RELIABILITY OF THE PETERSEN METHOD TESTED ON A ROE-DEER POPULATION

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Abstract: Since 1956 the roe deer (*Capreolus capreolus*) at the Danish game biology station have been marked with leather collars with serial numbers and colored buttons. In 1966 the collars were fitted with large reflecting numbers, making it possible to recognize individuals in the field, by day as well as by night, at distances up to 300 m. Seventy animals were so marked during the 1966 season. In the period just after the marking season, 1,735 observations were made of roe deer of which 1,336 were of animals individually marked. On this basis the calculation of the population was carried out, and the Petersen estimate, based on sight records of marked and unmarked deer, is evaluated in a situation in which considerable background data exist. Specifically, analyses are made as though individual identification were not obtained, and then individual identifications are used in evaluating the estimates. In this case it is found that more than two-thirds of the population must be captured and marked to obtain a reliable measure of population size.

In game research, the question of size of a population of animals is often encountered. As a rule, population estimates are based on guesswork or on calculations without real controls. The need for checks of estimates against known numbers was expressed clearly by Davis (1963:117) in his review of methods used for game population estimates.

In very few cases has it been possible to shoot or capture every animal and so ascertain the exact number of animals in a population. There is such a case at Kalø where the roe-deer population was exterminated in 1950 (Andersen 1953). Before the shooting, the foresters and game wardens were asked to estimate the size of the herd, not because the game biologists wanted to judge the ability of the men to estimate a population of roe deer, but to find out whether there were enough animals for an investigation of population composition, reproduction, and so forth.

In 1950 nobody doubted the estimate of about 70 animals and surprise was genuine when 213 animals were shot. This is more than three times as many as estimated by the professional forest and game personnel, even though the forests cover an area of only 340 hectares (about 740 acres).

In 1951 roe deer were reintroduced in the forest at Kalø, and from 1956 the growing number of animals in this new population has been followed through calculations based on the "Petersen Method" (Petersen 1896) or as it is often called, the "Lincoln Index" (Lincoln 1930). Until 1965 Andersen was in charge of this investigation (Andersen 1962).

In January and February every year, as many roe deer as possible were livetrapped, marked, and released in one of the two forests called Ringelmosen, with an area of about 170 hectares. The animals were given leather collars on which plastic buttons were fastened, a different color each year. A small copper tag attached to the collar showed a serial number and certain other information. Depending on snow conditions, from 28 to 75 animals were captured and marked in this way each year.

Immediately after the trapping period, during March and April, observations were carried out, and notes were made on the number of animals with colored collar of the year, number of animals with collars of earlier years, and number of animals without collars. In this way about 1,000 observations were made every year in the period just after the livetrapping.

Fig. 1. A roe buck marked with a reflecting number.

The Petersen method was then used to calculate the size of the population:

$$\frac{M \cdot n}{x} = \hat{N}, \text{ where}$$

M = number of marked, released animals,
n = total number of observations,
x = number of observations of animals with collars of the year, and
$\hat{N}$ = population.

In practice, the modification made by Bailey (1951) was used: $\hat{N} = \frac{M(n+1)}{x+1}$, and the standard deviation was calculated from the formula:

$$\text{SD} = \sqrt{\frac{M^2(n+1)(n-x)}{(x+1)^2(x+2)}}.$$

In the data presented here it does not seem to matter whether the calculations are made on the basis of the Petersen method or the Bailey index.

METHODS

Capture and Marking

In spite of all the work involved in the capture and the observations, the numbers calculated to show the size of the population seem to hold quite serious errors. Partly because of these errors the roe-deer investigation was intensified from January, 1966, and the marking technique was changed to individual marking by numbers (Fig. 1). The two rubber flaps with attached metal plates with reflecting numbers are fastened to the leather collars. All the deer trapped during the winter of 1966 carry numbers that can be seen through binoculars at a considerable distance. The reflecting material in the numbers makes possible night observations with a searchlight, but daytime observations are also made to the greatest possible extent.

