PRINCIPLES OF SOCIOBIOLOGICAL MODELLING OF MOOSE (*Alces alces andersoni*) OF THE NORTH AMERICAN TAIGA

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ABSTRACT: Principles of sociobiological [SB] control of taiga moose population well being are described. These principles are in contrast to the present models oriented to achieving maximum harvest, a policy dangerous to the ecosystem and undesirable in view of anti-hunting propaganda. The SB modelling is focused on the species-specific ranges of social infrastructures adapted to ecosystem equilibria. It is based on the knowledge that living populations are composed of overlapping generations of various fitness. Thus, there is not an average mortality rate as implied by life tables. In the models described here, we chose three fitness classes, each with a different set of mortality and recruitment parameters. The other important factor in population behaviour is the species-specific rate of maturation which is governed by inherited programs. These programs are flexible and within ranges are responsive to social and other extrinsic factors. The SB-modelling developed in this study relies on the experience that generations of similar social importance build cohorts of social classes [SC], for which intra- and inter-sexual optimum ratios can be simulated. In the field the SC-ratios can be monitored by observing morphological and behavioral cues.
Physiological parameters obtained from trapped or harvested individuals can be used to refine the SC-pattern. This is of paramount practical importance, because these SC-measurements indicate whether the population is in social order or disorder. In the SB-concept only those animals which are supernumerary for population and ecosystem well-being can be harvested. Practical aspects of the concept are discussed and shown graphically.

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Traditional game management is focused on production of wild animals to be harvested as "renewable resources" for sportsmen's satisfaction (Leopold 1947; Decker 1990),even at the expense of other species (Thomas 1979) and vegetation diversity (Burschel 1979). However, from the perspective of the ecosystem balance, and coevolutive mechanisms between herbivores and plants (Brown and Vincent 1987; Bubenik, A. 1989; Dodds 1990; Owen 1990; Palo and Robbins 1991; Roughgarden 1983), any game management system intended to maximize production of game, contributes to ecosystem disorder (Bubenik, A.1984, 1989).

This management objective aimed to maximum sustained yield [MSY] (Boer and Keppie 1988) is vulnerable to attacks by ecologists and naturalists, and paradoxically also by "timber-prerogative" foresters (Österr. Forstverein 1990; Parsons 1987), whose sylvicultural objective is no less dangerous than that of traditional game management (Bubenik, A. 1991;Schwab 1979). Unfortunately, the economic importance of timber-oriented forestry is apparently so great as to quiet environmentalists' opposition. Thus, it is the hunter, who as the real impetus for conservative game management (Franco 1991, Varićak 1991), is attacked by anti-hunters (Baker 1985; Ryder 1989).

However, the anti-hunting crusade is missing the point because hunting of game insettled or industrially exploited areas is necessary due to inadequate numbers of natural predators, abundance of food, resulting in uncontrolled recruitment and overpopulation of game. The solution to the predicament "to hunt or not to hunt?", or in hunter's words: "to be or not to be?", demands a new attitude towards game and hunting, and a revision of the historical hunter's role as game harvester

(Bubenik, A. 1984; 1991).

The current models, designed to ease the manager's job of harvest maximization are not concerned with the ecosystem as a unit (Balčiauskas 1990, Boer and Keppie 1988), even if they are "habitat oriented" (Allen *et al.*1988; Kansas and Raine 1990). Besides that, theterm "habitat" is too broad in comparison to "umwelt" (Bubenik, A. 1984; Von Uexküll1937, 1957). The "umwelt", as the world of the animal, is characterized by the neurophysiological cues the animal is searching for and uses to select as optimum grounds for breeding, calving, resting, feeding or playing (Bubenik, A. 1984).

By and large, the present models assume that demographic structures are either stable (Hennig 1988), or that their instability is generated only by environmental events (Ballard *et al.* 1986; Carley 1990; Johnson 1990).

Thus, the aim of such models is to inform the manager how many animals in general, or with respect to sex and age could be removed tomaximize harvest. However, they do not alert the manager to whether the population andecosystem is endangered (Bubenik, A. 1989). No attempt is made to mimic the patterns ofsociobiologically necessary losses and umwelt-related dispersal (Bubenik, A. 1984).

In order not to separate game control from ecosystem management (Dodds 1990), the concepts of modelling of game populations require an immediate revision. Their raison d'être must not be harvest of meat (Geist 1985) or trophies (Bajohr 1988; Varićak 1991), but the welling of game (Bubenik, A. 1971; 1984; Calhoun 1962; Harrison 1990) within overall ecosystem welfare.

