# CERVIDOS NATIVOS e INTRODUCIDOS en CHILE

## SEMINARIO INTERNACIONAL

# NATIVE and INTRODUCED DEER in CHILE

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# Consideraciones acerca de la regulación nutricional de la reproducción y dinámica poblacional en cérvidos.

# Aspects of nutritional regulation of reproduction and population dynamics in cervids.

**Resumen**

Podría ser común que las poblaciones de cérvidos libres estén limitadas nutricionalmente. Las patologías graves asociadas a desnutrición pueden ser raras (excepto en relación con la energía), y deficiencias subclínicas son difíciles de observar; sin embargo podrían ser muy importantes. La desnutrición puede afectar el potencial reproductor de hembras y así determinar la dinámica de la población. Más generalmente, la desnutrición también influye sobre la condición de los individuos, incluyendo el tamaño de las cornamentas de los machos y el sistema inmunológico. La desnutrición puede ser el resultado de una falta de macro y/o microelementos. Deficiencias de Co, Cu, I, Mn, y Se producen un efecto marcado sobre la reproducción de los rumiantes. Una deficiencia subclínica de Se disminuye la probabilidad de supervivencia de crías del ciervo cola negra (*Odocoileus hemionus columbianus*) durante el primer mes de vida. Aunque los ciclos de elementos esenciales se originan a partir del suelo local, es importante reconocer la posibilidad que tales ciclos no sean estáticos, y que algunos ciclos de elementos esenciales puedan ser sometidos a alteraciones rápidas por influencias antropogénicas. Los factores más importantes que pueden disminuir la biodisponibilidad del Se incluyen: a) la acidificación de los suelos, b) la contaminación de los suelos y las plantas con metales pesados, c) el uso de fertilizantes para las plantas, d) la tasa de la cosecha de la biomasa, y e) los cambios de composición en la comunidad de las plantas. La incidencia de desnutrición por insuficiencia de energía puede ser frecuente entre cérvidos, y pensamos que el número de poblaciones afectadas está aumentando contínuamente. Esto puede ser el resultado de a) el incremento de disturbios antropogénicos en áreas naturales donde los carnívoros principales están siendo reducidos o exterminados, b) un número creciente de poblaciones introducidas coincidente con sistemas de predadores insuficientes, y c) el normalmente insuficiente control de poblaciones con la caza recreativa. Este último aspecto está exacerbado por la opinión publica que se opone a la caza de hembras y crías. Desde el punto de vista del manejo, las poblaciones de hembras y machos pueden ser tratadas separadamente pero desde una perspectiva de la población total. Cuando es necesario el control de una población, se torna posible solamente si incluye un manejo adecuado de la población de hembras. Una superpoblación en clima templado frecuentemente resulta en mortandades masivas en invierno. Sin embargo, hemos observado una mortandad significativa del ciervo cola negra durante el verano por falta de suficiente energía. La falta de energía también puede afectar mucho el potencial reproductor de las hembras. La previsibilidad estacional del forraje posiblemente pudo haber sido la fuerza que resultó en la estrategia estacional de crianza que se da en cérvidos no-ecuatoriales. El cambio en fotoperíodo determina en forma general (melatonina) una vez cada año los ajustes fisiológicos en preparación para la ovulación. Sin embargo, el nivel de acumulación de grasa de reserva antes de la brama podría determinar finalmente el medio hormonal (estrógeno) necesario para producir la ovulación. Mecanismos bioquímicos podrían regular la probabilidad de ovulación de manera tal que las hembras solamente puedan ovular si el nivel de acumulación de grasa es suficiente para completar una preñez y lactancia sin comprometer la progenie o ellas mismas. Sin un control de la población, como es la predación, los cérvidos libres no muestran una estrategia que provea una reserva de grasa óptima a las hembras para asegurarse un éxito reproductivo óptimo. Más bien, tienden a saturar el hábitat de invierno y/o de verano hasta el punto que se producen mortandades masivas periódicamente. En una población de ciervo cola negra en la que faltaba suficiente energía, se ha observado un retraso del período de crianza de cerca de un ciclo del estro (22-28 días), al igual que hembras de las clases etarias jóvenes no gestantes. En ambientes modificados por el hombre aumenta la necesidad de manejo de las poblaciones de cérvidos libres. La existencia de una disponibilidad adecuada de energía puede ser determinada con una evaluación de la condición y parámetros reproductores de las hembras. El manejo tiene que concentrarse primero en el control de la población, y en segundo lugar puede involucrar una mejora del forraje. Las deficiencias subclínicas de elementos esenciales pueden ser determinadas solamente a través de ensayos de respuesta productiva. Ensayos sub-clínicos en poblaciones de cérvidos libres desafortunadamente son muy costosos. Las comparaciones con concentraciones conocidas en tejido normal (posiblemente de otras especies) pueden proveer aproximaciones que deberían utilizarse cautelosamente.

