Seasonal and age related changes in size of reproductive structures of red deer hinds *(Cervus elaphus).*

Rolf Langvatn

Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway

Abstract: Morphometric studies of uteri, ovary weights, and follicle diameters were carried out to investigate possible methodological applications. Size and anatomical appearance of the uterus varied with age and phase in the estrous cycle, both in parous and nulliparous females. The uterus thus may provide valuable information on reproductive status for known-aged animals. Weight of ovaries increased in young, but declined in old females, showing significant covariance with body weight in young and prime ages. Ovary weights increased from low levels shortly after parturition to a maximum towards the end of the gestation period. Ovaries containing a *corpus luteum* were heavier than those without. Compared to ovary weights, mean diameter of largest ovarian follicle varied in an opposite pattern during the yearly cycle. Maximum follicle diameter was largest in non-ovulated females. Weight of ovaries and follicle size appear to be of limited value as criteria in analysis of reproductive status and performance.

Keywords: uterus, ovaries, weights, follicle-diameter, criteria, methods.

Rangifer, 12 (2): 57–66

Introduction

Reproductive organs exhibit significant change in anatomical appearance and function over the lifetime of female individuals (McDonald, 1975; Nalbandov, 1976), thus providing a potential source of information on reproductive development and activity. In seasonal breeders like cervids, temporary structures in the ovaries may reflect reproductive status and history (Cheatum, 1949; Morrison, 1960; Strandgaard, 1972; Dauphinè and McClure, 1974; Haagenrud and Markgren, 1974), while the size and appearance of the uterus may provide supplementary information on fertility and reproductive activity (Valentincic, 1958; Markgren, 1969; Wegge, 1975).

Although examination of reproductive organs is widely applied as a way to reveal reproductive events, in particular age-specific fecundity (Golley, 1957; Wegge, 1975; Thomas, 1983), quantitative information on cyclic and lifetime changes in various parts of the reproductive tract of cervids is scarce (Leader-Williams and Rosser, 1983; Ahrens und Liess, 1987; Horak, 1989).

On a qualitative basis Markgren (1969) demonstrated how size and appearance of the uterus may be used to assess maturation and fertility in female moose *(Alces alces).* Markgren (op.cit) also indicated that size of Graafian follicles in ovaries may provide a possible criterion for the forthcoming estrus. However, these observations were not substantiated quantitatively. Ahrens and Liess (1987) showed that weight of uterus and ovaries differed between yearlings and older female fallow deer *(Dama dama)*, but did not relate their observations to effects inherent to the estrous cycle or pregnancy. Also, in red deer Valentincic (1958) demonstrated that size of uteri varied between yearling hinds and older females, and that occurrence of corpora lutea in the ovaries was associated with larger size both in uteri and ovaries. Development and seasonal variation in size of ovarian follicles in elk *(Cervus elaphus)* and red deer have been studied by Halazon and Buechner (1956), Valentincic (1958) and Morrison (1960). However, their descriptions are partly contrasting, and small samples size and limited statistical reporting of observations makes more generalized interpretation of their findings difficult.

In Norway, most female red deer are culled early in the hunting season (September to mid October) prior to the main period of breeding activity starting in mid October. Thus, access to reproductive tracts and ovaries from animals which have ovulated is limited. This applies especially to yearling hinds since they tend to ovulate later than older females (Langvatn unpubl. data). As part of a methodological study of reproductive organs in red deer (Langvatn 1992), this paper describes size and appearance of the uterus in females of different age and reproductive history, aiming to investigate the possible use of this organ as an additional source of information on reproductive events, primarily revealed through analysis of ovaries. In addition, seasonal and age related changes in the weight of ovaries and size of the largest ovarian follicles are described and discussed in relation to breeding cycles and reproductive status of the females.

Methods and material

In cooperation with local wildlife boards and hunters, jawbones and reproductive organs from 2174 female Norwegian red deer *(C. e. atlanticus)* were collected from different localities during the hunting seasons (10 September - 14 December) between 1970 and 1989. In addition to the material, hunters provided information on date shot, dressed weight, lactation and locality for each animal (Langvatn, 1986; Langvatn and Albon, 1986). Similar data and material were collected outside the hunting season from animals killed in accidents or selectively culled for scientific purposes.

Age determination. - Calves and yearlings were aged on basis of tooth eruption pattern (Mitchell and Youngson, 1969), while the method described by Reimers and Nordby (1968) was applied for age determination of older animals, including decalcification and microsectioning of roots of first incisors with its cementum layers and annuli.