This is too large and complex a task to be reported in a single paper. Thus, the aim of this paper has been limited to discussion and exploration of the importance of sociobiological principles in modelling only of native ungulate populations of the boreal zone.[1]

PRINCIPLES OF SOCIOBIOLOGICAL DEMOGRAPHY

First, we have to emphasize that "living populations cannot be treated as homogenous units, and conversely, in behavioral ecology the individual cannot be considered as being shaped (only) by evolutionary forces" (Lomnicki 1988). Numerous authors (Altman, M.1961, 1963; Bartecki and Jaczewski 1983; Bartoš and Perner 1985; Bubenik, A. 1982, 1984; Bubenik and Timmermann 1982; Bubenik, A. *et al.* 1956; Bubenik, A. *et al.* 1977, 1978; Bubenik, G. and Schams 1986; Geist 1968a,b; Greenwood and Craig 1987; Heimer and Watson 1986; Lomnicki 1988; Meile and Bubenik 1979; Niini 1982; Ozoga 1987; Pagel and Harvey 1990; Pemberton *et al.* 1988; Pinsker 1978; Prothero *et al.* 1980; Shackelton 1991; Singer, *et al.* 1991; Smith 1976; Verme 1991), have shown that maturation progress of an individual (at least in boreal ungulates) is dependent as much on its inborn fitness (Dobzhansky 1968) as on the social interactions generated by its demographic environment. Thus, the genetic uniqueness of individuals and their susceptibility to maturation stimulators (Bubenik, A. 1980, 1984; Prothero *et al.* 1980), as well as to social stressors (Leary and Allendorf 1989; Meile and Bubenik 1979; Ozoga 1987), should not be neglected and cannot be accounted for simply in statistical terms. The variability of individual fitness: inherited, acquired, particular and overall (Arnold *et al.* 1990), and

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[1] Other important factors such as the indirect indicators of sociobiological status and the reciprocal game-umwelt interactions (Bubenik, A. 1984) important in the arena of sociobiological game inventory and ecosystem management, can not be covered entirely. The different socio-physiological parameters of ungulates and quite different behaviour of ecosystems of temperate zones, require a different modelling concept.

that of intradependent neurophysiological responsiveness (Bubenik, G. 1982, 1986; Bubenik, G. *et al.* 1987; Bubenik, G. and Schams 1986; Weber and Pert 1989) is so complex that its numerical modelling would be extremely difficult (Lomnicki 1988).

Due to the variation in individual longevity, or, to simplify, in the average longevity of each generation (Bubenik, A. and Bellhouse 1980; Dobzhansky 1968; Lomnicki 1988; Pagel and Harvey 1990; Wright 1978), there is no reason to expect a smooth and stable age distribution in living populations with species-specific schedules of mortalities as represented in life tables (Fig. 1A) (Caughley 1970, 1977; Deevey 1947; Taylor and Carley 1988). In contrast, living populations are composed of overlapping generations (Bubenik 1984; Bubenik,A. and Schwab 1974; Lomnicki 1988; Schwab and Messner 1986) occasionally with significant differences in longevity. These differences generate the ragged age-class structures (Fig. 1B) observed in living populations (Bubenik, A. and Schwab 1974; Bubenik, A. *et al.* 1975; Garner, *et al.* 1990; Schwab 1979; Schwab and Messner 1986).[2]

Great differences in generations' longevity are more important than assumed, because population behaviour depends on the ratio of cohorts of animals of dissimilar social importance which contain more than one age class (Bubenik, A. 1984) (Fig. 1C). Production of generations with above or below normal longevity or excessive losses will generate social class [SC] distortions (Figs. 2A, 2C), inducing abnormal behaviour which may have a dangerous impact on both population and habitat well-being (Calhoun 1962; Donaubauer *et al.* 1990; Scanlon 1990; Thompson 1988; Timmermann and Gollat 1982).

The traditional terms of 'juvenile,' 'subadult' and 'adult' are inadequate to describe the demographic conditions and would lead to confusion (Bubenik, A. 1982, 1984; Eabry1970). They are based on the outmoded notion that any mammal, with the exception of humans, which enters puberty is considered to be an 'adult', just because it is fertile.

