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SEASON AND GROWTH STRATEGY IN RED DEER: EVOLUTIONARY IMPLICATIONS AND NUTRITIONAL MANAGEMENT

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Abstract: Red deer (*Cervus elaphus*), like many other species of deer, have highly seasonal cycles of live weight change even in the presence of surplus high quality feed. In this paper, we have used analyses of food intake and growth data from red hinds and stags kept indoors on high quality diets to compare males and females. We contrast the two sexes in terms of their annual patterns of food intake and growth, their energy requirements for growth and maintenance and their mature size. We hypothesize that the selection pressure on an increased mature size in males has led to a relatively greater efficiency of growth in males compared with females but that in contrast to the growth-oriented metabolism of the male, the female has a fat-biased metabolism. The consequences of seasonality and the differences in growth strategies between the sexes are examined in the light of possible evolutionary implications. We then draw some implications for the practical management of red deer.

Key Words: evolution, food intake, growth, nutrition, red deer, seasonality, selection pressure

Résumé : Le cerf rouge (*Cervus elaphus*), comme beaucoup d'autres espèces de cerfs, sont susceptibles aux cycles saisonniers très marqués dans leur poids même dans la présence d'un excès de nourriture de bonne qualité. Dans cette étude nous nous servons des analyses de la ration alimentaire et de la croissance des biches et des cerfs rouges gardés à l'intérieur au régime de bonne qualité pour effectuer une comparaison des mâles et des femelles. Nous contrastons les deux sexes en termes de leurs tendances annuelles pour la ration alimentaire et la croissance, leurs besoins d'énergie pour la croissance et le bien-être, et leur taille adulte. Nous formulons l'hypothèse que la pression sélective pour une plus grande taille adulte chez les mâles amena une efficacité relativement supérieure pour la croissance des mâles mais qu'en contraste avec le métabolisme en faveur de la croissance chez les mâles, le métabolisme des femelles est en faveur de la formation du gras. On examine les conséquences de la saisonnalité et des différences de stratégies de la croissance entre les sexes pour discerner les implications possibles pour l'évolution. Nous en tirons des conséquences pour la gestion pratique des cerfs rouges.

Mots-Clés: cerf rouge, croissance, évolution, nutrition, pression sélective, ration alimentaire, saisonnalité

Temperate and arctic species of deer exhibit highly seasonal patterns of live weight change (high growth rates in spring-summer and zero or low growth rates in winter) which persist even in the presence of excess high quality feed. These patterns are evident in both growing and mature animals of both sexes. Adult males exhibit a further cycle with a greatly reduced food intake and considerable loss of body weight during the annual rut (mating season). The seasonal pattern of feed intake and growth probably evolved in response to natural selection resulting from the seasonal nature of food supply. Such seasonal growth reflects an endogenously controlled system which prevents the animal from attempting to grow when feed supply is likely to be limiting and also conserves body reserves. In this paper, we will review aspects of seasonality in deer and examine some of the consequences of this selection pressure on the growth strategies of the two sexes. We will also compare information for red deer (*Cervus elaphus*) with other species and present data on an analysis of feed intake and growth in red deer with respect to season and differences between the sexes. We will then integrate our ideas on the apparent phenomena and attempt to relate them to the evolution of growth strategies in red deer. We will then draw some implications for the practical management of red deer.

Seasonality

Several species of deer show evidence of considerable seasonality in live weight change (French et al., 1956; Wood et al., 1962) which persist even under ad libitum feeding of high quality diets (McEwan and Whitehead, 1970; Bandy et al., 1970; Loudon et al., 1989). A seasonal cycle of food intake with higher intakes in spring-summer and lower intakes in winter is evident in both male and female deer (Blaxter et al., 1974; Suttie, 1987) with an additional rut-associated depression of food intake also evident in males (Suttie, 1981; Fennessy, 1982).

