Modelling carrying capacity for wild boar Sus scrofa scrofa in a forest/heathland ecosystem

Authors: Bruinderink, Geert W.T.A. Groot, and Hazebroek, Ed

Source: Wildlife Biology, 1(2) : 81-87

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1995.0013

Modelling carrying capacity for wild boar *Sus scrofa scrofa* in a forest/heathland ecosystem

Geert W.T.A. Groot Bruinderink & Ed Hazebroek

Groot Bruinderink, G.W.T.A. & Hazebroek, E. 1995: Modelling carrying capacity for wild boar *Sus scrofa scrofa* in a forest/heathland ecosystem. - Wildl. Biol. 1: 81-87.

The main habitat for wild boar in the Netherlands consists of a forest/heathland ecosystem. In this ecosystem we found an exclusive correlation between mast availability and nutritional condition in winter and reproduction of wild boar in the succeeding spring. This correlation was used to model carrying capacity in terms of a threshold density in winter, above which the average body weight is density-dependently reduced. The results of modelling carrying capacity of an area of forests and heathlands on poor, sandy soils, for wild boar are presented. The model is based on available mast and broadleaved grasses, the latter being the main substitute for mast during winter.

Key words: carrying capacity, density, mast, modelling, Sus scrofa scrofa, the Netherlands, wild boar

G.W.T.A. Groot Bruinderink & E. Hazebroek, Institute for Forestry and Nature Research (IBN-DLO), P.O.Box 23, NL-6700 AA Wageningen, the Netherlands

Received 14 November 1994, accepted 19 March 1995

Associate Editor: Nigel G. Yoccoz

In the Netherlands the last refuge areas for wild boar *Sus scrofa scrofa* are confined to habitats on poor sandy soils. Natural predators have been exterminated and an annual hunting toll, judged to be approximately equal to recruitment, controls population size. Traditionally, boar numbers were kept high by year-round supplementary feeding. In modern management, however, harvesting is no longer a major objective and cessation of supplemental feeding is strongly promoted. But little is known about the ecology of non-supplementary fed wild boar and patterns in their main food resources.

If predators are not regulating a population of ungulates and numbers are increasing, the animals' nutritional condition (body weight) and ability to breed may at one point become density dependent as a result of competition for limited food resources (Klein & Strandgaard 1972, Grubb 1974, Staines 1978, Mitchell & Crisp 1981, Albon et al. 1983, Sauer & Boyce 1983, Ratcliffe 1984, MacNab 1985, Fowler 1987, Clutton-Brock et al. 1992). This limiting effect of food availability may come down to one season (winter) and one single forage type. This was found, e.g., in the case of terrestrial lichens and caribou or reindeer *Rangifer tarandus* in Canada and Norway (Reimers et al. 1983, Skogland 1983, Gauthier et al. 1989). In the case of ungulates inhabiting the forested ecosystems of the temperate zone in the Holarctic region, this correlation was found between the fruits of oak *Quercus* spp. and beech *Fagus* spp., in short mast, and, e.g. white-tailed deer *Odocoileus virginianus* (Harlow et al. 1975, Pekins & Mautz 1988, McShea & Schwede 1994), wild boar *Sus scrofa* (Matschke 1964, Baber & Coblentz 1987), and red deer *Cervus elaphus* (Duvendeck 1962).

Our study on the diet and condition of non-supplementary fed wild boar in the Netherlands, revealed an exclusive mast dependency for boar to meet their winter-time energetic requirements; acorn mast was always depleted by the end of autumn, so beechnuts were the only mast available in winter. If beech mast was available in winter, wild boar grew heavy, with large body fat reserves. Fertility rate of sows ≤12, 13-24 and > 24 months of age amounted to 1.4, 3.0 and 4.5, respectively. Net recruitment following rich mast winters amounted to 1.7-2.5 piglets per adult sow. If beech mast was not available, the average body weight of juveniles and adults dropped by a factor of 2.6 (from 24 to 9 kg) and 1.6 (from 48 to 29 kg), respectively. Because of a poor nutritional condition, sows less than 2 years old did not get into oestrus. In sows more than 2 years old, the fertility rate was 1.2, but net recruitment was also nill.

Broadleaved grasses, supplied on game meadows, offered an alternative food resource for mast.