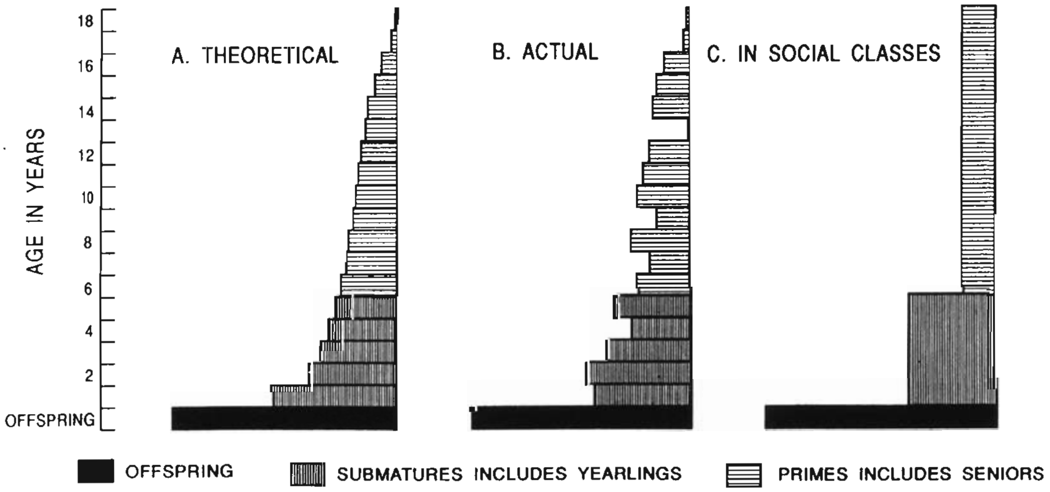

Fig. 1. Infrastructure of overlapping generations in a moose population with 50% submatures and 50% primes.

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[2] It is recognized that other "soft" and "hard" losses [not quite in terms of Wallace (1975,1977)] influence the shape of the age former include emigration as well as immigration and natural mortality, the latter, hunting, natural catastrophes, etc.

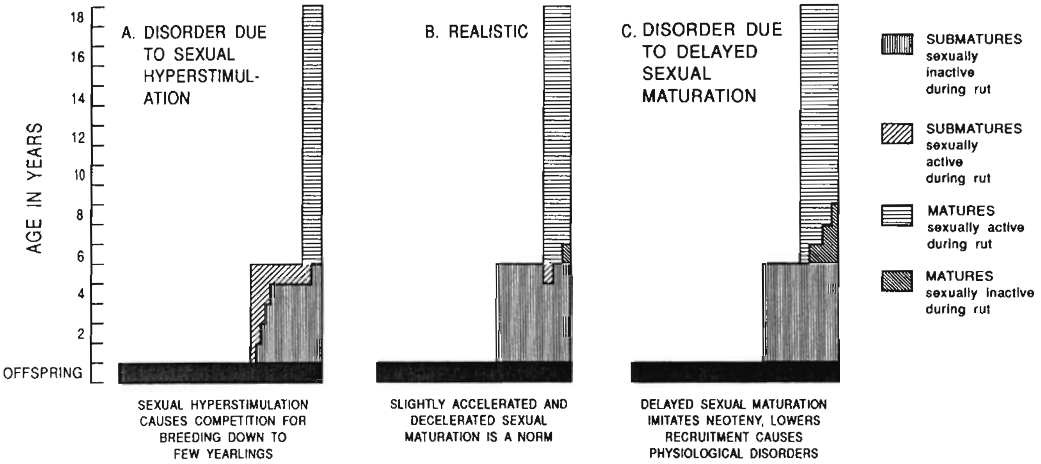

Fig. 2. Impact of social order and disorder on sexual behaviour and morphology of hypothetical moose population. (Simulated on behalf of studies in moose and other cervids.)

However, 'adult' means (e.g. Webster 1983) a fully developed and socially responsible individual and not simply any who entered into puberty. As well, in boreal ungulates the puberty is a recurrent process (Lincoln 1971). In respect to fertility, it develops gradually and has a great range of flexibility due to susceptibility to demographic and environmental conditions (Lomnicki 1988; Dobzhansky 1968; Bubenik and Timmermann 1982; Haines and Emes 1991).

Also in well organized ungulate societies the first puberty cycles either do not produce fertile semen or ova and in disorganized populations the onset of puberty may be delayed or accelerated (Dietrich 1979; Mitchell and Crisp 1981). The precocious sex maturation can shorten the longevity of offspring (Geist 1968a; Haines and Elmer 1991; Pemberton, *et. al.* 1988) and skew the sex ratios (Clutton-Brock 1985; 1988; Clutton-Brock *et al.* 1982; Gomendio *et al.* 1990; Scribner *et al.* 1984; Ozoga 1987). It is important to note that the speed or timing of the process of sexual maturation depends not only on genetical anlage, but also on externally induced mechanisms of a neuroendocrine nature (Bejšovec 1955; Bubenik, G. and A. Bubenik 1985; Bubenik, G. *et al.* 1987; Shackelton 1991; Singer *et al.* 1991), and on overall fitness (Mitchell and Crisp 1981; Ozoga 1987).