The seasonal pattern of growth reflected in feed demand reduces energy demand during winter, when the supply of high quality feed is likely to be limited and increases demand in spring-summer, when feed is likely to be abundant. Thus the animal is self-restricted to rapid growth only during seasons of abundant feed supply. Much of the weight gained by adult stags over spring and summer is fat which is depleted during the breeding season (Drew, 1985) when the stag eats little or no food. The rut inappetence also enables the stag to spend time in gathering and protecting his harem of hinds which increases the chances of mating and thus contributing his genes to the next generation.

Seasonal rhythms of deer, including the rut, are synchronised by daylength cues (Suttie et al., 1984) to a period of one year. It seems likely that the annual cycle of feed demand is a function of an underlying cycle in metabolic rate which is under endocrine control, although the precise relationship between the intake and metabolic rhythms is speculative. However several metabolic and growth hormones have well-defined seasonal rhythms in red deer (Suttie et al., 1989; Curlewis et al., 1988; Loudon et al., 1989) and further studies are underway at Invermay at present. In respect of an underlying metabolic rhythm, Silver et al. (1969) found that the fasting metabolic rate of white-tailed deer recorded in a respiration chamber (at 19°C) exhibited a 1.8 fold range, with a minimum in winter (December) and a maximum in summer (July). A similar range has been reported for fawns of the same species (Thompson et al., 1973). Unfortunately, there are apparently no comparable data available for red deer, although some very limited data are suggestive of such a rhythm (Suttie, 1981).

The potential impact of adverse climatic variables (eg. wind, rain, and low temperatures) on body heat loss indicates that a reduced feed demand alone during winter may not be a very satisfactory strategy, although a reduced drive to eat would be expected to reduce food searching and exposure to the elements. The essential associated strategies are behavioural approaches (eg. shelter-seeking) to reduce heat loss. In some situations, it is conceivable that with feed in short supply and/or of low quality, the energetic costs incurred in food searching, harvesting, and digesting may actually be greater than the energy yield to the animal. This highlights the importance of an integrated strategy. In looking at seasonal rhythms Moen (1978, 1985) has developed the concept of an annual metabolic rhythm expressed in terms of multiples of base-line metabolism (MBLM) for white-tailed deer (*Odocoileus virginianus*). For a non-pregnant, non-lactating doe, the computed MBLM maximum and minimum are 2.60 and 1.60 in October and February, respectively. The importance of behavioural adaptations to en-

vironmental stressors is indicated by the 2.0 fold difference in MBLM for a 40 kg doe at -30°C bedded down in a curled-up posture, compared with that for one standing in the open in a 1.8m/sec wind. However, metabolic strategies may also be involved, in that Moen (1985) reported that white-tailed deer may go further into metabolic depression as cold stress increases. He found no indication of increased metabolism with deer exposed to -20°C, in that their heart rate, respiration rate, body temperature and activity all decreased. However, in this respect, there may be species and perhaps individual differences, as Mautz et al. (1985) reported that white-tailed deer increased metabolic rate during lying by 1.5 fold as temperature declined from 7°C to -20°C, whereas black-tailed deer (*Odocoileus hemionus columbianus*) increased their rate by 1.7 times and mule deer (*O. h. hemionus*) by 1.2 times. The white-tailed deer also significantly increased the proportion of time spent lying down.

The net benefit of reduced metabolism, reduced food intake and behavioural strategies to limit energy loss is increased survival in a predictably harsh winter environment. The net cost is an obligatory cessation of growth for several months of winter which is generally not reversible even if conditions of food availability and quality and climate are unusually good during this period.

Food Intake and Growth Patterns in Red Deer

The analysis of food intake and live weight gain data is potentially of considerable value in identifying seasonal patterns and in comparing males and females, with the overall objective

Table 1. Summary of food intake and weight parameters for red deer stags and hinds (data from P.F. Fennessy and J.M. Thompson, pers. commun.).