The decrease in beech-mast consumption, the decline in body weight during winter, and therefore recruitment in the succeeding spring, were density dependent, so actually a density-dependent resource limitation on the nutritional condition and reproduction of wild boar was assessed (Groot Bruinderink et al. 1994). In this paper we present our results on calculating a threshold density above which condition is density-dependently reduced. Since both theory and empirical information support the conclusion that for species with life history strategies characteristic of large mammals most density-dependent changes occur at high population levels, close to the *K*-carrying capacity (Fowler 1981, MacNab 1985), we define this threshold value of density as the carrying capacity (CC) of the area.

Methods

Study area

The study was carried out from 1988 through 1993 in the largest wild boar refuge of the Netherlands, De Veluwe (52°00'-52°30'N, 5°20'-6°10'W). The study area was the Hoog-Soeren forestry, a 1,200-ha area encircled by a boar-proof fence. The area was inhabited by a population of wild boar that was not supplementally fed from 1987 onwards. Recruitment and boar numbers were assessed in three ways: a) by capture-recapture or resighting (Seber 1973); b) by two synchronous counts in spring covering the whole area, using temporary feeding places, and c) by analysis of cull data. The minimum number of boar per season was taken as the maximum value of a, b, and c.

From 1987-1990 the initial high numbers of wild boar (ca 200) were reduced by hunting to a more or less stable spring number of 30-40 head from 1990-1993, depending on mast availability and annual bag size (Table 1).

The area was dominated by humus podzols and brown podzolic soils on sandy Pleistocene material. Heathlands, dominated by *Calluna vulgaris*, *Erica tetralix* and *Molinea caerulaea*, covered about 30% of the area. The predominant forest type covering 40% of the area was Scots pine *Pinus sylvestris*, with bilberry *Vaccinium myrtillus*, cowberry *V. vitis idaea* and wavy hairgrass *Deschampsia flexuosa* as main understorey species. The deciduous forests with oak *Quercus robur*, *Q. petraea* and *Q. rubra* and beech *Fagus sylvatica* covered 20% of the area.

Mast

Because of the exclusive mast dependency, we could avoid the complexity of different forage types and seasons (Crête 1989, Hanley & Rogers 1989), and confine ourselves to quantification of mast production. In 1989, 1990 and 1992, the mast production of beech, of mixed stands of pedunculate oak and sessile oak (referred to as oak) and of red oak was measured in kg dry matter per ha (kg DW/ha) according to Ovington & Murray (1964). We used a random sample of forest stands old enough to produce fruits (i.e. > 25 years old; Goodrum et al. 1971). Area weighted means for the age of oak, red oak and beech were 78, 44 and 125 years; tree numbers amounted to 347, 826 and 451 per ha and bole diameters were 24, 22 and 37 cm, respectively.

Mast production figures are presented as geometric means. However, for the purpose of combining our data with observations on mast production from 1930 onwards (La Bastide & Vredenburch 1970), we also ranked our data as a percentage of the maximum mast according to Whitehead (1980): 0 = complete failure of mast; 1 = mast about 20% of maximum; 2 = 30-40%; 3 = 50%; 4 = 60% and 5 = 70-90% of maximum mast.

Table 1. Demography of the Hoog-Soeren wild boar population; ad includes animals > 12 months of age; juv includes animal ≤ 12 months of age. In Mast in winter "+" indicates rich and "-" poor mast years.

Year (i)	Mast in winter i-1→i	Spring numbers year i		Bag size in season i→i+1	
		ad	juv	ad	juv
1988	+	100	125	82	97
1989	-	40	1	0	0
1990	+	40	36	6	9
1991	+	30	48	10	10
1992	-	36	0	6	0
1993	+	30	75	10	16

Body weight

Our earlier presented results (Groot Bruinderink et al. 1994) were based on analyses of the body weight and stomach contents of 223 culled animals. In addition, we captured, weighed and ear-tagged 324 boar to assess population size and structure. Therefore, we have at our disposal 547 live weights and corresponding boar densities to provide a resource-based estimation of the CC of the wild boar habitat. Inventory of boar numbers, recruitment and sample techniques of the haphazard sample of 223 culled boar were described elsewhere (Groot Bruinderink et al. 1994). By feeding maize we lured the boar into two stationary and four mobile traps. This way we caught 324 boar at different spots all over the study area and assessed their live weights to the nearest kg. To analyse factors that affect body weight we recorded five parameters, both for culled and for trapped animals:

1) Time of year. We distinguished between three phenological seasons:
   - Autumn, 16 September-31 December. In this season mast availability is largest. The boar rut at the end of this season.
   - Winter, 1 January-15 April. In poor years mast is no longer available and boar have to feed on roots and grasses; piglets are born at the end of this season.
   - Spring/summer, 16 April-15 September. Boar feed mainly on grasses and herbs.
2) Mast availability. A binary distinction was made between rich and poor mast years. In rich years beech mast was available in winter, in poor years, no mast was available in winter.
3) Density. Boar density was expressed in kg metabolic weight per 100 ha (kg MW/100 ha), using the mass exponents as found by Jezierski & Myrcha (1975). Densities varied between years and seasons and ranged from 5.9 to 48.3 kg MW/100 ha. In the analysis we distinguished between five categories: ≤ 10, > 10 and ≤ 20, > 20 and ≤ 30, > 30 and ≤ 40, and > 40 kg MW/100 ha.
4) Sex.
5) Age. We used dental and morphological characteristics (Matschke 1967) to distinguish between two age categories: 1-12 months and older than 12 months.

Statistical methods

Analysis of factors affecting body weight was based on the regression screening technique (McCullagh & Nelder 1989). In this technique, for each term (main effect or interaction) two tests are performed. In the first test (the *marginal* test), the term is added to the simplest possible model, e.g. main effect A is added to a model containing only a general constant, but interaction A*B is added to a model already containing main effects A and B. In the second test (the *conditional* test), the term is dropped from the most complex possible model, e.g. main effect A is dropped from the model containing all main effects and all interactions not involving A, but interaction A*B is dropped from the full model with all main effects and interactions. All terms tested can be grouped into three categories: the ones that are significant ($P \leq 0.05$) in both tests, the ones that are significant in neither of the tests, and the ones that are significant in one of the tests only. Terms in the first two categories allow simple conclusions which are not expected to be affected much by confounding problems. The last category needs further testing using further orders of inclusion. For the regression screening we used the GENSTAT 5 statistical package (Genstat 5 Committee 1993).

The model

The inputs to the model consist of six parameters:

1) Areas (a_i, ha) for a subdivision of the total area in ecotopes $i = 1,...,p$; p represents three ecotopes: stands of oak, red oak and the game meadow ecotope with 'broadleaved grasses'.
2) Production of forage (p_i, kg/ha) per ecotope.
3) Digestibility coefficients (c_i, kg/kg) for the forage in each of the ecotopes. We used the apparent digestibility (c) of the organic matter for acorns and grass; c_{beech}, c_{oak} and c_{grass} in that order constituted 65%, 89% and 47% (ARC 1967; De Vor 1993; Briedermann 1990).
4) An estimate of the CC expressed as metabolic weight (MW) per unit digestible forage of any type (q, in kg MW/kg). We estimated CC for beech (in kg MW/ha) by assessing the threshold value for density, above which the average body weight was density-dependently reduced. Consequently CC for oak and grass can be estimated by correcting for dry matter production and digestibility by boar.
5) Mean winter live weights of adults (w_a, kg) and juveniles (w_j, kg).
6) Mass exponents for converting live weight to metabolic weight, for adults (k_a, dimensionless) and juveniles (k_j). According to Jezierski & Myrcha (1975) $k_a = 0.57$ and $k_j = 0.86$

The annual June-census revealed an adult/juvenile ratio of 1/0.9; during winter this ratio was 1/0.5. Since mean body weights in winter are also known, we can calculate winter-CC into the model output: the number of adults (n_a) and juveniles (n_j) corresponding to the winter-CC of the area.

Structure of the model

For each ecotope i the CC in kg MW per unit digestible forage (q) can be converted to the CC in kg MW per ha:

$$CC_i = p_i c_i q$$

The total CC of the area, still expressed in kg MW, then follows by weighted summation:

$$CC_{tot} = \sum_{i=1}^{p} a_i CC_i$$

The CC is related to the numbers of wild boar by

$$CC_{tot} = n_a(w_a)^{k_a} + n_j(w_j)^{k_j}$$

The total digestible forage available can be written as

$$DF_{tot} = \sum_{i=1}^{p} p_i c_i$$

The model assumes that DF_{tot} defines a threshold for nutritional condition needed for reproduction. Below a certain DF_0 value no reproduction occurred; at or above this value the ratio of juveniles to adults in winter was approximately 0.5/1.