The study area, consisting of Ringelmose wood and the surrounding farmland, covers about 420 hectares of which 250 are arable land and 170 are forest. Evenly distributed in the forest are 15 fenced enclosures measuring 2 × 20 m. A gate at one end can be closed by pulling a long wire; oat sheaves are used for bait. Food is kept in the traps all through the trapping period and the gates are left open so the animals can visit and leave at will. From one to three times a day a car takes a party around to all the traps, the gate is closed, a man investigates the trap, and in case of capture the animals are examined and the gates left open again.

During the 1966 trapping period from January 3 to February 7, 50 trips were made to the traps. Each trip took about 3 hours and involved 3–4 persons, so 400–500 hours were spent on trapping alone. Seventy animals were individually marked and

Table 1. Estimates of roe-deer population based on observations separated according to time, observers, and sex or age of deer.

M	n	x	$\hat{N}$	2 SD	$P = M/\hat{N}$	Source	
70	1,735	1,336	91	2	0.77	All 1966 data	
70	272	210	91	6	0.77	February	Month
70	560	434	90	4	0.77	March	Month
70	903	692	91	3	0.77	April	Month
70	597	448	93	4	0.75	Strandgaard	Observer
70	823	640	90	3	0.78	Christoffersen	Observer
70	315	248	89	5	0.79	Kristiansen	Observer
30	370	288	39	2	0.78	Bucks	Sex and age in April
40	482	358	54	3	0.74	Does	Sex and age in April
33	431	244	58	5	0.57	Adults	Sex and age in April
37	421	402	39	1	0.95	Fawns	Sex and age in April
10	141	59	24	4.6	0.42	Adult bucks	Sex and age in April
23	290	185	36	3.2	0.66	Adult does	Sex and age in April
20	229	229	20	0	1.00	Buck fawns	Sex and age in April
17	192	173	19	2.9	0.90	Doe fawns	Sex and age in April

3 others died in connection with the trapping procedure. The animals were aged on the basis of the third premolar, into two age-groups: fawns and animals older than 1 year. The third premolar is tripartite in fawns and bipartite in older animals. Finally the animals were sexed and weighed.

Field Observations

As soon as the trapping period ended on February 7, observations started. In early spring it is possible to observe roe deer at any time of day or night, but the most successful hours are in the early morning, late afternoon, and during the night. Although the area is transected by a network of wood roads and trails, no special routes were followed, but we tried to cover the whole area every day and every night.

Results are best when observations are made from a car because the animals are less disturbed than by a person on foot. During the night the car is necessary because the searchlight is powered by the electrical system of the car. The light can find the animals at a distance of more than 500 m and the collar numbers can be read up to 300 m. In daylight the readable distance is the same. In some areas the lack of roads makes it necessary to observe both from horseback and on foot. Altogether about 300 hours were spent on observations in the period February–April, of which 234 hours resulted in sightings.

RESULTS

The period February 7–May 1 produced 1,735 observations, of which 1,336 were of animals marked in 1966. On the basis of these numbers, the population can be calculated to be:

$$\frac{70(1735+1)}{1336+1} = 91 \text{ animals}$$

$$\text{SD} = \sqrt{\frac{(70)^2(1736 \cdot 399)}{(1337)^2(1338)}} = 1.0$$

However, the data can be broken up into their various components and separate calculations made, with the results shown in Table 1.

As shown in Table 1, whether the calculations are made on the basis of the total number of observations for the period or for each month does not seem to matter for the result is practically the same.

Table 2. Sex and age distribution among the individually marked roe deer.

	Males Less than 1 Year		Adult Males		Females Less than 1 Year		Adult Females		
	No.	%	No.	%	No.	%	No.	%	Total
Trapped and released	20	28	10	14	17	24	23	34	70
Observed February–April	438	35	110	9	334	26	375	30	1,257
Observed in April	229	35	59	9	173	27	185	29	646

There are other ways to divide up the data. In February and March two persons (Strandgaard and Christoffersen) were making observations: a third person (Kristiansen) was employed in April.