	Stags	Hinds
Food intake function		
Basic pattern		
Food intake at maturity, C (MJ ME/wk)	213	144
Appetence parameter, T* (wk)	38	20
Oscillation		
Food intake oscillation, d (MJ ME/wk)	47	25
Proportional oscillation (d/C)	0.22	0.18
Phase delay in food intake from photoperiodic oscillation (wk)	6.4	9.9
Liveweight function		
Mature liveweight, A (kg)	198	124
Marginal efficiency of liveweight gain (AB) (kg liveweight gain/MJ ME, scaled)	0.025	0.012
Maintenance efficiency, T_0 (kg liveweight maintained/MJ ME/wk)	0.94	0.87

furthering our understanding of deer growth and nutrition. In this respect, Parks (1982) proposed a theory of feeding and growth in animals which described growth as a three dimensional function of weight, age, and food intake, as opposed to the more conventional two-dimensional, weight by age concepts (Brody, 1945).

We have recently analysed data sets of weekly feed intake and live weight for red deer stags and hinds fed high quality diets (approximately 11 MJ ME/kg DM) *ad libitum* for up to 3.5 yr (P.F. Fennessy and J.M. Thompson, pers. commun.), using the functions proposed by Parks (1982). The data comprised weekly food intake and live weights for 16 stags (6 in Experiment 1 and 10 in Experiment 2) individually fed indoors from approximately 6 to 50 or 12 to 42 months of age. The hinds were approximately 6 to 50 or 12 to 42 months of age. The hinds were group fed (two pens, each of 6 hinds) from 10 to 18 months of age. The methodology is more fully presented in the appendix, but briefly, the rate of weekly food intake was described by a decreasing exponential function of age, to which a sine function was added to account for the seasonal oscillation in intake. The rut period was identified by inspection of the food intake analysis (the and these periods excluded from the food intake analysis (the first week of the rut was that in which intake had fallen by 20% compared with the previous 2 weeks and the time at which intake attained a new plateau was defined as the end of the rut). Live weight as a function of food intake was described using the controlled growth equation proposed by Parks (1982). The parameters for the food intake and live weight functions are presented in Table 1.

The mean food intake at maturity (C) and the sine oscillation about this mean intake (d) were markedly higher for stags than hinds, but when the amplitude of the oscillation was expressed as a proportion of mature food intake (d/C) the difference between sexes was much reduced. The magnitude of the seasonal oscillation (which excludes the rut) in these indoor fed deer (22 and 18% for stags and hinds, respectively) was higher than that reported for sheep (6%) (Blaxter et al., 1982). The magnitude of the oscillation in intake may also be expressed as a 1.56 fold and a 1.42 fold increase in food intake at the summer peak, relative to the winter trough in stags and hinds, respectively. Kay (1979) showed that with deer and sheep on 6 month photoperiodic cycles, the seasonal amplitude was greater in the deer; he also showed that the amplitude for the more primitive Soay sheep was greater than that for Suffolk x Finn-Dorset sheep.

The phase shift in food intake indicated a delay of 6.4 and 9.9 wk for oscillations in food intake behind the oscillations in day length, for stags and hinds respectively. These estimates are of the same order as the phase shift of 8.0 wk reported for antler casting for stags on manipulated day lengths by Suttie et al. (1984). The apparent difference in phase shift between the sexes of 3.5 wk must be treated with some caution as the estimate for the hinds was from only two pens of group-fed hinds, kept for only 0.75 of an annual cycle in day length, compared with the stags where the phase shift was estimated in 16 individually fed animals kept for 2.5 to 3.7 annual cycles in daylength. However, if the sex differences in phase shift are real, then two possible mechanisms may be operating. The seasonal rhythms themselves may differ between the sexes, or alternatively the systems which align the seasonal rhythms with photoperiod may differ between the sexes. If one considers the concept that there are

windows of responsiveness to changes in photoperiod it may be that the male opens this window earlier than the female and thus responds earlier. This is consistent with the male strategy of attempting to gain a selective advantage by altering physiological state early to take advantage of changing conditions and is consistent with a female strategy of less rapid but more consistent and less risky responses to a changing environment.