Thus, in disorganized societies we find more or less pronounced asynchrony between beginning and intensity of gonadal activity on the one hand, and physical and physiological asychrony and asymmetry of behavioral patterns on the other (Figs. 2A, 2C) (Bubenik, A.1984; Heimer 1987; Leary and Allendorf 1989; Meile and Bubenik 1979; Ozoga 1987; Shackelton 1991; Singer *et al.* 1991; Smith 1976). Both the asynchrony and asymmetry affect motivation, lead to derailed behaviour and generate morphological features which mimic a status of other social classes (Bubenik, A. *et al.* 1977; Bubenik G. and A. Bubenik 1985).

The extremely juvenile populations consume unnecessarily great amounts of food due to too many lactating females and growing individuals or they experience losses of prime males during the long rut (Bubenik 1984; Bobek *et al.* 1990; Payne and Wheeler 1968;Vitakova 1990). The reported temporarily frequent cases of arthritis, arthropathy or overall parodontal disorder (Peterson 1977; Timmermann and Lankester 1978) may be the result of weakened fitness, mainly due to low immunobiological resistance towards stress (Bower 1991). Pregnancy too early in life, as well as over exposure in sexual activity impairs the growth (Guiness *et al.* 1971; Shackelton 1991) by precociously high sex hormone levels. It also reduces the span of prime age and thus the life expectancy, despite a predisposition to high longevity (Bubenik, A. and Schwab 1974; Geist 1968a,b; Heimer and Watson 1986; Stringham and Bubenik 1974).

The negative impact of asynchronous maturation processes is easily identified by morphological and/or behavioral cues. (Bubenik, A. 1984; Bubenik, A. *et al.* 1977, 1978) which are important for assessment of the degree of disorganized status and for sociobiological population control. Thus, we need symbolic terms for individuals in similar social importance, i.e. similar maturation or social classes (Wilson 1975). In this paper we describe the SC-s by following terms: '**offspring**', individuals who need maternal care; '**submatures**' or '**teenagers**' (Altmann 1961) in analogous, but not anthropomorphic sense (Bubenik, A. 1980; Lorenz 1974), are animals whose timing of gonadal activity is delayed and semen reserve or diameter of follicles is small in comparison to the '**mature**' or '**prime**' individuals. For the modelling we use also the '**yearlings**' as a subclass of 'submatures' because this is the age with which the infrastructure begins and assessment of yearlings is relatively reliable. Most 'primes' are mature in every respect and thus potentially fully developed breeders; this, of course, does not predispose all prime males to actually become breeders[3]. **Postprime**' or '**seniors**' (Altmann 1963) are animals whose gonadal activity begins to decrease (Bubenik, G. and Schams 1986). We did not include the class of postprimes, i.e. virtually senescent individuals due to their scarcity in wild as well as in hunted populations (Altmann 1963).

The fact that a social class is a cohort of individuals with similar demographic impact is of paramount importance for modelling. Theoretically, each SC is so independent of generation survival that if some of its age classes are over- and others under represented (due to high or low life expectancy), the SC-ratio does not change substantially. It is the SC-ratio which determines whether the structure is well organized or disorganized (Figs. 1C, 2A, 2B,2C). From an ecosystem point of view the population stays in a status of well-being if the SC and sex-ratios remain within the species-specific range and if the growth of palatable plants and rate of succession on preferred feeding grounds is not impaired.

It is also quite natural that in well organized populations, the social classes are never precisely delineated by chronological age. There is always an overlapping of a few faster, or slower maturing individuals (Fig. 2B). For simplifying the modelling we assume that in generations of normal or supra-normal longevity the usual distribution of early and late maturating individuals in neighbouring SC-cohorts is equal (Fig. 3). Two or more age classes exhibiting different maturation progress indicates social disorder as shown in Figs. 2A and 2C.

The social order of a population can be monitored using observations of SC based on:i) age (which is problematic), or ii) behavioral and morphological features. Fig. 4 illustrates a tabulation framework for assessing social order and it illustrates this framework applied to the three hypothetical populations depicted in Fig. 2.