Uteri. - Uteri were autopsied and tissue samples preserved in 10% formalin for later processing. However, a sample of 210 fresh uteri from females of different age and reproductive status were trimmed and weighed. The trimmed uterus consisted of the *corpus uterii* and *cornua*, less ovaries and ligaments, cut free from the vaginal tract at the *cervix.*

Ovaries. - Ovaries were cut free at the hilum, weighed separately, and stored in formalin for analysis. The analysis of the ovaries included describing size and appearance of various luteal structures and their regressing stages. Size of largest follicles was determined by measuring the maximum and minimum diameters at right angles across the exposed face of the structures. The two diameters were averaged (Leader-Williams and Rosser, 1983).

Reproductive status. - Information on lactational status and occurrence of a *corpus rubrum (corpus albicans)* as described by Valentincic (1958), Markgren (1969) and Langvatn (1992) was used to assess if the hind had given birth during the immidiate, preceding calving season (June). Corpora albicantia assumingly older than the corpus rubrum (Gibson, 1957; Valentincic, 1958; Haagenrud and Markgren, 1974) were indicative of multiple parturitions in animals three years and older. Young age (1-3 years), no lactation, and no indication of regressed luteal structures characterized nulliparous females (no offspring). Presence of corpora lutea in the ovaries (but no blastocyst or implant in uterus) indicated a recent ovulation and estrus.

Statistical analysis. - Tests for homogeneity of variance and distributions in the data (e.g. kurtosis, skewness) were used to check if assumptions of normal error distributions were met. T-tests and one-way analysis of variance were used to compare mean values of weight of uteri

Table 1. Variation in weight of uterus (dependent variable) with body weight (covariate), month of sampling, age, estrus (ovulated, non-ovulated), and whether the hinds given birth or not earlier (previous parturition), - (independent factors). Regression approach model with simultaneous assessment and correction of factors, covariate and interactions.

	Body weight F	p	Cow.raw regr.coeff.	Age F	p	Estrus F	p	Previous parturition F	p	Month of sampling F	p
All females											
≥1 year	$F_{1,165}=0.193$	0.661(N.S.)	0.020	$F_{3,165}=29.630$	<0.001***	$F_{1,165}=60.929$	<0.001***	$F_{1,165}=64.915$	<0.001***	$F_{3,165}=1.347$	0.263(N.S.)
Within age groups:											
yearling hinds	$F_{1,48}=0.629$	0.432(N.S.)	0.041			$F_{1,48}=11.523$	0.001***	(a)		$F_{3,48}=0.600$	0.553(N.S.)
2 year old hinds	$F_{1,37}=1.394$	0.245(N.S.)	0.084			$F_{1,37}=14.124$	0.001***	$F_{1,37}=128.680$	<0.001***	$F_{3,37}=2.362$	0.108(N.S.)
3 year old hinds	$F_{1,25}<0.001$	0.986(N.S.)	0.003			$F_{1,25}=9.283$	0.005**	$F_{1,25}=13.133$	0.001***	$F_{3,25}=0.215$	0808(N.S.)
hinds≥4 year old	$F_{1,37}=0.638$	0.429(N.S)	-0.151			$F_{1,37}=5.670$	0.023 *	(b)		$F_{3,37}=0.960$	0.392(N.S.)

(a) Parous yearling hinds did not occur
(b) Nulliparous hinds ≥ 4 years did not occur

and ovaries, as well as mean diameter of the largest ovarian follicles. Factorial and covariate models for analysis of variance were used to examine the effects of month of sampling, age (categories, see below), previous parturition, and estrus, with body weight as a covariate, on the weight of uteri and ovaries and size of follicles. Relationships between dependent variables and factors such as age and time periods also were examined with linear regression analysis.

Results

Weight of uteri. - Calves of Norwegian red deer have never been reported to conceive, nor have yearling hinds been found to lactate. The weight of the uterus in calves was significantly lower than in older age groups of non-ovulated females (one-way analysis of variance, Scheffe's procedure; $F_{3, 112}$ 114.023, $p< 0.05$; - Fig. 1). Calves were excluded from further analysis concerning weight of uteri.

The assumption of homogeneity of variance in sampled categories of females appeared to be met (Cochran's C, all $p \geq 0.10$). Analysis of variance (regression approach model) showed significant variation between weight of uterus and age (categories: 1, 2, 3 and ≥ 4 years), parous or nulliparous status, and whether the hind had ovulated or not that season. Month of sampling was not significant, nor was there significant covariance with body weight after controlling for age. The analysis is summarized in Table 1, both for the entire sample of hinds (≥ 1 year old), and within age groups.