The parameter, t*('star) is the age at which animal attains 0.63 of its mature food intake and therefore an animal with a higher appetite will have a lower t* value. The sex difference in t* is of particular interest in that the rate of increase in food intake was markedly greater in females (who attained 63% of their mature food intake at 20 wk in early May during the southern hemisphere autumn) compared with males, where t* was 38 wk of age (i.e. in August during early spring). As t* is a time variable, it would be expected to be positively related to mature weight, with the stags, having a greater mature weight, having a larger t* than the hinds (Taylor, 1980). However, even after scaling for mature weight ($A^{0.27}$) (Taylor, 1980) a sex difference in t* was still apparent with scaled estimates of 9.1 and 5.4 metabolic wk for stags and hinds, respectively. The scaled estimate for t* in hinds was very similar to the values for rams and ewes obtained by Thompson et al. (1985), whereas the estimate for stags was considerably higher. The effect of this difference in t* on weekly food intake is such that both young male and female deer would be expected to have similar intakes at around 26 wk of age, with the divergence between the sexes becoming very evident in the following spring-summer.

The most interesting feature of the growth/food intake analysis is the difference in (AB), (the marginal efficiency of conversion of food ME to live weight gain, free of a live weight maintenance component). The post weaning (AB) value for stags at 0.025 was twice as high as that for hinds at 0.012. Consequently, the results suggest that red stags have a similar, or even slightly greater feed efficiency than sheep and cattle (Parks, 1982; Thompson and Barlow, 1986), while hinds are clearly less efficient. By contrast, Thompson et al. (1985) reported that in sheep, females had a slightly greater (AB) value than males.

The maintenance efficiency of the animal is described by the parameter T_0, which is equivalent to the ratio of mature weight over mature food intake (A/C). The marked seasonal oscillation in food intake would suggest that either similar oscillations would be evident in T_0, or alternatively the oscillations in mature food intake were matched by similar oscillations in mature weight, with the net effect that T_0, or maintenance efficiency, was constant over the period of the experiment (up to 3.5 yr of age). To examine these options, an oscillation for T_0 was included in the live weight model, and although there was some suggestion of an oscillation it was variable in magnitude and failed to account for a significant proportion of variation in any of the animals. This supports the contention of Parks (1982) that T_0, or maintenance efficiency, is constant throughout life. This is surprising in view of the well-defined seasonal oscillations in metabolic rate in both sheep fed at maintenance (14%, Blaxter and Boyne, 1981) and white-tailed deer (Silver et al., 1969) and suggests that some other factors may be overriding an inherent oscillation in the data. This may well be the case in that the rate of growth and food intake are autocorrelated such that real changes in T_0 could be interpreted

Table 2. Mean liveweight change (kg ± S.D.) over the rut (pre-rut maximum to rut minimum) for two groups of red deer stags.

Rut	Live weight change (kg ± S.D.)	
	Experiment 1 (n = 6)	Experiment 2 (n = 10)
Yearling	-4.7 ± 2.3	+1.3 ± 3.0
2 year	-9.6 ± 3.8	-17.3 ± 13.5
3 year	-28.2 ± 10.7	-29.4 ± 15.7

as being a component of feed efficiency.

In marked contrast to the situation with feed efficiency, the parameters for live weight maintained/MJ ME/wk (T_o or A/C) were marginally higher for stags than for hinds (0.94 and 0.87 kg/MJ ME/wk, respectively). Use of the growth curve parameters to calculate the ME requirement by scaling mature food intake by mature weight ($C/A^{0.75}$) gave a ME requirement of 0.57 and 0.56 MJ ME/$kg^{0.75}$/day, values which were virtually identical to estimates of the feed requirements for maintenance derived using short term data sets from the same animals (Fennessy et al., 1981a; Suttie et al., 1987) and by other workers (Kay and Staines, 1981). Thus, once a hind reaches maturity, her feed requirements for maintenance are as expected (that is with little apparent difference between the sexes after scaling for mature live weight), and the high energetic costs of growth are not carried through to maturity. Our conclusion therefore is that there has been selection pressure on both sexes to limit maintenance costs in adulthood.