$$n_a = 2\,(n_j)$$

The total number of wild boar $n = n_a + n_j$ can be calculated from:

$$CC_{tot} = n_a(w_a)^{ka} \qquad (DF_{tot} < DF_0)$$

$$CC_{tot} = n_a\{(w_a)^{ka} + 0.5(w_j)^{kj}\} \qquad (DF_{tot} \geq DF_0)$$

which results in:

$$n_a = CC_{tot}/(w_a)^{ka} \qquad (DF_{tot} < DF_0)$$

$$n_a = 2\,n_j = CC_{tot}/\{(w_a)^{ka} + 0.5(w_j)^{kj}\} \qquad (DF_{tot} \geq DF_0)$$

Assumptions

The model is based on the following three assumptions:

1) All stands of oak and beech older than 25 years potentially produce mast.
2) Other food resources (including minerals) or water are not limiting in winter.
3) The animals have access to the whole area.

Results

Production of forage

In 1989, 1990, and 1992, beech-mast production (p) amounted to 8.2, 500.0 and 152.0 kg DW/ha; for oak the comparable figures were 1100, 0.02 and 0.39 kg DW/ha, and for red oak 383.0, 0.40 and 0.0 kg DW/ha. The oak mast of 1989 and the beech mast of 1990 are considered maximum crops, i.e. value 5 in the mast-ranking system. We assume that red oak crops may reach maxima similar to the other oak species.

In terms of the mast-ranking system, the median value for mast production of European or red oak over the past 63 years was 2, which was ca 35% of 1100 kg DW/ha: 385 kg DW/ha (Table 2). As for the study period, the median for beech over the past 63 years was 2, which corresponds to ca 35% of 500 kg DW/ha: 175 kg DW/ha. The over-winter standing crop of a game meadow that was constantly grazed and rooted by red deer, roe deer and wild boar was estimated to be 500 kg DW/ha (Barret 1971, Hone 1980). So p_{beech}, p_{oak} and p_{grass} were 175, 385 and 500 kg DW/ha, respectively.

Table 2. Mast rating figures for beech, European oak and red oak 1930-1993, based on data in La Bastide & Vredenburch (1970) and the present study. Mast rating figures: 0 = failure of mast; 1 = ca 20% of maximum mast; 2 = 30-40%; 3 = 50%; 4 = 60%; 5 = 70-90%; n.r. = not recorded.

Rating figures	Beech	European oak	Red oak
0	13	4	3
1	14	6	2
2	17	18	31
3	1	17	14
4	9	7	4
5	5	1	0
n.r.	4	10	10
median	2	2	2

Table 3. Indications of significance for marginal (mprob) and conditional (cprob) tests of regression screening of season, mast availability, sex and age on body weight. Interactions of third order were not significant.

Term	mprob	cprob
season	0.000	0.000
mast	0.000	0.000
sex	0.013	0.029
age	0.000	0.000
season.mast	0.000	0.410
season.sex	0.000	0.340
mast.sex	0.032	0.726
season.age	0.000	0.000
mast.age	0.000	0.005
sex.age	0.660	0.243

Body weight

Body weight was affected by season, age, sex and mast availability (Tables 3, 4, and 5). On average, males weighed 19.7 (± 2.0) and females 18.2 (± 2.0) kg. After correction for effects of season, age, sex and mast availability, a density of 10 kg MW/100 ha was assessed as the threshold density above which body weight was density-

Table 4. Live weights of wild boar in kg (±SD) from Veluwe (the Hoog-Soeren population) according to season and age class.

Age classes	≤ 12 months	N	> 12 months	N
Season				
autumn	15.6 (±1.3)	126	53.6 (1.4)	61
winter	19.6 (±1.6)	63	34.3 (1.7)	71
summer	10.2 (±1.4)	171	28.8 (1.8)	55

Table 5. Live weights of wild boar in kg (± SD) from Veluwe (the Hoog-Soeren population) according to age class and mast availability in rich and poor years.