Within age groups weight of uterus in general varied significantly with estrus, and in hinds two years and older also with previous parturition. Month of sampling was not significant after controlling for the effect of estrus in any age category, nor was there significant covariance with body weight.

One-way analysis of variance (Scheffe's procedure), showed no significant differences in weight of uterus between hinds four years and older, neither in ovulated nor in non-ovulated individuals ($F_{9,10} = 0.264$, $p > 0.05$, and $F_{10,11} = 0.528$, $p > 0.05$ respectively). However, the same analysis did show significant differences in mean uteri weights between non-ovulated females in the age groups shown in Figure 1, both for parous and nulliparous hinds ($F_{2,52}$ =

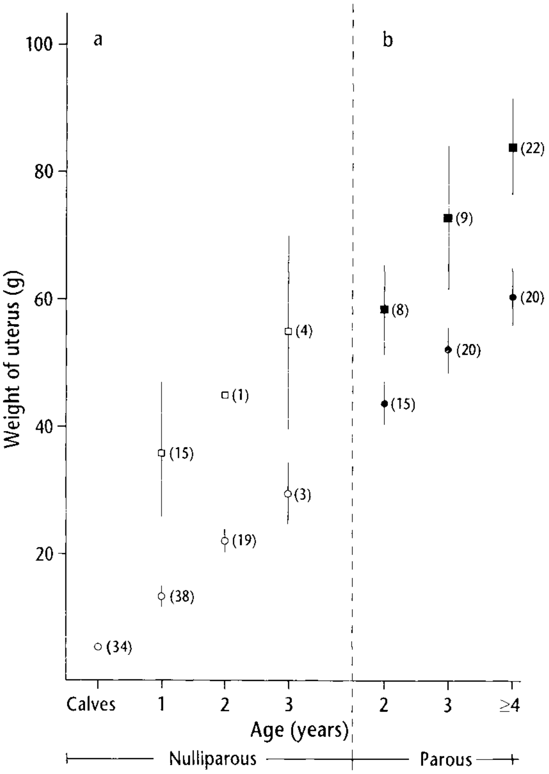

Fig. 1. Mean weight of uteri (± 95% confidence limits) for nulliparous (a) and parous (b) red deer females. Circles=non-ovlulated, squares=ovulated. Sample size in brackets.

19.340, $p < 0.05$, and $F_{2,57} = 63.748$, $p < 0.05$). Within ovulated, parous hinds significant differences in the weight of the uterus was demonstrated (Fig. 1b) only between two and four years old ($F_{2,36} = 8.376$, $p < 0.05$), while no such difference occured between ovulated, nulliparous females (Fig. 1a; – $F_{2,17} = 3.517$, $p = 0.053$).

As indicated in Figure 1, differences in mean uteri weights were significant between ovulated and non-ovulated hinds in all age groups, irrespective of their previous breeding history (t-tests, all $p < 0.001$). Also, in two and three year old non-ovulated hinds, uteri were significantly heavier in the parous compared to the nulliparous group (2 year old: $F_{1,32} = 158.997$, $p < 0.001$, 3 year old: $F_{1,21} = 26.695$, $p < 0.001$).

On the basis of corpora albicantia and lactation, three year old hinds were classificied as primipara or multipara (first and second time breeders). Mean ute~us weight for the two groups were 47.0 g (S.D. ± 5.03) and 54.5 g (S.D. ± 6.9) respectively, the difference being significant ($t = -2.50$, d.f. = 18, $p < 0.05$). Primiparous two and three year old hinds did not differ in mean uteri weights ($t = 1.15$, d.f. = 20, $p = 0.263$). The sample size did not allow further analysis of whether the increase in uterus weight was associated with number of parturitions.

Although mean uteri weights for non-ovulated yearling hinds did not increase significantly with month (see above), or fit a regression line with date of death ($R^2=0.049$, $F=1.734$, $p=0.197$), values for both 70 and 90 percentiles increased from September to October (70 percentile: 14.0 g – 15.5 g, 90 percentile: 15.9 g – 22.2 g). Kurtosis and skewness increased in the same period (kurtosis: -0.024 – 1.470, skewness: 0.124 – 1.173). This may indicate that, had they not been shot, growth of the uterus in some individuals might have continued towards a size associated with ovulation in this age class, and that some of the yearling hinds shot might have started reproduction at a later date that season. A similar trend was not apparant in non-ovulated, nulliparous two year old hinds.