## Abstract

It may be a common occurrence that free-ranging populations of cervids are limited nutritionally. While overt pathologies associated with undernutrition may be rare (except in relation to energy), subclinical deficiencies are difficult to observe, yet may be very important. Undernutrition can affect the reproductive potential of females and, therefore, determine the dynamics of the population. More generally, undernutrition will also influence the condition of individuals such as body size including antler size of males, and the immune system. Undernutrition may occur due to a relative lack of macro and/or micro elements. Amongst trace elements, deficiencies of Co, Cu, I, Mn, and Se have a pronounced effect on reproduction of ruminants. Se in particular has been shown to affect reproduction of cervids. Subclinical deficiency of Se was shown to lower the probability of survival of young black-tailed deer (Odocoileus hemionus columbianus) during their first few months of life. Although trace element cycles originate from local soil, it is important to recognize the possibility that such cycles are not static, and some trace element cycles may be subject to rapid alterations through anthropogenic influences. In the case of the Se cycle, the most important factors which may lower subsequent Se bioavailability include a) acidification of soils, b) soil and plant contamination with heavy metals, c) use of plant fertilizers, d) rate of biomass removal, and e) changes in plant community composition. The incidence of undernutrition due to insufficient energy may be frequent amongst cervids, and we believe is occurring in a steadily increasing number of populations. This may be related to a) increased anthropogenic disturbance in natural habitats where top carnivores are being reduced in numbers or exterminated, b) an increasing number of introduced populations concurrent with inadequate predatory systems, and c) the usually inadequate control of populations through recreational hunting. The latter aspect frequently is exacerbated by public opinion opposing the hunting of females and young of the year. For management purposes the female and male populations can be treated separately, while considering the whole population. When population control is necessary, it can only be achieved by including adequate management of the female population. In temperate climate, overpopulation frequently results in mass die-offs during the winter, however, we observed a significant die-off of black-tailed deer during the summer time due to inadequate energy availability. Summer die-offs are more difficult to discern in forested areas because the animals tend to be dispersed. Lack of energy may further have a strong effect on the reproductive potential of females. Seasonal predictability of forage may have been the driving force resulting in the seasonal breeding strategy found in non-equatorial cervids. The change in photoperiod determines in a general way (melatonin) the timing for physiological adjustments in preparation for ovulation. However, the level of storage fat obtained before the breeding season may ultimately determine the hormonal milieu (estrogen), which is necessary for ovulation to occur. Biochemical mechanisms may regulate the probability of ovulation in such a way that females only ovulate if their body energy stores are adequate to carry a pregnancy to term and lactate without compromising progeny or themselves. Without population regulation such as through predation, free-ranging cervids do not exhibit a strategy providing optimal fat reserves to adult females ensuring optimal reproductive success. Rather they tend to saturate winter and/or summer habitat to the extent that mass die-offs occur periodically. In a population of black-tailed deer lacking sufficient energy we observed a delay of the breeding season by about an estrus cycle (ca. 22-28 days), as well as unbred females of young age classes. In man-modified environments, it is becoming increasingly necessary to manage free-ranging populations of cervids. The existence of inadequate energy availability can be determined by evaluation of body condition and reproductive parameters of females. Management should first focus on population control and secondarily, may involve improvement of the forage base. Subclinical deficiencies of trace elements can only be determined with production response trials. Such clinical trials in free-ranging populations of cervids unfortunately are a costly enterprise. Comparisons with known normal tissue concentrations (possibly of other species) may provide approximations which should be used cautiously.