The calculations based on the observations of Christoffersen and Kristiansen give the same results. A small deviation is found in Strandgaard's observations, perhaps because he observed by artificial light mainly at night, and the other two observed mainly in the morning and afternoon.

The calculations show clearly that the information we receive on the basis of the observations (n and x) contains no errors that can be traced to the three observers responsible for them, or to the long period of time involved. But they do not show whether the observed animals satisfactorily represent the population.

An Analysis of the Extracted Sample

During all observations, sex and age are determined whenever possible and in April, for instance, 852 out of 903 observations were of sexed and aged animals. Of these 852 observed deer, 646 carried collars of the year (reflecting numbers).

Calculation: $\hat{N} = \dfrac{70(852+1)}{646+1} = 92$ animals. This is almost the same result as that obtained on the basis of all the observations.

Resolved into bucks and does there are still no major changes in our calculated results, but if we divide our material into fawns and adults the result is divergent (Table 1).

The explanation can be found in Table 2. Compared to the observations, the marked animals do not represent the real population in the study area. It appears that the bucks less than 1 year of age are present in too small a number among the marked animals (or are observed too often) while the older bucks are too numerous among the marked individuals (or are observed too infrequently). Among the does there seems to be an even distribution among the marked animals and in the observations. But further explanation is required to understand Table 2.

The observations suggest a large representation of young males among the trapped animals, since 1,735 observations do not contain a single male less than 1 year of age without a reflecting number, indicating that the group was trapped 100 percent. Altogether there are 20 males less than 1 year old. The conclusion is that young males are easy to trap and are often spotted in the field. Andersen (1953) reported a similar situation during the 1950 shoot: male fawns were much more susceptible to being shot than were female fawns.

There are 10 animals marked in the adult male group, but we know of at least an additional 9 animals, with collars from earlier years. We therefore succeeded in trapping only one-half of this group.

Females less than 1 year old are easier to trap and observe than adult females. A total of 17 young females have been captured and through observations we know

Table 3. Numbers of roe deer based on calculations compared to minimum numbers determined from 1,735 observations.

	Number of Roe Deer on Basis of Calculations	Minimum Number of Roe Deer Determined from Observations
Total	91	85
Males	39	39
Females	54	46
Fawns	39	38
Adults	58	47
Male fawns	20	20
Female fawns	19	18
Male adults	24	19
Female adults	36	28

of 1 more animal belonging to this group, which adds up to 94 percent success.

Adult females are represented by 23 among the individually marked animals and we know of at least 5 more animals belonging to this group.

Altogether we can identify 39 bucks of the calculated 39 and 46 of the calculated 54 females. Totally we can identify a minimum of 85 of the calculated 91 animals. We know there are 38 male and female fawns and the calculations show 39.

It must be taken for granted that the calculated population of about 90 animals is nearly correct in view of the fact that the 70 test animals represent 77 percent or ¾ of the calculated population. The fact that 77 percent of the population is captured and marked does not mean that the 70 animals are a representative sample of the population of the Ringelmose forest. The fawns are too numerous among the marked individuals because they are easier to trap than the older animals. In the trapped and marked part of the population the fawns amount to 52 percent, whereas fawns are only 41 percent in the calculated population. When the herd was exterminated in 1950, Andersen (1953) found 43 percent fawns.

That fawns are disproportionately represented in the marked individuals is confirmed by the observations, as there is only one fawn among the unmarked animals, while we have found quite a number of adults with collars from earlier years which means that they were not trapped in 1966.

From a mathematical point of view, the sum of the last four estimates in Tables 1 and 3 gives the best estimate of the total population $(24 + 36 + 20 + 19) = 99$ (SD = 6.3). However, from our experience we feel that the first estimate (91) is more correct.

An Estimation of Population Size Based on Extracted Samples

Because we recognize the marked animals individually, we can estimate the population on the basis of partial samples of the marked animals. For instance, if we had marked only 5, 10, 15, 20 . . . , the basis of estimation in April would have been

$M = 5, 10, 15 \ldots$

$n = 852$

$x =$ number of observations of the first 5, 10, 15, 20 . . . , individuals marked with reflecting numbers.