Anatomical appearance of uteri. – Compared to non-ovulated hinds, uteri from ovulated hinds in all age groups showed relatively more developed cornua and a more bulgy corpus, as well as increased vascularization. It also appeared relatively easy to distinguish between parous and nulliparous uteri from anatomical appearance. Uteri from nulliparous hinds are "slimmer" with relatively smaller cornua, less developed ligaments (e.g. *lig. latum*), and a thinner uterine wall *(myometrium).* The pale yellow or pinkish white colour sometimes gives an almost translucent impression and underlines the "virginity" compared to the more muscular, darker and more vascularized uterus from parous hinds.

Weight of ovaries. – There was no significant difference in weight between right and left ovaries in any age class (paired t-tests: all p ^{3} 0.05), the overall means being 0.75 g and 0.76 g respectively. In non-ovulated females weight of ovaries differed significantly between age classes (Fig. 2; – $F_{21,1353} = 19.456$, p ⅓ 0.05). However, this was largely due to calves having smaller ovaries than older females. As a group, calves, yearlings and hinds older than 16 years had smaller ovaries than hinds 2–16 years of age ($t = -5.27$, d.f. = 393, p ⅓ 0.001), the respective

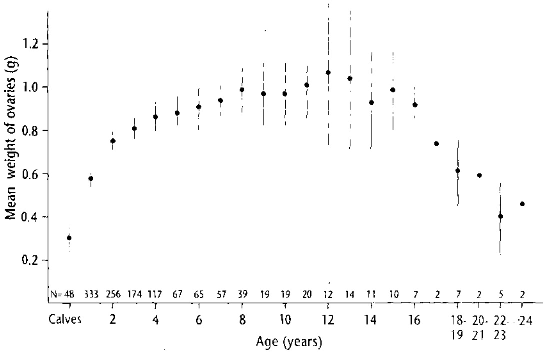

Fig. 2. Mean weight of ovaries (± S.D.) for different age classes of female red deer. Sampling period September–December.

means being 0.67 g and 0.92 g. There were no significant differences in ovary weight between hinds 2–16 years of age ($F_{14,288}$ = 2.981, p > 0.05, Scheffe's proc).

Within age groups (calves, yearlings, hinds 2–16 years and hinds ≥ 17 years) there was significant covariance between ovary weights and body weight, except in hinds 17 years and older (Table 2). Weight of ovaries also varied significantly with month in yearling hinds and hinds 2–16 years old, but not in calves and hinds older than 16 years. During autumn (September–December), weight of ovaries from hinds one year and older showed a small but steady increase with date (y = 0.76 + 0.0023x, R^2 = 0.014, $F_{1,383}$ = 5.261, p = 0.022), mainly as a result of a gradually larger proprotion of ovaries

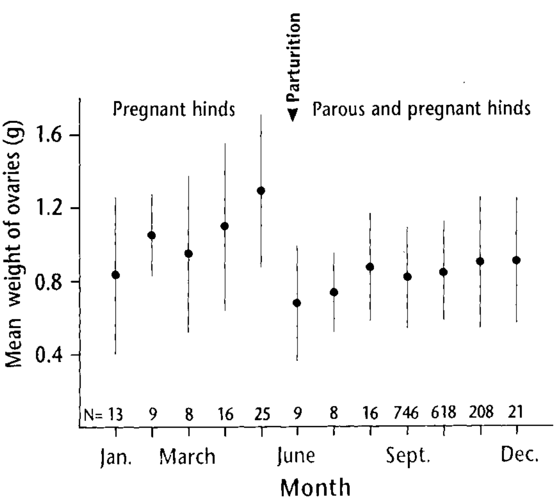

Fig. 3. Mean weight (± S.D.) of ovaries in pregnant or parous hinds one year and older in different months of the year.

containing corpora lutea entering the sample with time. Overall, ovaries from hinds that had ovulated weighed significantly more (0.97 g) than non-ovulated hinds (0.80 g; – t = -3.77, d.f. = 393, p <0.001).