Age classes	≤ 12months	N	> 12 months	N
Mast				
poor	15.3 (± 1.3)	166	33.5 (± 1.7)	134
rich	11.8 (± 1.7)	194	50.6 (± 1.8)	53

dependently reduced ($P \leq 0.001$; Table 6). Therefore, as a threshold value for CC_{tot}, 10 kg MW/100 ha is suggested. Since in fact CC_{tot} was CC_{beech}, CC_{tot} could be converted to the total area of beech which was 167 of 1200 ha:

$$CC_{beech} = (1200/167) \times 0.10 = 0.7 \text{ (kg MW/ha)}$$

Since $CC_{beech} = p_{beech}c_{beech}q$, it follows that $q = 0.0062$. Consequently, $CC_{oak} = 385 \times 0.89 \times 0.0062 = 2.1$ (kg MW/ha) and $CC_{grass} = 500 \times 0.47 \times 0.0062 = 1.5$ (kg MW/ha).

Mean winter live weights

Mean winter live weights for adults (w_a) and juveniles (w_j) were 43.2 (± 1.5) and 14.6 (± 0.4) kg, respectively.

Model output

Output if $DF_{tot} < DF_0$:
Under these circumstances reproduction in year i fails, and n stands for number of adults in winter of year $i \rightarrow i+1$.
For 1 ha of beech: $n_a = 0.7/8.6 = 0.08$
For 1 ha of oak: $n_a = 2.1/8.6 = 0.24$
For 1 ha of grass: $n_a = 1.5/8.6 = 0.17$

Output if $DF_{tot} \geq DF_0$:
Piglets are born in numbers that are about equal to adult numbers; in the succeeding winter this ratio is about 1/0.5.
For 1 ha of beech: $n_a = 2n_j = 0.7/13.6 = 0.05$
For 1 ha of oak: $n_a = 2n_j = 2.1/13.6 = 0.15$
For 1 ha of grass: $n_a = 2n_j = 1.5/13.6 = 0.11$

Table 6. Effect of boar density (kg MW/100 ha) on body weight (kg ± SE) after correction for season, sex, age and mast availability (model predictions).

Boar density	Body weight (± SE)
≤ 10	26.50 (± 1.10)
10-20	19.30 (± 1.08)
20-30	17.67 (± 1.05)
30-40	19.80 (± 1.06)
> 40	18.49 (± 1.03)

Discussion

Since the decrease rate of mast consumption was density dependent, we believe that competition for beech mast was the causal ecological explanation for the density-dependent decrease of body weight during winter and reproductive success in the succeeding spring.

An over-winter decline in body weight is a normal phenomenon in mammals of the temperate zone, the winter being the main energetic bottleneck to pass (Putman 1988, Wallis de Vries 1994, Wolda et al. 1994); for this reason we corrected for season in the regression screening of body weight.

The model is based on the assumption that the animals have access to the whole area. Food availability has been shown to trigger seasonal migration in many ungulate species (Helle 1980, Gordon 1989, Larter & Gates 1994), including wild boar (Singer et al. 1981). Habitat evaluation models show that the CC of patches of habitat hardly determines numbers of animals using these patches; the fact that animals were able to disperse and explore new habitats had a larger impact on their numbers (Hobbs & Hanley 1990). Home ranges of 120-150 km^2 for males and 40-60 km^2 for sows are quite normal in wild boar (Janeau & Spitz 1984). And again, their migratory activity is correlated with mast availability: activity ranges in a poor mast winter are 3 to 5 times larger than in rich winters (Singer et al. 1981). However, for wild boar inhabiting the forest/heathland ecosystem in the northwestern parts of Europe, migration possibilities are limited, because their feeding strategy is believed to conflict with agricultural interests (Groot Bruinderink 1977, Briedermann 1990, Anon. 1993). We believe that in the small natural areas of this region still inhabited by wild boar, the calculated CC may offer a guideline for establishing spring densities *c.q.* for cropping a wild boar population (MacNab 1985).

Although the model was based on one population only and only covered 1,200 ha of forests and heathland, the studies of the diet of wild boar from the 90,000-ha Veluwe and other forested areas on the sandy soils of northwestern Europe, did not reveal any natural substitute for mast (Groot Bruinderink 1977, Briedermann 1990). Therefore, we suggest that the model applies to all these situations.

Our paper presents an estimated CC for beech and oak, based on the median value of mast production over the past 63 years. Since annual crop rating figures can be converted into kg DW/ha, CC can be calculated for any beech or oak crop, assuming linear correlationship. In addition, consequences for CC of application of supplemental feeding can be calculated.