Other examples are given in Table 4.

The calculated population size varies considerably not only because the marked animals do not accurately represent the total population. The fact that some individuals were observed more often than others also plays a major part.

In these data the extremes are one animal seen only once after trapping and marking and another seen 25 times in the month of April alone.

In Fig. 2, the population calculated on the basis of the first 5, 10, 15, 20 . . . , individually marked animals is shown. In the same way the number of observations

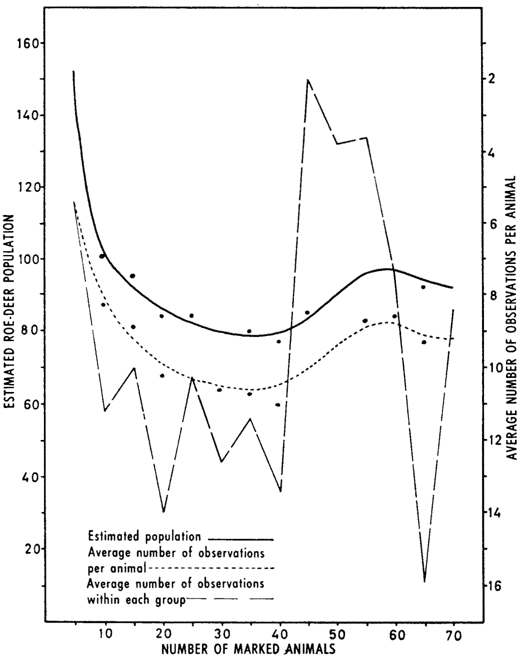

Fig. 2. The relation between the estimated roe-deer population and the number of marked individuals seen in extracted samples.

of the first 5, 10, 15, 20 . . . , marked animals is shown. The correlation between the two curves is quite clear. In both cases the group division follows the same sequence in which the animals were trapped and marked.

A closer study of each single group reveals that a constant course in the calculated population is merely apparent. The number of observations within the single groups is the basis for the third curve in the diagram and the considerable variations are easily seen. The extremes are found in the group 41–45, in which there are only 10 observations in April, while the group 61–65 contains 79 observations in the same period. Supposing that the sample (M) had included only 5 animals and all of them had fallen in the group 41–45, the calculation would have been: $5(852+1)/(10+1) = 388$ animals ($2\ \text{SD} = 222$).

If only the animals within the group 61–65 had been marked, the result would have been: $5(852+1)/(79+1) = 53$ animals ($2\ \text{SD} = 12$).

Roe Deer Are Individualists

If we increase the number of observations, the errors shown above become even more significant. The calculations in Fig. 2 represent the month of April only. If all the observations from the period February–April are included, the difference between the single groups becomes even more striking. The same two groups will still make up the extremes, the group 41–45 containing 13 observations, ($\hat{N} = 584$, $2\ \text{SD} = 300$) and 61–65 holding 148 ($\hat{N} = 55$, $2\ \text{SD} = 9$).

The observations show an extremely variable behavior of the different individuals. Some are seen frequently, feeding and going about their lives in full view of the observer, while others are observed only by sheer luck, fleeing as soon as the car stops. Some deer forage in the fields at the edge of the forest, sometimes for a whole day, while others never leave the security of the forest. The main part of the herd is very stationary, but some animals seem to move about to a large extent. These factors play an important part, but other circumstances such as death, emigration, and immigration are worth attention.

Among the 70 marked animals, 2 were found dead and 1 was never observed after it was marked. There is every probability that the latter animal is dead, but whether the same probability holds for the unmarked part of the herd is not known. However, if only 1 deer has disappeared among 70 marked animals, it is probable that none has disappeared among the about 20 animals which were not marked. The same conclusion holds true for emigration. Five marked animals have been observed outside the research area, but we do not know whether the same number of the animals not individually marked has emigrated. Two of the marked roe deer have been seen on the neighboring estate (about 2.5 km from Kalø) together with an animal bearing a collar from an earlier year.

There appeared to be no immigration during the trapping period. Among the 1,735 observations in the period February–April, there is no evidence of strange deer being observed in the study area.