Sample size of data from outside the period September–December did not allow detailed statistical analysis. However, some possible trends may be indicated: Ovaries from nulliparous and non-pregnant hinds one and two years weighed on average 0.26 g (n=9, range 0.23 g – 0,31 g) from December to April. Mean weight from June to August averaged 0.65 g (n=18, range 0.59 g – 0.76 g) and declined thereafter as a consequence of a gradually increasing proportion of maturing hinds ovulating, leaving the less developed individuals with smaller ovaries in the sample.

In pregnant or parous hinds one year and older, weight of ovaries follow a different trend (Fig. 3), increasing from December to shortly before parturition in early June. Then weights dropped to a minimum after parturition, before increasing again throughout summer and autumn.

Size of ovarian follicles. – Size of ovarian follicles varied within pairs of ovaries as well as between individuals. The largest follicle measured had a diameter of 15.0 mm, while the mean diameter for largest follicle across age classes was 5.2 mm. Overall, there was no significant difference in size of largest follicle between age classes ($F_{21,1058}$ = 2.49 p > 0.05). Even calves often had follicles with diameters overlapping the range of older females (see Fig. 4). However, grouped together, calves and hinds 17 years and older had significantly smaller diameters of largest ovarian follicles compared to hinds 1–16

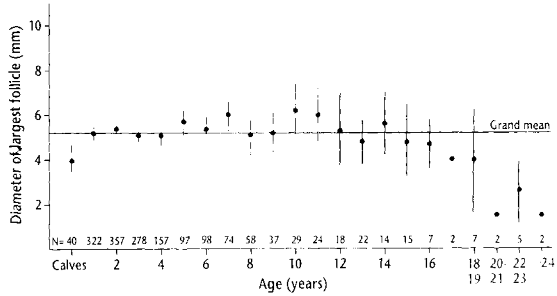

Fig. 4. Mean diameter of largest follicle in pairs of ovaries from female red deer of different age. Sampling period September–December.

years of age, respectively 4.5 mm and 5.3 mm (t = –3.23, d.f. = 93.94, p = 0.007, sep.var.est).

Analysis of variance showed that overall, size of largest follicle varied with age (categories: calves, yearlings 2–16 years and ≥ 17 years, $F_{3,1909}$ = 4.592, p = 0.003), estrus ($F_{1,1909}$ = 32.754, p < 0.001) and month of sampling ($F_{11,1909}$ = 4.117, p < 0.001). Covariance with body weight was also significant ($F_{1,1909}$ = 8.188, p = 0.004). Excluding calves from the analysis, however, age was no longer significant ($F_{2,1866}$ = 2.767, p = 0.063), leaving other factors and covariate with unchanged significance levels.

Within age categories the picture was somewhat different (Table 2). In calves and yearling hinds, but not in hinds two years and older, size of largest follicle was positively correlated with body weight. Month of sampling was important only in hinds 2–16 years of age, and follicle size declined from mid summer to parturition next spring (y=6.886–0.292x, R^2=0,025, $F_{1,1637}$ = 42.289, p = < 0.001). Estrus (with or without corpora lutea) showed significant association with follicle size both in yearlings and 2–16 year old hinds. Mean diameter of largest ovarian follicle did not vary with any independent factor or covariate in hinds 17 years and older, that perhaps also being due to a small sample size in this age group.

Size of largest follicle declined with date during summer and autumn in hinds 2–16 years old (Fig. 5), and Figure 6 illustrates this more

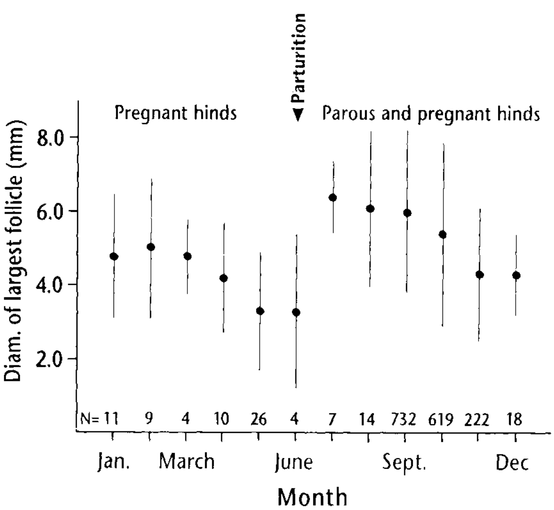

Fig. 5. Mean diameter (± S.D.) of largest follicle in pairs of ovaries from hinds one year and older in different months of the year.

Table 2. Relationships between mean weight of ovaries and mean diameter of largest follicle (dependent variables) and body weight (covariate) and month of sampling and estrus (independent factors).