Acknowledgements - We are obliged to the Royal Forestry 'Het Loo' for permission to work in the area. We thank H. van der Voet of the

Agricultural Mathematics Group (GLW-DLO) at Wageningen and A.T. Kuiters (IBN-DLO) for their helpful comments on the manuscript. W. Lamers assisted in measuring mast production. The study was part of the Research Program on Forest Grazing of the Institute for Forestry and Nature Research (IBN-DLO), the Winand Staring Centre (SC-DLO), and the Agricultural University of Wageningen. We received a grant from the Ministry of Agriculture, Nature Management and Fisheries.

References

Albon, S.D., Mitchell, B. & Staines B.W. 1983: Fertility and body weight in female red deer: a density-dependent relationship. - Journal of Animal Ecology 52: 969-980.

Anon. 1993: Nota Jacht en Wildbeheer - Ministerie van Landbouw, Natuurbeheer en Visserij, 51 pp. (In Dutch).

ARC 1967: The nutrient requirements of farm livestock. No. 3, Pigs. - Agricultural Research Council, London, 278 pp.

Baber, D.W. & Coblentz, B.E. 1987: Diet, nutrition, and conception in feral pigs on Santa Catalina Island. - Journal of Wildlife Management 51: 306-317.

Barret, R.H. 1971: Ecology of the feral hog in Tehama County, California. - Ph.D. Thesis, University of California, Berkeley, 368 pp.

Briedermann, L. 1990: Schwarzwild. - VEB Deutscher Landwirtschaftsverlag, Berlin, 540 pp. (In German).

Clutton-Brock, T.H. , Price, O.F., Albon, S.D. & Jewell, P.A. 1992: Early development and population fluctuations in Soay sheep. - Journal of Animal Ecology 61: 381-396.

Crête, M. 1989: Approximation of K carrying capacity for moose in eastern Quebec. - Canadian Journal of Zoology 67: 373-380.

Duvendeck, J.P. 1962: The value of acorns in the diet of Michigan deer. - Journal of Wildlife Management 26: 371-379.

Fowler, C.W. 1981: Density dependence as related to life history strategy. - Ecology 62: 602-610.

Fowler, C.W. 1987: A review of density dependence in populations of large mammals. - In: Genoways, H.H. (ed.); Current Mammalogy, Volume 1. pp. 401-441.

Gauthier, L., Nault, R. & Crête, M. 1989: Variations saisonnières du régime alimentaire des caribous du troupeau de la rivière George, Québec Nordique. - Nature Canada 116: 101-112. (In French).

Genstat 5 Committee 1993: Genstat 5 Reference Manual. - Clarendon Press, Oxford, 796 pp.

Goodrum, P.D., Reid, V.H. & Boyd, C.E. 1971: Acorn yields, characteristics, and management criteria of oaks for wildlife. - Journal of Wildlife Management 35: 520-532.

Gordon, I.J. 1989: Vegetation community selection by ungulates on the isle of Rhum. II. Vegetation community selection. - Journal of Applied Ecology, 26: 53-64.

Groot Bruinderink, G.W.T.A. 1977: Maaginhoudonderzoek van het wilde zwijn (Sus scrofa) op de Veluwe.- Lutra 19: 73-86. (In Dutch).

Groot Bruinderink, G.W.T.A., Hazebroek, E. & van der Voet, H. 1994: Diet and condition of wild boar, Sus scrofa scrofa, without supplementary feeding. - Journal of Zoology, (Lond.), 233: 631-648

Grubb, P. 1974: Population dynamics in the Soay sheep. - In: Jewell, P.A., Milner, C. & Boyd, J.M. (eds.); Island Survivors: the ecology of the Soay sheep of St. Kilda, pp. 242-272.

Hanley, A. & Rogers, J.J. 1989: Estimating carrying capacity with simultaneous nutritional constraints. - U.S. Department of Agriculture, Forest Service, Research Note PNW-RN-485, 29 pp.

Harlow, R.F., Whelan, J.B. & Skeen, J.E. 1975: Deer foods during years of oak mast abundance and scarcity. - Journal of Wildlife Management 39: 330-336.

Helle, P. 1980: Food composition and feeding habits of the roe deer in winter in central Finland. - Acta Theriologica 25: 395-402.

Hobbs, N.T. & Hanley, T.A. 1990: Habitat evaluation: do use/availability data reflect carrying capacity? - Journal of Wildlife Management 54: 515-522.