Calculation of a Population on the Basis of Captures and Recaptures

We can use the Petersen method in the same manner to calculate the population on the basis of the relation between captured and recaptured individuals. The factors in the formula are then:

M = number of individuals captured in the first period
n = number of individuals captured in the second period
x = number of individuals captured in both the first and the second periods, or number of recaptures.

Dividing the data into two groups of approximately the same size, the first period gave 35 individuals (M), while the second period gave 51 individuals (n) of which 18 (x) were marked by captures in the first period. Calculation: $\hat{N} = 35\ (51 + 1)/(18 + 1) = 96$ (2 SD = 34).

The result resembles very closely the one obtained on the basis of the observation technique although the 2 SD is much greater. If the first period had produced only 14 roe deer (the actual number caught the first 2 days) and the second period 21 new ones (rest of the first week), this material contains five recaptures in the second period, and the calculation is: $\hat{N} = 14\ (26 + 1)/(5 + 1) = 63$ (2 SD = 42). The deviation is then so great, compared to the real population, that the value seems dubious. The rule about sufficient data can also be applied in this case.

Table 4. Estimates of population size based on extracted samples.

M	$\frac{M\,(n+1)}{x+1}$	$\hat{N}$	2 SD
The first 5	$\frac{5\,(852+1)}{27+1}$	152	56
The first 10	$\frac{10\,(852+1)}{83+1}$	102	21
The first 15	$\frac{15\,(852+1)}{133+1}$	95	15
The first 20	$\frac{20\,(852+1)}{203+1}$	84	10
The first 25	$\frac{25\,(852+1)}{254+1}$	84	9
The first 30	$\frac{30\,(852+1)}{317+1}$	80	7
The first 35	$\frac{35\,(852+1)}{374+1}$	80	6
The first 40	$\frac{40\,(852+1)}{441+1}$	77	5
The first 45	$\frac{45\,(852+1)}{451+1}$	85	5
The first 50	$\frac{50\,(852+1)}{470+1}$	91	6
The first 55	$\frac{55\,(852+1)}{488+1}$	96	6
The first 60	$\frac{60\,(852+1)}{525+1}$	97	5
The first 65	$\frac{65\,(852+1)}{604+1}$	92	4
The first 70	$\frac{70\,(852+1)}{646+1}$	92	4

DISCUSSION

It seems that whether we use the observation technique or the recapture technique, the calculations based on the Petersen method can lead to quite large errors. Of course, these are not caused by the applied mathematical methods but are solely due to the fact that the biological data on which the calculations are based do not represent the actual population. One violates the assumption on which the Petersen formula is based, if one tries to throw all sexes and ages together in the formula. However this does not prevent application of the formula to the various identifiable segments of the population, which now requires only that *marked adult bucks* are just as apt to be observed as *unmarked adult bucks,* that *marked adult does* are as apt to be observed as *unmarked adult does,* etc. (Table 3).

However, during practical work in the field, it is often difficult to distinguish between the single groups. In the present example, for instance, it has been possible to distinguish doe fawns from adult does only because there has been only one unmarked individual among the doe fawns. If there had been more unmarked does, it would have been impossible in practice to distinguish these two groups with certainty. It is our impression that biologists often find themselves in a situation where the requirements of the Petersen formula can be fulfilled only with difficulty.

Here the Petersen estimate, based on sight records of marked and unmarked deer, is evaluated in a situation in which considerable background data exist. Specifically, analyses are made as though individual identification were not obtained, and then individual identifications are used in evaluating the estimates.

Whether the extracted sample represents the population it is taken from, is a question encountered with nearly every collection of biological data used for population analysis. If the sample is equivocal, the calculation will eventually lead to an erroneous result.

Concerning roe deer, two factors play a decisive part. First, there is individual variation in their behavior which affects the likelihood of their being observed. This makes it very difficult to extract a representative sample. Second, as mentioned above, it is not possible in the field to distinguish with certainty between doe fawns and adult does.