## Introduction

Undernutrition in seasonal free-ranging populations of cervids may occur frequently. The most prominent outcome is a massive die-off due to energy deficiency during the winter. Other overt pathologies related to undernutrition, especially in regard to trace elements, have been rarely reported (Kistner 1982). However, subclinical deficiencies may occur more frequently, albeit they tend to go unnoticed due to unspecific symptoms (Robbins 1983). Amongst trace elements, deficiencies of Co, Cu, I, Mn, and Se can have a pronounced effect on reproduction of ruminants (Underwood 1977).

Energy deficiency in cervids of high reproductive potential may be related to the uncontrolled population growth response after introduction as an exotic or by altering the predator-prey relationship. However, deficiencies of macro and micro elements may not be related to animal density.

Although weather conditions alone may result in undernutrition energetically, introductions of exotic cervid species and/or changes in the predator-prey relationship are more important factors. Introductions of cervids have occurred extensively worldwide (Niethammer 1963, Simberloff 1981) and population dynamics in relation to habitat remain of both practical and theoretical interest. Predator-prey relationships are becoming increasingly important as large predators continue to be displaced or their numbers reduced by man. Indirectly, alterations of the food base for herbivores may also have the same effect as a reduction of predator density by allowing herbivore densities to increase while predators remain territorial.

Undernutrition may not be distributed homogeneously throughout a population. The feeding requirements and behavior amongst different age and sex classes may be distinct and include spatial segregation. In the male population typical indicators of the nutritional status include body size and the quality of antlers. The effects on the female population appears to be more pronounced, exerting a strong influence on reproductive success.

First, we will utilize the trace element selenium (Se) to demonstrated the subclinical effects of deficiency on reproduction of free-ranging black-tailed deer (Odocoileus hemionus columbianus) and discuss the dynamic nature of the Se cycle. Next, we will describe the circumstances of a massive die-off among black-tailed deer due to energy deficiency and discuss how energy may regulate reproduction. Lastly, we will provide suggestions on how this information may be incorporated into sound management of cervid populations.

## Trace element deficiency and reproduction: selenium as an example.

We studied a free-ranging deer herd in California, USA, which had spring fawn-to-doe (FTD) ratios of less than 30/100 since 1978. Since veterinary records of domestic ruminants showed that Se was playing an important role in calf survival and weight gain rate, we initiated a field trial to evaluate the effect of Se supplementation on the reproductive success of local deer.

Adult females were supplemented with Se using iron-Se alloy boluses (95:5 by weight). In 1984, one Se bolus and in 1985-87, 2 boluses were administered. Ages were obtained later based on cementum annuli analysis. The number of fawns of Se-supplemented females was ascertained in autumn after migration to the winter range, when experimental females were also shot and necropsied. The control measure was obtained by counting fawns, adult females and adult males during herd composition counts in autumn. Se in blood and the activity of the corresponding enzyme glutathione peroxidase were determined as described previously (Flueck 1991).

The distribution of whole blood Se levels of unsupplemented animals (n = 135) indicates that 80% fall below 0.050 ppm which is considered deficient for cattle, while 15 % fall between 0.051 and 0.075 ppm, which is considered low-marginal for cattle. Se supplementation increased blood levels by factors of 1.9 in 1984 and 3.6 in 1985-87 (n = 40). The response variable was the number of fawns per adult female surviving until the time after the autumn migration. The productivity attributable to Se supplementation is the difference of productivity ratios among supplemented (n = 94 F + D) and unsupplemented groups (n = 2051 F + D). Thus, while the Se supplementation added 10 fawns per 100 adult females in 1984, the increased survival rate remained fairly constant over the period from 1985 to 1987, amounting on the average to 51 added fawns per 100 adult females (Flueck 1989). Supplementation with Se demonstrated: 1) the role of Se in the initial survival of fawns; 2) that additional factors unrelated to Se result in fawn mortality; and 3) that those additional mortality factors vary greatly from year to year. Possible reasons for these additional mortalities include other nutritional deficiencies, herd health problems, and predation.

## The dynamics of the Se cycle.

Although mineral cycles originate in bedrock and soil, it is important to note that such cycles are not necessarily static. For instance, the incidence of overt Se deficiency in many areas has increased recently (B.B. Norman, pers. comm., Jenkins and Hidiroglou 1972, Gissel-Nielson 1975, Stoszek *et al.* 1980, Fischer 1982, Millar 1983, Griffiths 1986). While increased exposure to a number of substances can result in an increased demand for Se, there are several factors which may contribute to an apparent decline of soil Se availability to plants and animals: a) soil acidification; b) soil contamination with heavy metals; c) use of plant fertilizers; d) rate of biomass removal; and e) changes in plant community composition.

