the whole of the open season (June 16–February 29). In Fig. 9 the weight of the baculum through the year is

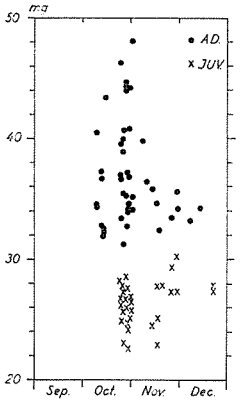


Fig. 8. The distribution in time of values of the eye lens weight from squirrels from Kalø. Two separate symbols indicate the result of age determination based on epiphyseal closure of the limb bones.

*Fig. 8. Den tidsmæssige fordeling af øjelinsevægten for egern fra Kalø. Ved hjælp af to signaturer er resultatet af aldersbestemmelsen på grundlag af epifyselukning hos de samme dyr angivet.*

compared with age determination based on epiphyseal closure. In the autumn months there is some degree of overlap of the baculum weights of the juvenile and adult groups. The baculum weight of 92 % of juvenile animals during August–December does however lie under 20 mg., while for 88 % of the adults it is greater than 20 mg. During January and February the baculum weights of juveniles are however so great that it is not possible to separate them from adults. In addition, the possibility always exists that some epiphysis have become ossified by this time, even although the individuals were born in the previous year.

If only these two criteria were available for use, one would have to presume that they were equally good. If some degree of inaccuracy is permissible, then they can be used up to and including the month of October. The material from November and December was insufficient to gauge the degree of inaccuracy present, but it is quite plain that by January and later the methods cannot be used any longer.

*Baculum and eye lens*

The final pairing of criteria is the comparison of the baculum weight with eye lens weight. As the eye lenses originate however from such a short period of time, the time factor in this case will be disregarded. In this way the last pairing of criteria can be carried out, and all three methods compared at the same time.

In Fig. 10, the two sets of weights are

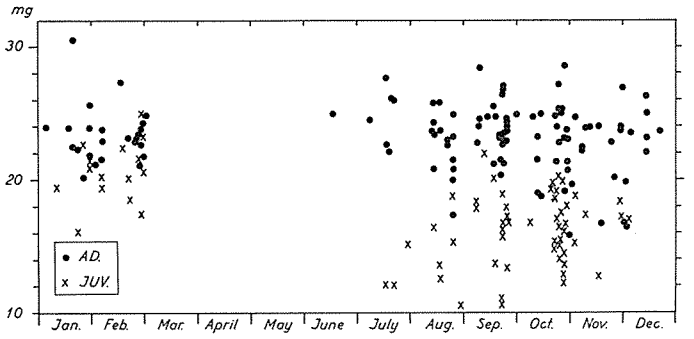


Fig. 9. The weight of the baculum in relation to the time of shooting of each individual. Two separate symbols indicate the result of age determination based on epiphyseal closure.

*Fig. 9. Baculumvægten angivet i forhold til nedlæggelsestidspunktet. Ved hjælp af to signaturer er resultatet af aldersbestemmelsen på grundlag af epifyselukning angivet.*

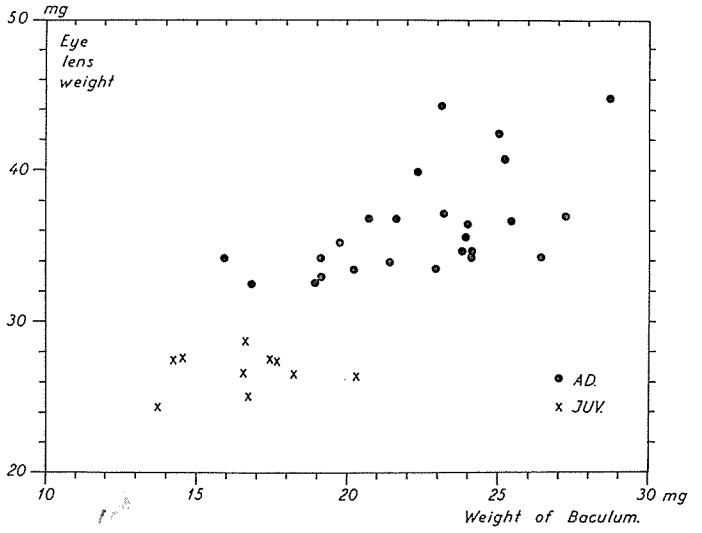


Fig. 10 Comparison of the three methods used for age determination. The weights of the baculum and eye lens are indicated on the axes, while ossification of the epiphysis is indicated by the symbols used in plotting the first two parameters.