Therefore it seems necessary to capture and mark at least two-thirds of a roe deer population to be sure that the extracted sample is representative of it. We are not able to determine whether this statement can be applied to other species of animals. Where the size of the population is calculated on the basis of a sample which makes up only a small percentage of the calculated population, we are skeptical about the results.

The standard deviation, which is often referred to in connection with calculation of a population, seems to be rather unimportant. It shows the mathematical reliability of the calculation but does not say anything about the reliability from a biological point of view. This fact is illustrated rather clearly in our example where a roe-deer population is calculated on the basis of the groups for every fifth animal. With an increase in the number of observations (n and x) from 852 and 79 to 1,633 and 148 respectively, the standard deviation decreases from 12 to 9, without altering the fact that the calculated population ($\hat{N}$) in both cases is only about one-half of the actual population.

Because the content of this paper is part of an intensive and continuing roe-deer investigation, we have not included detailed descriptions of the techniques of trapping, marking, and observing. However, an analysis of the basis of the calculations used in estimating the size of the population is so important and fundamental that it is worth while to point out the danger in using the Petersen method.

LITERATURE CITED

ANDERSEN, J. 1953. Analysis of a Danish roe-deer population (*Capreolus capreolus* (L)) based upon the extermination of the total stock. Danish Rev. Game Biol. 2(2):127–155.

———. 1962. Roe-deer census and population analysis by means of modified marking and release technique. Pp. 72–82. *In* E. D. Le Cren, and M. W. Holdgate (Editors), The exploitation of natural animal populations. Blackwell Scientific Publ., Oxford, England. 399pp.

BAILEY, N. T. J. 1951. On estimating the size of mobile populations from recapture data. Biometrika 38(3–4):293–306.

DAVIS, D. E. 1963. Estimating the numbers of game populations. Pp. 89–118. *In* H. S. Mosby (Editor), Wildlife investigational techniques. 2nd ed. The Wildlife Society, Washington, D. C. 419pp.

LINCOLN, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. U. S. Dept. Agr. Circ. 118. 4pp.

PETERSEN, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Rept. Danish Biol. Sta. for 1895. 6:1–77.

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CHARACTERISTICS OF MULE DEER HERDS AND THEIR RANGE IN NORTHEASTERN UTAH[1]

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Abstract: Mule deer (*Odocoileus hemionus*) which winter in Daggett County, Utah, are divided by the Uinta-Mountain crest into two distinct herds when on their summer ranges; migration routes and, in large part, winter ranges are also separate. The time, rate, and extent of migration vary from year to year as environmental conditions vary. During 1959–60, big sagebrush (*Artemisia tridentata*) and mountain mahogany (*Cercocarpus* sp.) were the key mule deer foods on the winter range, but bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier* sp.), forbs, and grasses were important supplemental foods. Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus edulis*) were important as emergency foods and escape cover. The Daggett deer winter range was heavily used by large numbers of big game and domestic livestock; preferred browse species were severely hedged or highlined wherever accessible and there was a low rate of seedling establishment. Predation, starvation, accidents, parasites, and disease contributed to deer mortality during the study period but losses were not large, mostly fawns and older deer with poor teeth. In December and January of 1958–59, there were 85 fawns and 42 bucks per 100 does; the next year there were 80 fawns and 42 bucks per 100 does. Net productivity during the study period was about 31 percent. Most deer were fat in the fall and gradually lost body condition as spring approached.

Records show that mule deer of the Uinta Mountains have had periods of scarcity during 1835–40, 1870–73, and 1906–20. These declines were associated with "obvious" overgrazing of the winter range. A major die-off of deer occurred in the Uinta Mountains in the harsh winter of 1948–49 (Utah Fish and Game Dept. 1952:2) presumably owing to lack of forage. Although this die-off increased the concern of wildlife biologists for this range and its deer, the real impetus for this study was the impending construction of the Flaming Gorge Dam on the Green River.

Conducted in 1959 and 1960, this is the first detailed investigation of mule deer that winter in Daggett County, in the eastern Uintas. The primary objectives were to investigate (1) deer migrations, (2) the sta-

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