### a) *Soil acidification*

Anthropogenic production of protons is substantial. With respect to the ability to neutralize, mitigate, or recover from the effects of acid deposition, many areas are considered sensitive (Root *et al.* 1980). Frost in 1972 suggested that the emission of sulfur dioxides and $H^+$ ions may lead to a reduction of Se available to plants and animals since a decrease in soil pH was known to elicit a reduction of plant uptake of Se (Allaway et al. 1967, Geering *et al.* 1968, Gissel-Nielsen 1971). Consequently, others have considered acid precipitation to be in part responsible for a declining Se cycle (Frost 1972, 1983, Fischer 1982, Mushak 1985, Kieffer 1987). Soils with equivalent Se concentration can produce Se toxicity or Se deficiency in animals depending on soil pH. For instance, Se deficiency in North Dakota has been encountered recently due to immission from sulfur oxides (Hastings 1979), even though North Dakota is traditionally known to have high levels of Se and, at times, toxicity problems in livestock. Other processes causing soil acidification such as fertilization and removal of biomass have to be considered as well.

**b)** *Soil and plant contamination with heavy metals*

During the process of soil acidification increased amounts of heavy metals become available for plant uptake. Direct aerial immissions or contamination of fertilizers may also contribute significant amounts. Heavy metals such as cadmium and mercury, however, are antagonistic to Se and demand an increased intake of Se for compensation. Furthermore, increased solubilization of heavy metals may tie up Se in the soil by forming metal selenides (Allaway *et al.* 1967, Comb and Comb 1986:2, Frost 1987).

**c)** *Use of plant fertilizers*

All forms of agriculture are essentially exploitive in nature due to removal of products. This is well recognized and is reflected in the widespread need for fertilizers, including trace elements. Correction of a nutrient deficiency in plants by adding fertilizer (phosphate, nitrogen, sulphate) often increases the incidence of Se responsive diseases (Stefferud 1956:431) and produces lower Se levels in animal tissues (Millar 1983, Gupta and Watkinson 1985). Fertilizers can produce a dilution effect (Se is absorbed passively), reduce soil pH, interfere with plant absorption of Se, and interfere with Se uptake by animals.

**d)** *Rate of biomass removal*

Se cycles rather rapidly, especially when plant available Se is minimal. Under these circumstances most of the bioavailable Se is tied up in the standing biomass (Swaine 1978), decaying organic matter and in the organic soil horizon (Gissel-Nielsen and Hamdy 1977). Se bioavailability then appears to require substantial local recycling, i.e. the biomass should decay locally. An accelerated rate of biomass removal by harvesting and exporting vegetation or herbivores can consequently result in an exhaustion of plant available Se.

Fire acts as a potent mineralizing agent, causing the rapid transformation of organic compounds to inorganic ones. Removal of Se by volatilization during fires may be substantial in systems with marginal to low Se concentrations since much of the plant available Se occurs in the standing biomass (Swaine 1978). Additionally, much higher concentrations of sulfur as compared to Se exist in the plant material, and a likely result of combustion is sulfur dioxide reducing selenicals to insoluble elemental Se, and the formation of insoluble metallic selenides (Swaine 1978, Comb and Comb 1986:2, Frost 1987). Frequent prescribed burning may thus contribute to the loss of Se from the cycle.

Ruminants return Se through urine and feces to the soil in relative insoluble, inert forms which are unavailable to plants (Butler and Peterson 1963, Peterson and Spedding 1963). Plant uptake of Se from sheep feces amounts to less than 0.3% and suggests that continuous foraging by ruminants over many years could reduce the available Se in the soil (Butler and Peterson 1963, Peterson and Spedding 1963). The intensity of grazing and browsing thus may be an important aspect of the Se cycle.