	Age groups	Body weight F	Body weight p	Cow.raw regr. coeff.	Month of sampling F	Month of sampling p	Estrus F	Estrus p
Weight of ovaries	calves	$F_{1,32}$=5.838	0.022*	0.015	$F_{5,32}$=0.775	0.550 N.S.		
	yearling hinds	$F_{1,287}$=7.891	0.005**	0.006	$F_{9,287}$=2.293	0.013**	$F_{1,287}$=2.013	0.038*
	hinds 2–16 yrs	$F_{1,1187}$=28.308	<0.001***	0.006	$F_{11,1187}$=5.200	<0.001***	$F_{1,1187}$=35.883	<0.001***
	hinds ≥ 17 yrs	$F_{1,53}$=1.494	0.227 N.S.	0.006	$F_{8,53}$=0.973	0.467N.S.	$F_{1,53}$=4.339	0.042*
Diam. of largest foll.	calves	$F_{1,37}$=4.584	0.039*	0.121	$F_{5,37}$=0.590	0.71 N.S.		
	yearling hinds	$F_{1,351}$=6.902	0.009**	0.038	$F_{9,351}$=1.446	0.167N.S.	$F_{1,351}$=9.306	0.002**
	hinds 2–16 yrs	$F_{1,1432}$=3.228	0.073 N.S.	0.012	$F_{11,1432}$=2.556	0.003**	$F_{1,1432}$=26.385	<0.001***
	hinds ≥ 17 yrs	$F_{1,12}$=0.002	0.963 N.S.	0.003	$F_{7,12}$=0.373	0.901 N.S.	$F_{1,12}$=0.733	0.409 N.S.

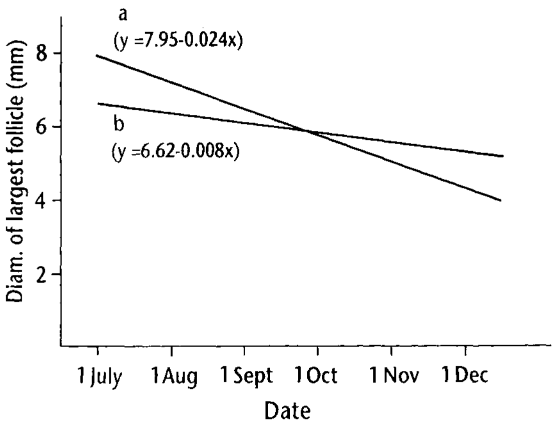

Fig. 6. Mean diameter of largest ovarian follicle with date in hinds one year and older. a=non-ovulated and ovulated hinds 2–16 years old. b=non-ovulated hinds 1–2 years old.

generally, also including the regression line for non-ovulated hinds 1–2 year old. Difference in slopes of regression lines in Figure 6 may partially illustrate the moderating or suppressing effect a corpus luteum or pregnancy is likely to exercise on development of follicles. Mean size of largest follicles in non-ovulated hinds was 4.5 mm, and significantly larger than the mean of 4.0 mm in ovulated hinds ($t = 5.13$), d.f. = 896.38, $p < 0.001$, sep.var.est.). Possibly, this effect applies to development and dynamics in the ovaries as a whole, since mean weight of ovaries in non-ovulated hinds (no corpus luteum) was significantly heavier than non-luteinized ovaries in pairs where the contralateral ovary contained a corpus luteum ($t = -2.54$, d.f. = 1561, $p = 0.011$), the respective weights being 0.83 g and 0.78 g in hinds 2–16 years old.

Discussion

As indicated by Valentincic (1958), the weight of the uterus in red deer may provide an easy way to assess if a female has given birth earlier (parous) or not (nulliparous). However, it is clear that this is reliable only when females have not ovulated or are pregnant at the time of sampling (Fig. 1). Variation in time of ovulation and uterine development relating to conception could make comparison between ovulated, nulliparous hinds and parous hinds (ovulated as well as non-ovulated) unfeaseable and confounding.

Within both nulliparous and parous females there is a clear difference in weight of uteri between ovulated and non-ovulated individuals in the age groups 1, 2, and 3 year old, and in parous hinds also in 4 years and older, Thus, knowing the age and parous status (e.g. lactation) of female sampled in autumn, it is possible to assess if that female has ovulated or not with reasonable confidence on the basis of weight of the trimmed uterus.