*Fig. 10. Sammenligning af de tre anvendte aldersbestemmelsesmetoder. Ud ad akserne er vægten af baculum og øjelinse afsat, mens epifysens forbening fremgår af signaturen der er anvendt til afsættelse af de to første størrelser.*

drawn as the variables. In the diagram, two symbols were used to indicate whether a particular animal was classified as juvenile or adult from examination of epiphyseal closure. The two symbols comprise two separate groups of points; this is understood to indicate that the age determination was performed correctly. The distribution also shows that there is an overlap in the case of the baculum weight, which implies that some degree of uncertainty will be present if it is used as the only criterion. If however the eye lens weight is used there is no overlap. It is also evident from the figure that with sufficient experience, it is possible to differentiate between juvenile and adult animals by examining the epiphyseal closure. As the majority of the material is from October, this conclusion must be restricted to apply up to and including this month. This is also true of the other two criteria.

## The breeding season

According to different authors, the time of birth of the first litter in Denmark varies from late February (Bræstup 1935) to April–May (Boas 1923). Most authors are agreed that there are two litters per year, but no mention is made of the time of birth of the second litter. This point has for instance relevance in relation to the fixing of the open season; in 1968 this was altered from the whole year round to include only the period June 16 to February 29.

It was intended to investigate the duration of the breeding period with the help of the material available. The material is more suited to such an investigation than

to a study of the number of litters, as it comprises only dead animals. Each specimen can of course only give an impression of an isolated case, and cannot explain what happens to a single individual over a longer period of time.

## MATERIAL AND METHODS

The majority of the material originates from the 407 animals mentioned previously (p. 3). In addition, cand. mag. P. VALENTIN JENSEN of the Zoological Museum, Copenhagen, kept records of the specimens sent to the Museum in 1942; this material has very kindly been made available to the author. It also covers the period during which the species is now protected, and will be used to give supplementary information on gravid females.

The time of sexual maturation has been studied for a few species of the genus *Sciurus*. The data obtained from various foreign species indicate that there is no particular pattern for the genus (ALLANSON 1933, BROWN & YEAGER 1945, BRAUER & DUSING 1961). The only information concerning the species in this study is a short note (ROWLANDS 1938). His figures indicate that in England there is a short anoestrus period in the autumn, although the material in exactly the period in question (September–November) is rather little.

The breeding season is usually defined on the basis of the condition of the females, but it is not impossible that a study of the sexual development of males might contribute to a more precise determination of the time limits of the breeding season. For this reason, two organs of special relevance were removed during the treatment of the animals shot. The size of the testicle is probably the most frequently employed measurement of sexual maturity in males. The testicles were dissected out and weighed with an accuracy of 0.1 g. The two Cowper's glands were very variable in size and occasionally very obvious. They consist of two spirally coiled glands, situated under the tail on each side of the root of the penis and the anus. They were dissected out to the point where they open out into the corpus spongiosum of the bulb, and weighed with an accuracy of 0.1 g. In cases in which the weight of the gland is given as 0.0 g., this indicates that their weight was considerably less than 0.1 g. and not that they were absent altogether. In young animals they are difficult to find as they are only about 3 mm. in diameter, but in the sexually active adult animals they may reach a diameter of about 20 mm.

In subsequent discussion, breeding period is taken as the time from when the young are born and until they can fend for themselves. The most direct method of determining the breeding period is to discover whether a female is suckling her young. On skinning the animals, the presence of large teats was recorded, as was the occurrence of mammary glands. If these were well-developed and functioning, they appeared as a thin greyish glandular mass on the inner side of the skin, where they were easily recognized.

The commencement of the breeding period can be determined by a study of the presence of embryos in the uterus. The uterus of every female was therefore removed and examined for the presence of visible embryos. It is certain that several very early embryos may have been overlooked in the examination, but as in so many cases, the results must be considered according to the means.