The estimated mean mature live weight for the sexes (predicted from T_o and the mean mature food intake, C) indicate a sexual dimorphism ratio for mature weight of 1.6 (198/124). The computed mature live weights of the two sexes differ from the actual recorded peak live weights at around 4 years for stags and hinds of 202 and 113 kg respectively, a ratio of 1.8. Notwithstanding the possible minor errors in mature live weights, both estimates are substantially higher than the male/female ratio published for sheep (Thompson et al., 1985) and cattle (Taylor et al., 1985) of 1.4. We believe that the greater sexual dimorphism in deer provides support for the concept of different selection pressures between the sexes in deer, in contrast to the two domestic ruminant species where sexual dimorphism is less.

Variability Through the Rut and Winter

The variability in the magnitude of the rut among groups of stags is of special interest. This is particularly the case in terms of the patterns of food intake and live weight change over the rut and following winter. The intensity of the rut (as reflected in changes in feed intake and live weight) in red stags tends to increase with age but also varies markedly between stags of the same age at least up to the 3 year old stage. This is readily

apparent both from live weight change over the rut (Table 2) and from food intake data (eg, the lowest weekly food intake recorded for each stag). The distributions of such intake data are shown in Fig. 1.

The first (yearling) rut is of special interest. In Experiment 1, (stags born in 1977), all 6 stags lost weight over the rut and following winter while in the following year (Experiment 2, stags born in 1978), the 10 stags housed in the same complex, on average gained weight over the rut and maintained a positive live weight gain until well into the winter before undergoing a small live weight loss (Table 3). The reasons for the difference between years is not obvious but it may be that the proximity of the older stags (ie. the 1977 born stags) to the yearling stags in Experiment 2 suppressed the rut in the latter group, such that they maintained reasonable levels of feed intake through the rut period (the relatively high food intake is evident in Fig. 1). If rut suppression is the reason for the difference it raises some interesting questions. Is the suppression due to pheromones and could such a phenomenon be used in the practical management situation to minimise weight loss or even obtain a weight gain in yearling stags around the first rut? More controlled studies are necessary to further investigate this apparent phenomenon.
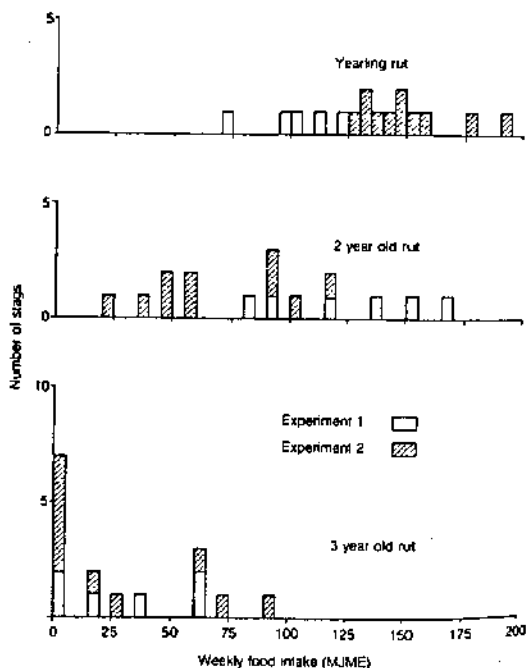

Fig. 1. Distribution of the minimum weekly food intake for 16 individually fed stags during the rut over 3 years (Experiment 1, n = 6; Experiment 2, n = 10).