The size of uterus tends to increase with age both in nulliparous and parous individuals up to three and four years respectively, thus providing a good indication of age in the two groups, given the females have not ovulated or conceived. Ahrens and Liess (1987, also citing R. Hofmann pers.comm) suggest that in wild cervids one or two pregnancies are required to have the uterus fully developed in terms of size and appearance. From this study (Fig. 1), it seems more likely that 2–3 pregnancies are required for red deer. No difference in size of uterus occurred in hinds four years and older. The sample size did not, however, allow conclusions about size of uteri in very old hinds (> 20 years), but if anything, the few specimens in the material tended to have rather small uteri.

Although uteri did not increase in weight with time, controlled for the effect of estrus, there appeared a possible positive trend in yearling hinds. One conceivable explanation of this observation is that growth in uterus from September to the end of hunting season is largely due to an increasing proportion of individuals approaching estrus (McDonald, 1975; Nalbandov, 1976), and had they not been shot, they probably would have ovulated at a later stage and exhibited correspondingly heavier uteri.

In Norwegian red deer, yearling hinds generally ovulate later than older hinds, mainly from the end of October to late November or even into December. Red deer hunting in Norway mainly takes place in September and October, prior to most ovulations in yearling hinds. Use of uteri weights to estimate proportions of ovulating and non-ovulating females appear most reliable if sampling takes place late in the season, thus distinguishing more precisely between those females who have ovulated or are likely to, and those who are not. In principle this also applies to older hinds, although they are likely to conceive earlier. However, since more than 95% of hinds two years and older conceive (Wegge, 1975; Burkey, 1989; Langvatn, 1990), weight of uteri as a methodological approach probably in most usefully applied on yearling hinds, especially since their later ovulation period reduces possibilities to assess ovulation on the basis of corpora lutea.

In summary, weight of uteri may provide an additional source of information to estimate certain reproductive events like estrus period and parous status. It may also be indicative of age, given knowledge about parous status and whether the female has ovulated or not. Under circumstances where it is difficult to get samples of uteri and ovaries from the period at or after the main estrus activity, uteri weights may be of help in estimating the proportion of females likely to ovulate and conceive. In Norway, this is particularly useful in yearling hinds, since they tend to ovulate towards the end, or after the present hunting season.

In terms of methodological application, weight of ovaries *per se* does not seem to reflect any particular relationship to reproductive events, past or approaching. This is perhaps also the reason why so few authors (Leader-Williams and Rosser, 1983) have reported on this variable in wild cervids. European red deer attain fertility at an age of 1–2 years (Kröning und Vorreyer, 1957; de Crombrugge, 1964; Lowe, 1969; Wegge, 1975), and after peak reproduction in prime ages, pregnancy rates decline in old hinds (Mitchell, 1973; Guinness *et al.*, 1978; Albon *et al.*, 1986; Burkey, 1989). Very young and very old age classes also have smaller ovaries (Fig. 2), thus coinciding to some extent with reproductive performance in general. However, weight of ovaries alone can not be regarded a reliable criterion in this connection, since although size of ovaries from calves and yearlings may corresponc to those of hinds > 16 years, their histological appearance differs significantly, as also shown for moose (Markgren, 1969). Ovaries from young, nulliparous females are lighter and more "translucent" compared to the more "dense" and vascularized ovaries in old hinds. Young females also tend to have a relatively broad ovarian cortex with more antral follicles compared to old hinds where the medullar zone and stromal connective tissue in the cortex seem more conspicuous (conf. Dellmann and Brown, 1976). The trajectory of mean ovary weights (Fig. 2) for hinds from three to approximately 16 years of age probably illustrates correlation with body weight more than reproductive performance, since all these age groups show 99–100% pregnancy rates in Norwegian red deer (Burkey, 1989). Leader-Williams and Rosser (1983) and Horak (1989) found a similar relationship between ovary weights and age (up to nine years) in South Georgian reindeer and roe deer, respectively. Their observations on development of ovaries from calves and differences in weight of ovaries with and without corpora lutea also parallel the findings in this study on red deer (see also Valentincic, 1958).

In reindeer, Leader-Williams and Rosser (1983) found that in parous hinds, weight of ovaries declined after early pregnancy and then increased and declined before parturition. In contrast the data from this study suggest an increase from low values after parturition to highest values just before parturition (Fig. 3). However, this trend did not fit a linear regression line ($R^2=0.007$, $F_{1,404}=3.001$, $p=0.084$). Trauger and Haugen (1965) found that in young white-tailed deer, ovaries increased in size during pregnancy.