*Males*

In Fig. 11, the weight of the testicles of each individual is shown in relation to the date of shooting. The use of different symbols makes it possible to differentiate between juvenile and adult animals. The age determination criterion used was that of epiphyseal closure, as it was previously shown (p. 13) to be sufficiently accurate until the end of October.

Seasonal changes in testicular weight of adult males are best illustrated by the monthly averages indicated in the figure. In July a few of the testicles are of some weight, and comparison with the results for August, when no pair of testicles weighed more than 0.2 g., indicates that in July the testicles are in a state of degeneration. In the subsequent autumn months their weight begins once more to increase, and continues to do so until the monthly average weight reaches a maximum value in January. Whether the drop in the monthly value from January to February is a biologically genuine one cannot be stated, as there is insufficient data for the subsequent months.

The number of juvenile animals was much less, and no average value was calculated. It is evident however that the testicular weight in September and October is rather lower than that of the adult animals, indicating that growth begins sometime later. In January and February, with one exception the juvenile weights have reached the same level as the adult testicular weights.

It is not definite that the reproductive condition of the squirrel is alone associated with the size of the testicles, and therefore a very variable accessory gland is also taken into consideration. This is the paired Cowper's glands, and in Fig. 12 the weight of the two glands is shown in relation to the date of shooting of each individual. Different symbols indicate whether the animals were juvenile or adult, age determination being based on the epiphysis as before.

Only a few results from July were available, but on average they are greater than those of subsequent months. This would appear to indicate that just like the testicles, the Cowper's glands are in a state of degeneration in July. In the latter part of the year the glands are very small and only occasionally do they exceed 0.5 g. Even although the material cannot confirm it, the growth which takes place must happen very rapidly around the turn of the year, and much more rapidly than testicular growth which takes place gradually during the autumn. In the months of January and February the weight of a pair of Cowper's glands may reach as much as 5 g., but it never exceeds 2.2 g. in any of the animals classified as juveniles. There are amongst the adults many values however which are very low; these may originate both from older animals and from young of the previous year, in which the epiphysis is already ossified.

The reproductive ability of the male squirrel is certainly not determined by the size of the testicles alone, as it is extremely unlikely that those squirrels which in autumn have large testicles are able to reproduce while they possess such small Cowper's glands. In Fig. 11 and 12, the two sets of weights are shown independent of one another. In Fig. 13 the weights of the two organs are compared, to determine whether there is any association or regular relationship between the two. The majority of the paired results have fairly low values. Although the data available are of course single observations of the condition of an individual at the time of shooting, they originate from a relatively long period of time, and thus an indication of the course of development may nevertheless be gained.

It appears that the testicles grow fairly quickly to their maximum size, their weight normally being about 1 g. Only then do the Cowper's glands begin to grow, and their weight increases up to a value of 5 g., without any further increase in testicle size. ALLANSON (1933) found that in the grey squirrel there was a linear correlation between the two glands, but this is not the case here. The sequence of weight increase observed is also in agreement with the temporal difference in growth of the two organs, as is illustrated by a comparison of Figs. 11 and 12.

The weight of the Cowper's glands of all juvenile animals was less than 2.2 g., even in those animals with a maximum testicle weight. There appears to be a cluster of points where the weight of the Cowper's glands is at least 3.3 g., which are all from adult animals. The fact that they are clustered may possibly be due to

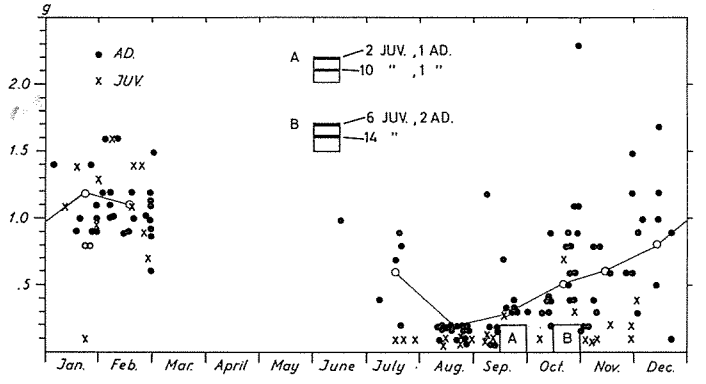


Fig. 11. Seasonal changes in the weight of the testicles of the male squirrel. Two separate symbols indicate the age determination on the basis of epiphyseal closure. The complete line connects up the monthly average for adult animals.