**e)** *Changes in plant community composition*

The Se concentration varies greatly in different plant species and also in different parts of plants (Burridge *et al.* 1983). White clover (*Trifolium repens*), for instance, is a poor accumulator of Se (NRC 1983:20) and contains less Se than ryegrass which, in turn contains less than browntop (*Agrostis tenuis*). Thus, changes in plant community structure such as results from improving a low-producing browntop pasture to a high-producing rye-white clover pasture can lead to a decline in animal Se status and lowered production, particularly in areas of marginal Se status, and independent of soil Se conditions (Burridge *et al.* 1983, Clark and Towers 1983, Millar 1983).

## Energy deficiency and reproduction

Energy deficiency can be defined as occurring when the number of herbivores per unit forage energy results in less than the genetically determined maximal body size, all other factors being optimal. The degree of energy deficiency is expressed in a gradient of responses. In seasonal cervids, the most important period is late summer and autumn when sufficient fat has to be accumulated (Mautz 1978). The amount of fat necessary to survive the winter is approximately proportional to the severity of the winter season. Severe undernutrition results frequently in mass die-offs during the winter and early spring. Less severe undernutrition will be expressed in smaller body size of individuals including the antlers of males. Furthermore, the degree of undernutrition of females in autumn may determine the timing of the rut and pregnancy rates.

Mass die-offs during the summer time are possible as well, although they can be difficult to discern in forested areas where the animals tend to be dispersed. This may occur when several winters were favorable, or when the winter range is large in relation to the available summer range. Without adequate population control, animal density may increase and the condition of the herd decrease. In a black-tailed deer herd in California we measured continuously decreasing marrow, kidney, and brisket fat levels over four years. During the last autumn (the peak of fat accumulation), marrow fat averaged 37% and was less than 15% in several individuals. In the summer of 1987, we observed a mass die-off estimated at 30-40% of the female population around the time of parturition which coincides with maximal energy demand due to lactation. The average age of the female population of 8.3 years dropped to 4.5 years in the following year (Flueck and Smith 1990 in prep.). Furthermore, reproductive information on this herd substantiated the severity of energy deficiency. In 1987, the peak of parturition was delayed by about 3 weeks; several examined females 2 and 3 yrs of age had never been pregnant; and, the growth rate of fawns was as low as 25% of the published rate under optimal conditions (Flueck, unpubl.). FTD counts in autumn and the following spring also indicate drastic changes in the population dynamics. Normally, the spring FTD ratio is lower or at the most equal to the preceding autumn ratio. However, the ratio from autumn to spring in 1987/88 increased indicating further selective mortalities. The shortage of available energy also may have resulted in an early autumn migration in 1987 and clearly demonstrated that weather per se had no influence on the timing (Flueck unpubl.).

**Reproduction in cervids**

Proximate environmental mechanisms which optimize the timing of ovarian cycles in seasonal breeders are of two types. Some provide consistent, predictable stimuli and act as general timers ("Zeitgebers") which initiate the seasonal development of the ovaries so that ovulation occurs during a favorable season. The most reliable of these in non-equatorial regions is the seasonal change in the photoperiod. Thus, the further one moves away from the tropics, the more pronounced seasonal breeding becomes, and the more precise the timing (Follett 1985, Tyler 1987b). The other group of stimuli represents adjusting factors which modulate the timing of ovulation to conform to immediate environmental conditions.

The reproductive performance of the female population is reflected in herd productivity and depends strongly on the capability of optimally partitioning the seasonally available energy. Thus, the peak of energy demand (lactation) generally coincides with the peak of forage production (Loudon and Kay 1984). However in addition, non-equatorial cervids have developed a strategy of lipogenesis in autumn and fat mobilization in winter and spring to survive the harsh winter, and to supplement the energy requirements of reproduction. This is controlled intrinsically and results in weight loss during winter even when high quality feed is available ad libitum (Ullrey *et al.* 1967, Moen and Severinghaus 1981). Thus, the ability to lay down fat in winter is limited irrespective of the amount of food available. As part of this strategy, fat in particular may provide necessary signals to the central nervous system and gonadotropin regulatory areas either directly, by estrogen production, or indirectly, by the effects of relative fatness on temperature control and metabolic rate, or by both means.