In moose (Markgren, 1969) and reindeer (Leader-Williams and Rosser, 1983), calves may have follicles of a size comparable to mature Graafian follicles in adult females. This is also the case in red deer, thus excluding the possibility of using follicle size alone as a indication of fertility. Also, as evident from the work by Halazon and Buechner (1956) functional corpora lutea may originate from follicles with diameters well within the range of follicle size in calves.

There was a relatively small variance around the mean diameter of largest ovarian follicle over the "life span" in red deer. Only calves and very old hinds (≥ 17 years) tended to diverge in that respect. Because published information is not available, it is difficult to know how this compares to other species, although Valentincic (1958) and Markgren (1969) described ovaries from old female red deer and moose to be often small and with few antral follicles. Among hinds ≥ 17 years, there were clearly some in menopause (sterile) with ovaries weighing from 0.10 to 0.32 g. Histological examination revealed no developing (secondary) follicles, and the cortical stroma appeared dense, consisting mainly of connective tissue (Valentincic, 1958). It seems likely that, allowing for individual variation, red deer hinds approach cessation of their reproductive capability from approximately 17 years of age. Burkey (1989) reported a significant decline in pregnancy rates in hinds older than 19 years.

The association between size of largest follicle and body weight in calves and yearlings may be related to covariance between body weight and the weight of ovaries. Valentincic (1958) states that size of follicles relates to the size of ovaries, smaller ovaries offering limited possibilities for the development of large follicles.

In many cervids, number and size of large antral follicles increase during the follicular phase (*proestrus-estrus;* – Halazon and Buechner, 1956; Morrison, 1960; Harder and Moorhead, 1980; Leader-Williams and Roser, 1983). According to Harrison and Weir (1977), the period for development of the follicle from a primordial state is about 10 days in the cow. Assuming a similar period in cervids, it is not surprising that many large follicles during anestrus and early proestrus phases were obliterative atretic with infolded and hypertrophic granulosa and theca layers (see also Halazon and Buechner, 1956; Harder and Moorhead, 1980; Leader-Williams and Rosser, 1983). In contrast to observations by Halazon and Buechner (1956) in elk, ovaries from Norwegian red deer contained many large follicles (> 2 mm) during the anestrus period shortly after parturition. In fact, in hinds two years and older (as well as yearlings) the largest follicles on average occurred in this period, whereafter the mean diameter declined gradually during follicular and luteal phases (Fig. 5). The decline in follicle size from July to December (Fig. 6) may be caused by a gradual reduction in representation of large follicles as they turn atretic or later rupture and luteinize (Fig. 6a). It may also reflect the suppressing effect progesterone from corpora lutea exercises on development of new antral follicles (Brokx, 1972), as illustrated by the difference in slope of lines a and b in Figure 6. This also applies to the whole period of pregnancy, probably accentuated by increased amounts of progesterone from the gravid uterus (McDonald, 1975; Nalbandov, 1976). Peripheral plasma progesterone levels in white-tailed deer were low during anestrus in does in August–September, but increased at the time of ovulation, and stayed high during winter (Harder and Moorhead, 1980).

Morrison (1960) and Markgren (1969) found no major differences in size or number of large antral follicles between pregnant and non-pregnant females in elk and moose respectively. From this study however, it seems clear that heavier ovaries and smaller antral follicles in general coincides with estrus (corpora lutea) and pregnancy.

In conclusion, weight of the uterus may serve as a useful measure to substantiate assessments of reproductive events such as parous status, fertility, and estrus within different age groups. Application is perhaps of special interest in 1–2 year old hinds entering first reproduction. If ovulation rates can not be calculated on the basis of corpora lutea, weight of uteri, sampled shortly before the peak estrous period, may be indicative of what proportion of the hinds that is likely to ovulate at a later stage.

Not surprisingly, changes in weight of ovaries and size of ovarian folliclies were associated with reproductive events like ovulation and pregnancy. However, variation with age, body weight and phase in estrous cycle makes it difficult to see any applicable value of these measures that surpass or significantly support other criteria for reproductive events used in population dynamics and ecological studies.

Acknowledgements

This study would not have been possible without the consent of a large number of municipal wildlife boards. L. Ingdal assisted in sampling and laboratory work, and S. D. Albon, T. Hanley and N. Chr. Stenseth gave valuable comments on earlier drafts of this manuscript. To all these persons I wish to express my sincere thanks.

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Manuscript accepted 27 April, 1992