*Fig. 11. Ændringerne i vægten af to testikler i løbet af året hos hanegern. De to forskellige signaturer angiver aldersbestemmelsen på grundlag af epifyselukning. Den indlagte linie forbinder de månedlige gennemsnit for voksne dyr.*

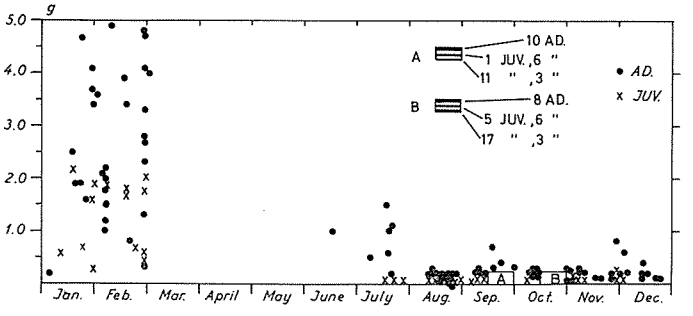


Fig. 12. The weight of the two Cowper's glands in relation to the time of shooting of each individual. Two separate symbols indicate the age determination on the basis of epiphyseal closure.

*Fig. 12. Vægten af to cowperske kirtler i forhold til nedlæggelsestidspunktet for hanegern. De to forskellige signaturer angiver aldersbestemmelsen på grundlag af epifyselukning.*

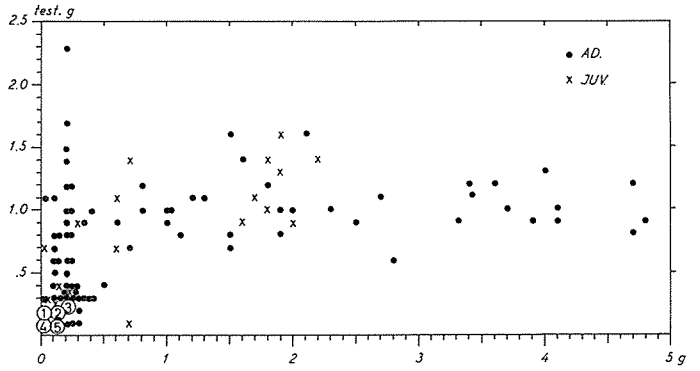


Fig. 13. The relationship between the weight of the testicles and the Cowper's glands in the male squirrel. The two separate symbols indicate the age determination on the basis of epiphyseal closure. 1 (6 juv., 7 ad.), 2 (1 juv., 13 ad.), 3 (1 juv., 20 ad.), 4 (36 juv., 3 ad.), 5 (6 juv., 2 ad.).

*Fig. 13. Forholdet mellem vægten af to testikler og to cowperske kirtler hos hanegern. De to signaturer angiver aldersbestemmelsen på grundlag af epifyselukning.*

this weight being part of a stage of longer duration than the transitional states of growth and degeneration. It may therefore be interpreted as representing the animals being in a functional stage, and that this minimum value must be reached before an individual is capable of reproduction.

*Females*

The breeding period is here defined as the period between the birth of the young and their attainment of independence from the parents. This is fairly much the same as the period of suckling. Although the period of gravidity is not included in the breeding period, information concerning this has also been considered, as it can be used to determine the time of birth and thus the commencement of the breeding period. The data on the condition of the mammary glands and uteri are given in Table 6; the two sections of the table are independent of each other, as there was frequently only data on one factor for a given individual.

Embryos may be found in the period January–July. The gestation period is about 38 days (EIBL-EIBESFELDT 1951), and as it must be presumed that the very earliest stages are not discovered on examination of the uteri, it is reasonable to assume that birth occurs less than a month after embryos are discernible. The majority of embryos found in January are not likely to be born until the latter part of February. The last offspring are born in August, but the two records from July do not form a basis for a more precise determination of the completion of the period of birth. Although the results are few, they indicate that young are produced during the whole of the period of February to August. The amount of data does not indicate whether there are any peaks on the birth curve, that is, whether there are several separate litters.