The seasonal change in adult body weight with a maximum in autumn is well documented. In adult females, the weight gain is primarily from the deposition of storage fat (e.g. Anderson and Medin 1965, Mitchell and Brown 1973, Anderson *et al.* 1974, Reimers *et al.* 1982, Tyler 1987b). Moreover, the probability of ovulating especially in fawns and yearlings, is dependent on the body weight at mating (e.g. Mitchell and Brown 1973, Blaxter and Hamilton 1980). Under nutritional constraints, lactating females may not obtain the necessary body weight to ovulate, and often conceive only every other year (e.g. Clutton-Brock *et al.* 1982, Loudon and Kay 1984). This may also explain the significant changes in ovulation rates observed between years (e.g Barron and Harwell 1973). Furthermore, poor nutrition has been related to delayed conception and parturition dates (e.g. Haagenrud and Markgren 1973, Mitchell and Lincoln 1973, Clutton-Brock *et al.* 1982), and under severe undernutrition, elk have been found not to conceive at all (Morrison 1960). In this context, the practice of 'flushing' needs mentioning. It is accomplished by introducing female ruminants to a feeding area of much greater quality several weeks before anticipated oestrus. The level of exposure to the high quality food induces a higher rate of ovulation (dose-response) especially in multiovulatory species (Rattray et al. 1981, Wilson 1984), but only if females were in poor condition before flushing (Clark 1934, Ransom 1967, Rattray *et al.* 1981).

**Regulatory mechanisms of ovulation**

Seasonal oestrus in non-equatorial cervids is spontaneous (non-coitus-induced) and is governed by the change in day light hours. Artificially reducing the photoperiod or melatonin treatment has been used to advance the timing of oestrus in well-nourished deer (Budde 1983, Webster and Barrell 1985, Adam *et al.* 1986). However, melatonin did not have this effect in lactating red deer (Nowak *et al.* 1985).

There appear to be additional regulatory systems which fine tune reproduction (Wayne et al. 1988). For instance, not all females will ovulate during the breeding season (White and Fancy 1986), and lactational status has been shown to modulate the timing of oestrus (Harper 1971, Loudon and Kay 1984, Adam *et al.* 1985, Fink 1986, Emery 1988). Estrogen-dependent ovulation appears to be a major regulatory mechanism of reproduction. Specifically, elevation of estrogen in the blood above a critical concentration for a certain amount of time will induce a short-lived, high-level release of pituitary gonadotropins which then causes ovulation to occur (Brodie 1979, Schwartz *et al.* 1977, Fink 1986, Baird and Short 1977, Mori *et al.* 1987). This hormonal pattern was also evident in ovariectomized ewes supplemented with subcutaneous implants releasing constant amounts of estrogen (Worthy *et al.* 1985), thereby suggestive of additional endogenous sources of estrogens.

The important association of body weight and ovulation rate in cervids may thus occur because ovulation rate may be related to the ratio of lean body mass to fat mass as documented for humans (Frisch 1980, 1984, 1988). Specifically, fat mass determines the extent of endogenous estrogen production by converting androgens to estrogens (Siiteri 1982) and influences the direction of estrogen metabolism to more potent or less potent forms (Fishman *et al.* 1975, Schneider et al. 1983). In addition to modulating the preovulatory gonadotropin surge, estrogen may also be a factor in the maturation process of oocytes (Bahr *et al.* 1977).

What evidence exists supporting the view that fat mass in female cervids controls reproduction by modulating the hormonal milieu which allows ovulation to occur ? In areas where food availability changes seasonally, cervids synchronize the breeding period to occur before winter (Klein 1985, Verme *et al.* 1987). This has been explained by the effect of nutrition on body weight due to its relationship to breeding success (Mitchell and Brown 1973; Albon et al. 1983; Skogland 1986; Tyler 1987a,b). A more refined explanation for cervids is the relationship of amount of fat reserves or lean body mass to fat mass ratio and ovulation rate (Harper 1971, Lenvik *et al.* 1982, Dauphiné 1976, Klein and White 1978, Thomas 1982, Albon *et al.* 1986, Cothran *et al.* 1987, Ozoga 1987, Verme and Ozoga 1987). High fat reserves in adult white-tailed females at the beginning of the breeding season appear to be a prerequisite for conceiving two young instead of one, and early breeders had the highest amount of fat (Cothran *et al.* 1987, Ozoga 1987). Similarly, female white-tailed fawns on a high energy diet in autumn ovulated whereas fawns on low energy diet did not (independent of protein levels) (Abler *et al.* 1976). In caribou, a body weight increase of only 10% was associated with a change from essentially zero to 95% probability to conceive (Thomas 1982, Reimers 1983, White 1983), while in red deer, a body weight increase of 50% doubled the number of calves born and surviving until September (Blaxter and Hamilton 1980). Strong correlations between fat stores, reproductive rate, and onset of puberty were also found in Roosevelt elk (Harper 1971).