Hone, J. 1980: Effect of feral pig rooting on introduced and native pasture in North-eastern New South Wales. - Journal of the Australian Institute of Agricultural Science 46: 130-132.

Janeau, G. & Spitz, F. 1984: Budget espace temps des sangliers (Sus scrofa) en forêt de Grésigne.- INRA 22: 123-133. (In French).

Jezierski, W. & Myrcha, A. 1975: Food requirements of a wild boar population. - Polish Ecological Studies, Warszawa, 1: 61-63.

Klein, D.R. & Strandgaard, H. 1972: Factors affecting growth and body size of roe deer. - Journal of Wildlife Management 36: 64-79.

La Bastide, J.G.A. & Vredenburch, C.L.H. van 1970: The influence of weather conditions on the seed production of some forest trees in the Netherlands. - Stichting Bosbouwproefstation "De Dorschkamp", Wageningen, Med. 102, 11 pp.

Larter, N.C. & Gates, C.C. 1994: Home-range size of wood bison: effects of age, sex, and forage availability. - Journal of Mammalogy, 75: 142-149.

MacNab, J. 1985: Carrying capacity and related slippery shibboleths. - Wildlife Society Bulletin 13: 403-410.

Matschke, G.M. 1964: The influence of oak mast on European wild hog reproduction. - Southeastern Association of Game and Fish Commissioners Conference 18: 35-39.

Matschke, G.M. 1967: Ageing European wild hogs by dentition. - Journal of Wildlife Management 31: 109-113.

McCullagh, P. & Nelder, J.A. 1989: Generalized linear models. 2nd ed. - Chapman and Hall, London, 511 pp.

McShea, W.J. & Schwede, G. 1994: Variable acorn crops: responses of white-tailed deer and other mast consumers. - Journal of Mammalogy 74: 999-1006.

Mitchell, B. & Crisp, J.M. 1981: Some properties of red deer (Cervus elaphus) at exceptionally high population density in Scotland. - Journal of Zoology (Lond.), 193: 157-169.

Ovington, J.D. & Murray, G. 1964: Determination of acorn fall. - Quarterly Journal of Forestry 58: 152-159.

Pekins, P.J. & Mautz, W.M. 1988: Digestibility and nutritional value of autumn diets of deer. - Journal of Wildlife Management 52: 328-332.

Putman, R. 1988: The natural history of deer. - Christopher Helm, London, 191 pp.

Ratcliffe, P.R. 1984: Population density and reproduction of red deer in Scottish commercial forests. - Acta Zoologica Fennica 172: 191-192.

Reimers, E., Klein, D.R. & Sørumgård, R. 1983: Calving time, growth rate, and body size of Norwegian reindeer on different ranges. - Arctic and Alpine Research 15: 107-118.

Sauer, J.R. & Boyce, M.S. 1983: Density dependence and survival of elk in Northwestern Wyoming. - Journal of Wildlife Management 47: 31-37.

Seber, G.A.F. 1973: The estimation of animal abundance and related parameters. 2nd edition - London: Griffin, 654 pp.

Singer, F.J., Otto, D.K., Tipton A.R. & Hable, C.P. 1981: Home ranges, movements, and habitat use of European wild boar in Tennessee. - Journal of Wildlife Management 45: 343-353.

Skogland, T. 1983: The effects of density dependent resource limitation on size of wild reindeer. - Oecologia 60: 156-168.

Staines, B. W. 1978: The dynamics and performance of a declining population of red deer (Cervus elaphus). - Journal of Zoology (Lond.), 184: 403-419.

Vor, H. de 1993: De vertering van celwandrijke voeders door wilde zwijnen en Meishan varkens. - Report Vakgroep Veevoeding, Landbouwuniversiteit Wageningen, 59 pp. (In Dutch).

Wallis de Vries, M.F. 1994: Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. - Oecologia, 100: 107-117.

Whitehead, C.J. 1980: A quantitative study of mast production in the southern Appalachian region of Georgia, North Carolina, and Tennessee. - Tennessee Wildlife Research Agency, Technical Report 80: 2. 97 pp.

Wolda, H., Dennis, B. & Taper, M.L. 1994: Density dependence tests, and largely futile comments: Answers to Holyoak and Lawton (1993) and Hanski, Woiwod and Perry (1993). Short communication. - Oecologia 98: 229-234.