The presence of well-developed mammary glands and large teats may together be presumed to be a good indicator of suckling, except in those cases where birth is very imminent. These conditions were found in the material during the months of February to September. In February there was however only 1 animal out of 24 in this state, and this indicates that

| Month *Måned* | Embryos *Fostre* Present *Med* | Absent *Uden* | Mammary glands *Mælkekirtler* Well-developed *Veludviklede* | Not developed *Ikke udviklede* |
|---|---|---|---|---|
| Jan. | 2 | 16 (9) | – | 16 (9) |
| Feb. | 12 (5) | 22 (16) | 1 | 23 (16) |
| Mar. | 3 | 7 | – | 1 |
| Apr. | 3 (1) | 1 | 3 | 1 |
| May | 1 | 7 (1) | 3 (1) | – |
| June | 4 | 5 (2) | 5 | 2 (2) |
| July | 2 (2) | 15 (8) | 10 (8) | 7 (2) |
| Aug. | – | 11 (9) | 7 (4) | 7 (5) |
| Sep. | – | 36 (31) | 3 (2) | 32 (29) |
| Oct. | – | 30 (27) | – | 27 (27) |
| Nov. | – | 9 (6) | – | 9 (6) |
| Dec. | – | 6 (4) | – | 5 (4) |

Table 6. Evidence of breeding activity in female squirrels from Denmark. The number of animals classified with certainty as adults is given in parenthesis. The two sections of the table are not associated with each other.

*Tabel 6. Tegn på yngleaktivitet hos danske hunegern. I parentes er anført oplysninger om sikkert bestemte adulte dyr. De to halvdele af tabellen er uafhængige.*

only a small proportion of the females give birth before March 1.

In the following months there was only little material collected, and not until September was it of a sufficient size to draw definite conclusions about the frequency. In this month, only 3 out of 29 adult females were suckling their young, and the breeding season is evidently drawing to a close by this time.

In five cases, suckling females with well-developed mammary glands and large teats were found to have very small embryos in the uterus. The size of the embryos excluded the possibility that the development of the mammary glands was that which takes place immediately prior to birth. The five cases originate from the months of May to July, that is, long after the early births in February and March. It was previously assumed that each female had more than one litter per year; these cases prove that the assumption was true.

## DISCUSSION AND CONCLUSIONS

The occurrence of embryos in the uterus proves quite definitely that a few litters are born by the end of February, but many more are presumably born in the beginning of March. Subsequently, gravid females may be found up to and including July, and as a result young are born throughout the period and well into August.

This is in agreement with the information gained from a study of the condition of the mammary glands. The earliest suckling female was found on February 23, and it was even recorded as apparently just having given birth. The only information from March is on one animal, and thus no conclusion can be drawn about the general condition of females in that month. Suckling females were found in each of the subsequent months up to and including September. This is also in fair agreement with the data on the times of birth; the final litters are born in August, and although the suckling period lasts about 2 months (FRANK 1952), this does not necessarily provide a contradiction. It must be remembered that the data come from one observation on an individual animal, and thus quite a large variation in the material may easily occur.

In the case of male squirrels, it is probable that the testicular weight is not the only factor governing reproductive condition, but that at least the size of the Cowper's glands must also be considered. Whether even this is sufficient is not

quite clear. BROWN & YEAGER (1945) considered that Cowper's glands were »a good criterion by which to judge the sexual condition«, but HOFFMAN & KIRKPATRICK (1956) concluded that the size of »male squirrel reproductive glands are inadequate for determining sexual development«. This statement was based on a histological examination of several reproductive organs, and part of the purpose of the present study was to determine whether sexual development could be recognised in a simpler way. The result need not necessarily be true for every single animal, but at least for the great majority of the population, such that the condition of the population as such could be described.