Body fat in turn, has been shown to be responsible for estrogen production. Extraovarian estrogen can originate from adipocytes located in the abdominal cavity, omentum and bone marrow among others, and can amount to about 30% of circulating estrogen in pre-menopausal women and to all the estrogen in postmenopausal women (Schindler *et al.* 1972, Nimrod and Ryan 1975, Longcope *et al.* 1978, Forney *et al.* 1981, Kirschner *et al.* 1982, Frisch 1988). Increased obesity in human females results in increased androgen production and a higher rate of peripheral aromatization to estrogens (Kirschner *et al.* 1982). Injection of androgens into nonpregnant red deer for instance, resulted in oestrus within a few days (Short 1979).

There appear to be additional mechanisms which have some modulatory effect on the timing of ovulation, but which may not be related to fat metabolism. *Behavioral responses particularly* are known to *influence* the endocrine milieu (Cheng 1986). The presence of rutting males appears to elicit such an effect (Moore 1985, Moore and Cowie 1986, Fisher and Fennessy 1987, McComb 1987, Verme *et al.* 1987).

There are many advantages to early ovulation. A 35 day advance in ovulation through melatonin treatment resulted in female red deer calves weighing 49.7 kg more by weaning than controls and resulted in an increased probability of winter survival (Blaxter and Hamilton 1980, Adam *et al.* 1986, Adam and Moir 1987, Milne *et al.* 1987).

## Management implications

Se is important to health and reproduction of mammals including cervids. Trends of increased incidence of Se responsive disease have been noted. This may be mainly the results of decreased Se availability through changes in the Se cycle. However, due to its basic biochemical functions, Se demand may also be increased under increased exposure to toxic oxygen species. Broad scale application of Se may be used to correct a deficiency situation (Flueck *et al.* 1989).

Most difficult of all is to recognize if there exists a subclinical or 'silent' deficiency of trace elements in animals. This is of importance especially in free-ranging cervids because it is difficult to make adequate observations on individuals and even more difficult to make repeated observations on the same individual. In principal, analytical methods should not be used as a sole criteria for analyzing trace element status. A subclinical deficiency can only be positively identified by production response trials where the productive performance of treated animals is compared to untreated or control animals foraging under the same conditions. Most importantly however, one should not expect requirements and/or bioavailability of certain trace elements to remain constant. When a deficiency is suspected, analysis of tissue samples will provide a good start for an investigation.

Without population regulation such as through adequate predation, free-ranging cervids tend to saturate habitats to the extent that high periodic mortality rates result and not that females obtain optimal fat reserves ensuring optimal reproductive success (Klein 1985). This genetically based behavior is indicative of opportunistic and fast reproducing species which can take advantage of rapidly changing environments. Under such circumstances it is beneficial to have control mechanisms of reproduction based on environmental stimuli such as through the extent of lipid stores. If this hypothesis should be confirmed, the implications to management of wild cervid populations are as follows: for high reproductive rates to occur, the female population must be provided with optimal forage and a habitat structure which allows females to obtain adequate fat reserves for successful breeding at the optimal time of the year.

To have any major impact on cervid reproductive efficacy, the principal management efforts should focus on summer and autumn conditions. There are 2 basic approaches for dealing with free ranging populations. First, the vegetation and habitat can be modified to provide more or better forage. However, due to the great reproductive potential of cervids, these efforts are worthless if not accompanied by adequate population control. Without population control, such habitat improvements which are normally expensive, may add but a few additional members to a population, but certainly will not affect the condition of the population and hence, reproductive efficacy. The second option is to ensure that the number of animals in relation to the food supply allows adequate fat deposition before winter. Unless predation and diseases exert adequate control already, the only feasible approach is through hunting. However, it needs to be emphasized that the female population particularly needs to be regulated. Where control through harvesting is indicated, it needs to be determined if recreational hunting by itself is sufficient. Aside from any goals set in regard to population turn-over rate (i.e. harvest rate), the importance of adequate population control in man-modified environments is the preservation of the habitat.

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