Table 3. Mean liveweight change (kg ± S.D.) and numbers gaining liveweight in two groups of yearling red deer stags during three periods: over the rut, from pre-rut to the winter minima, and from pre-rut to the winter maxima.

	n	Pre-rut to rut minimum		Pre-rut to winter maximum		Pre-rut to winter minimum	
		Weight change	n	Weight change	n	Weight change	n
Experiment 1	6	-4.7 ± 2.3	0	-3.0 ± 3.2	1	-6.5 ± 3.3	0
Experiment 2	10	1.3 ± 3.0	8	+8.5 ± 3.7	8	+3.0 ± 3.9	9

Evolutionary Aspects

The difference in efficiency between stags and hinds is an intriguing observation and suggests that the selection pressures on the sexes in red deer may well be very different from those operating on the two sexes in sheep and cattle. However there is also the possibility that domestication has brought about major changes in the domestic species, but this seems unlikely. Rather an evolutionary perspective seems more appropriate.

Our hypothesis, akin to that of Clutton-Brock et al. (1982a), is that the selection pressure operating on red deer males is the attainment of a large body size at maturity to improve a stag's chance of access to hinds. The result of this pressure is an increase in absolute growth rate and a greater adult body size. Adult body weight and early growth rate are highly correlated in red deer (P.F. Fennessy, pers. commun.) as with domestic ruminant species. The objective for the stag is to attain a large skeletal size prior to closure of the epiphyses associated with puberty. Under such pressure, the drive is to grow in size and stature; the accumulation of fat reserves is simply incidental to the increase in size. Interestingly, some results from both Scottish and New Zealand work suggest that there may be negative selection pressure on extremely high early growth, through the penalty associated with precocious puberty (as assessed by the date of pedicle initiation), which if it occurs in the autumn may ultimately lead to permanent stunting and a reduced mature body size (Suttie, 1981; P.F. Fennessy and J.M. Suttie, pers. commun.). In contrast, the selection pressure on a female is to reproduce successfully over a lifetime; that is to attain her pubertal target weight and to start breeding at the first opportunity as a yearling, and to successfully rear a calf to independence as frequently as possible, in order to maximise her lifetime reproductive rate.

In these respects, the Rhum studies of Clutton-Brock et al. (1982a) are of considerable interest, in that male calves were heavier at birth and sucked more frequently than females, both factors which support the concept of the genetic impetus towards a high growth rate to achieve a high mature weight in males. The relatively low fat reserves of the male calf also mean that there are benefits of a larger body size, such that the greater the body size, the greater the chance of the calf surviving the environmental stresses of the first winter (Clutton-Brock et al., 1982a). Therefore we hypothesize that the higher feed efficien-cy of the males may be a result of this selection pressure on mature size and hence on growth rate. This is not to say that there are no advantages of larger size in females; there are (eg dominance and access to food, Clutton-Brock et al., 1984) but the scale within females is very much less than the scale of difference between males and females. In other species such as reindeer and caribou (*Rangifer tarandus*), or perhaps even North American wapiti (*Cervus elaphus* spp.), it is conceivable that there may be selective pressure on leg length to cope with snow and/or the necessity to migrate (K.L. Parker, pers. commun.). It is the greater variance in reproductive success among males than females so elegantly shown by Clutton-Brock and his coworkers (Clutton-Brock et al., 1982a; Clutton-Brock, 1988) that imposes the far greater selection pressure on mature size in males. In contrast, the selection pressure on females is simply to reproduce successfully, a strategy which puts little pressure on growth rate beyond the need to ensure that live weights and fat reserves are sufficiently high principally to cope with the adverse conditions of winter. In fact, in an environment where periodic food shortages occur, it could be argued that the selection pressure on females is towards the smallest size compatible with successful rearing of a calf. In this situation, fat reserves would assume a far greater importance and in this respect it is significant that Albon et al. (1986) have shown that female fertility in a free-ranging red deer population in Scotland was positively and independently related to both body weight and kidney fat weight. Overall therefore, we describe the female as having a fat-biased metabolism, in contrast to the growth-oriented metabolism of the male. It is not that males do not make good use of their fat reserves; they do, but the important point is that the primary drive in males is towards the attainment of large size in contrast to the situation with females.