A comparison of the testicles with the Cowper's glands showed that it is probable that the size of the glands is the determining factor for the state of the animal. This is supported by the fact that testicular weight reaches a maximum value long before the Cowper's glands reach a sufficient size to be considered as those of a reproducing individual. On the basis of the material available it is not possible to state the exact time of year at which this size is reached, but it is certainly accomplished by the latter part of January. Due to the uneven distribution of the material, it may of course have already been reached by the turn of the year; this would agree excellently with the condition of the females. As was mentioned, the earliest gravid females were found at the end of January.

One may therefore conclude that in January, the sexual development of the earliest maturing individuals has reached such a stage that fertilization may take place. Due to the close season it was not possible to follow changes in the males during spring and summer, but in January and February the size of the Cowper's glands can evidently be used as an indicator of development. Throughout the whole summer, newly-born litters may be found. The breeding season terminates in September or perhaps even October, as the final offspring are produced in August and the suckling period lasts about two months.

## Summary

407 squirrels were collected from different localities in Denmark during 1968–1972. In addition a further 108 specimens from the Zoological Museum, Copenhagen, were used in taxonomical studies.

On the basis of cranial measurement, body weight, body length and tail length, it is quite definite that squirrels from the island of Bornholm belong to the subspecies *Sciurus vulgaris vulgaris* L. 1758. Animals from northern Sealand, Funen and Djursland (East Jutland) are presumed to belong to the subspecies *Sciurus vulgaris fuscoater* ALTUM 1876, this being in agreement with the colour of the fur.

As the animals from Kalø, Djursland, were age determined, it was possible to compare a sample of random age distribution with one consisting entirely of adult animals. The results for the latter group were the larger, and it is presumed that the use of age determined samples in systematic studies would give less ambiguous results.

In adult females, cranial measurement, body weight and body length are slightly larger than in adult males.

Three methods were used for age determination; manual and visual examination of epiphyseal closure on the radius, the weight of the baculum, and the eye lens weight. By comparison, it was found that

epiphyseal closure and eye lens weight can be used with very good accuracy, at least up to and including the month of October. Due to insufficiency of the material from the following months, it is not possible to state how late in the year these criteria may be relied on. If the baculum weight is used, an uncertainty of about 10 % must already be accepted by August–September.

The duration of the breeding period has been studied. Offspring are produced from the end of February until August, and suckling females were found up to and including September. This is in agreement with male reproductive conditions; in males, it was found that the weight of the paired Cowper's gland in particular was the decisive factor for reproductive condition. This gland reaches a sufficient size in January, and the gestation period of the females is just over one month.

## Dansk resumé

Systematik, aldersbestemmelse og reproduktion hos danske egern *(Sciurus vulgaris* L.).

Fra forskellige lokaliteter i Danmark er indsamlet 407 egern i årene 1968–1972. Til systematiske undersøgelser er yderligere undersøgt 108 eksemplarer fra Zoologisk Museum i København (tabel 1).

For bestandene fra Nordsjælland, Fyn og Djursland ses kranielængden at være den samme som for den tyske underart *Sciurus vulgaris fuscoater* ALTUM 1876, mens de bornholmske egerns kranier er af størrelse som den skandinaviske underart *Sciurus vulgaris vulgaris* L. 1758 (figur 2).

De bornholmske egern vejer kun ca. 3/4 af egern fra de andre undersøgte bestande, og har kortere hale (tabel 2). Derimod er der ikke nogen sikker forskel med hensyn til kropslængde. Også observationer over pelsfarve støtter, at de bornholmske egern er den skandinaviske underart.

Da dyrene fra Kalø er aldersbestemte, er det muligt at udskille de voksne dyr. Herved kan man sammenligne en prøve med tilfældig aldersfordeling og en prøve bestående udelukkende af voksne dyr. For såvel kraniemål (p. 6) som kropsmål og vægt (tabel 3) ligger værdierne for voksne dyr højest. Ved at anvende prøver af ukendt alderssammensætning indfører man en ukendt usikkerhed som følge af varierende ungeprocent og væksten af de unge dyr. Sammenligning af voksne dyr i samme aldersklasse til systematiske undersøgelser kan muligvis give mere entydige resultater.

Både kraniemål, vægt og kropslængde er hos voksne hunner en smule større end hos hannerne (p. 6 og tabel 4).

Tre metoder er blevet anvendt uafhængigt til aldersbestemmelse. Ved slutningen af dyrenes vækst forbenes en vækstzone i de lange rørknogler; denne zone kan erkendes hos ikke-udvoksede dyr. En adskillelse synes at være ret sikker til og med september måned (tabel 5).

Vægten af penisknoglen stiger stærkt omkring kønsmodningen, og hos mange dyr kan man derved adskille hannerne i kønsmodne og ikke-kønsmodne dyr. Denne metode synes dog ikke særlig god hos egern (figur 5).

Vægten af øjelinsen hos de fleste pattedyr vedbliver at stige gennem hele livet. Da unger fødes på bestemte tider af året, vil fordelingen af øjelinsevægtene ikke være en jævn kurve, men opdelt i aldersklasser. I det aktuelle tilfælde synes man at kunne skelne mellem unge og voksne dyr på grundlag heraf (figur 6).

Ved parvis sammenligning af metoder-

ne (figur 7, 8 og 9) konstateredes det, at epifyselukning og øjelinsevægt kan anvendes med meget stor sikkerhed, i hvert fald til og med oktober måned. Grundet materialets lidenhed i de følgende måneder kan man ikke udtale sig om, hvor langt hen på året kriterierne er påviselige. Bruger man baculumvægten, må man allerede i august–september affinde sig med en usikkerhed på ca. 10 %.

Yngleperiodens længde er belyst ved undersøgelser af både hanner og hunner. Efter tilstanden af uterus at dømme fødes der unger fra slutningen af februar til ind i august (tabel 6). Diegivende hunner er fundet fra slutningen af februar til slutningen af september.

Hos hannerne blev testiklerne og de cowperske kirtler vejet. Det synes sandsynligt, at den reproduktive tilstand først og fremmest bestemmes af de cowperske kirtlers størrelse (figur 12). En tilstrækkelig størrelse opnås i januar. Det stemmer tidsmæssigt med forholdene hos hunnerne, da drægtighedstiden er lidt over en måned.

## Резюме на русском языке

Систематика, возрастные критерии и воспроизводство датской белки (*Sciurus vulgaris* L.)

В течение 1968–1972 г. из разных местностей Дании было собрано 407 белок. Кроме того, для таксономических исследований использовалось 108 экземпляров из Зоологического Музея г. Копенгагена.

На основании измерений черепа, веса тела и длины тела и хвоста точно определено, что белки с острова Борнхольма принадлежат к подвиду *Sciurus vulgaris vulgaris* L. 1758. О животных из Северной Зеландии, с острова Фионии и из Дьюрсланда (в Восточной Ютландии) можно предполагать, что они принадлежат к подвиду *Sciurus vulgaris fuscoater* Altum 1876, что соответствует цвету их шкуры.

Так как животные из Калё в Дьюрсланде определялись по возрасту, предоставлялась возможность сравнения образца случайного распределения по возрасту с образцом, полностью состоявшим из взрослых особей. Результаты этой последней группы были более широки, и можно предполагать, что применение определенных по возрасту образцов в систематических исследованиях могло бы дать менее сомнительные результаты.

У взрослых самок размеры черепа, вес тела и длина тела были немного больше, чем у взрослых самцов.

Для определения возраста применялись три способа: физическое и визуальное обследования срастания эпифизы с radius, вес baculum, и вес хрусталика глаза. Сравнением было установлено, что срастание эпифизы и вес хрусталика глаза с удовлетворительной степенью надежности могут служить критериями, по меньшей мере до истечения октября. Ввиду недостаточности материала, собранного в течение следующих месяцев, невозможно судить о том, до какого времени под конец года можно еще полагаться на эти критерии. Если определение производится по весу baculum, то уже в августе-сентябре нужно считаться с ненадежностью в прибл. 10%.

Изучалась также длительность периода выводки. Детеныши производятся с конца февраля до августа, и кормящие самки встречались до конца сентября. Это соответствует способности к размножению у самцов. Было установлено, что у самцов решительным фактором для способности к размножению прежде всего является вес парной glandula Cowperi. Эта железа достигает достаточной величины в январе, а период беременности у самок продолжается немного дольше одного месяца.

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