It is also interesting that calculations from artificial rearing data (Fennessy et al., 1981b) indicate that the (AB) for both males and female calves is similar on a milk diet (0.039 and 0.034 for males and females, respectively). Therefore there is evidence that the lower energetic efficiency of females so evident post weaning may not operate in the preweaning environment and thus the young female is not penalised by a lower efficiency factor preweaning. Since female calves grow at only slightly lower rates than males preweaning it means that they have reached a much higher proportion of their mature weight by weaning than have their male counterparts. The logical extension to this hypothesis is that selection pressure on the

female is towards a metabolism which will support the accumulation of fat reserves, (a fat-biased metabolism), rather than towards absolute size, although to date we are unaware of any complete body composition data on females to support or refute such a concept. However limited data relating to particular fat depots do support this concept (Clutton-Brock et al., 1982b; J.A. Stevenson and K.R. Drew, pers. commun.).

Seasonal feed availability places a constraint on the strategy of rapid growth of the male in that growth is restricted to the times of feed abundance. Rather than allowing feed supply *per se* to determine growth, a seasonal growth rhythm has evolved which obliges a stag to cease growth in winter (although a young stag does have some potential for winter growth, this is much below that recorded in spring). Whether the ontogeny of this rhythm is actually seasonal or whether it is implicit in all deer growth and has been merely entrained with season cannot be determined. A major consequence of this rhythm is that a stag can conceivably gain an advantage over its peers in terms of growth if it is to increase its food intake and hence growth rate earlier in the spring. The penalty for this is that the stag which increases growth early in the year with the late spring is more likely to die with the increase in feed demand (consequent on the increase in metabolic rate) which is not satisfied by the available feed supply; consequently the stag will in fact lose weight rather than gain, and place itself at risk.

Although the female too has a growth rhythm which is inevitably constrained by the seasonal rhythm of feed abundance, this rhythm is of far less consequence in terms of evolutionary significance as the female strategy of rapid gain while sucking (which results in females attaining a much higher proportion of their mature live weight while sucking) followed by a steady gain to adulthood is in no conflict with season. Fat reserves in the female also provide a reserve to meet environmentally-induced shortfalls in feed supply over winter. The difference between stags and hinds is elegantly borne out in the present study where the seasonal oscillation in food intake is less in females than in males.

Implications for the Farming of Deer

In the practical situation in New Zealand, where deer are run outdoors in winter, the environmental factors (low temperature, wind and rain) necessitate an increased food intake to compensate for the increased body heat loss. This is particularly critical in adult stags with their low fat reserves following the rut (Drew, 1985). It has been estimated that this increases energy requirements of adult stags outdoors during winter by about 50% compared with stags indoors (Fennessy et al., 1981). Provision of shelter reduces the energy requirement and consequently is a common practice among New Zealand deer farmers. It is also interesting that observations of red stags in New Zealand suggest that they will continue food searching in adverse weather conditions, rather than reduce activity and seek shelter to conserve energy reserves. However it may be that in a sense they have little choice in that their energy balance is critical as evidenced by stag deaths (the so called winter death syndrome) following sudden weather changes. Such deaths are now unusual with a greatly improved appreciation by farmers of the critical nature of the stags energy balance. In this respect it is very interesting

that even with *ad libitum* feeding of high quality diets over winter, stags will only maintain body weight; this situation holds even with indoor feeding of high quality diets. The management of adult stags during the rut may also have an impact on fat reserves at the start of the winter. For example in breeding stags, there is evidence that single-sire mating results in a lower body weight loss over the rut than multiple-sire mating systems, presumably through reduction in conflict and harem-protecting activities. In contrast to the situation with stags, hinds with their greater fat reserves entering the winter, are in a much less critical state. Practical recommendations on winter management of hinds recognize this and recommend nutritional practices designed to take weight off hinds over winter (Fennessy and Milligan, 1987). Overall, an appreciation of seasonality, the natural growth patterns, and the impact of the environmental situation on energy requirements will greatly assist in the development of practical and cost-effective management systems for deer.

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