Through field observation of morphological and behavioral parameters of a representative sample of moose during the first half of the rut, (Bubenik A. *et al.* 1977, 1978) and during antler casting, the cells in the table (Fig. 4) can be filled. Check station data can also be used to complete the tabulation. The table of observed data can be compared to theoretical templates and the degree and nature of social disorder be estimated. The

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[3] It depends on female's choice whether any prime male or a specific one is accepted as a mate.

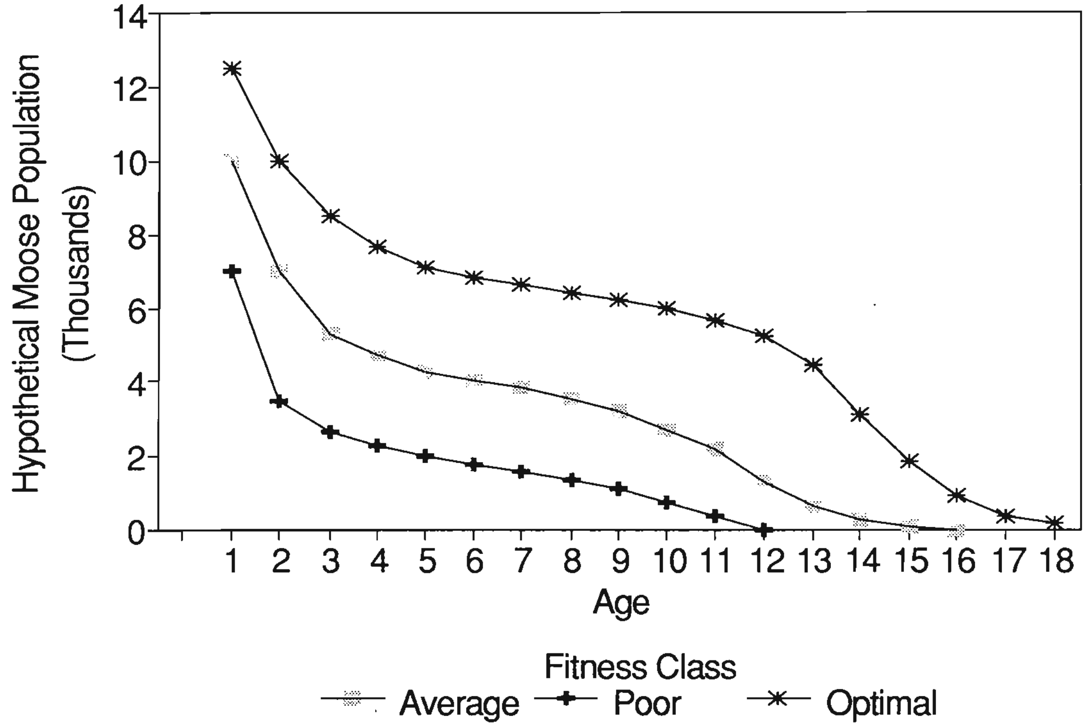


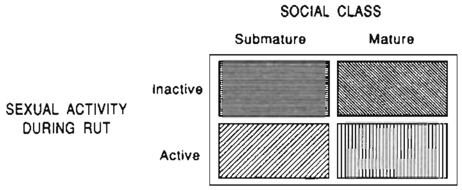
Fig. 3. Mortality analysis by fitness class.

theoretical templates can be established through observation and studies of morphophysiological parameters of individuals under controlled conditions, and of populations known to be in good social order. From this comparison a harvest strategy can be proposed in order to restore the population to social well-being.

Thus, there are three problems in sociobiological modelling: i) simulation of the range of 'optimal' infrastructure, ii) determining the frequency of generations with normal ('A' for average), optimal ('O') and subnormal ('P' for poor) longevity, and iii) determining the actual SC-ratios of both sexes (Fig. 4).

SIMULATION OF OPTIMUM SOCIAL STRUCTURE

Using some of the sociobiological parameters of optimum (**O**), average (**A**) and poor (**P**) generations (many are unknown), we simulated variation in their longevity as the most probable cause of deformation of species-specific SC and sex-ratios and their impact on population behaviour. The impact of such generation-change can be noticed only after the females of such a generation enter



	A) DISORDER		B) ORDER		C) DISORDER	
	sm	m	sm	m	sm	m
Inactive	35	0	45	5	45	15
Active	20	45	5	45	0	40
SOCIAL CLASS RATIO	55 : 45		50 · 50		45 : 55	

(numbers in tables are percentages)

Fig. 4. Tabulation of the social order illustrated in Fig. 2.

reproductive age and produce offspring. In well organized moose populations the reproductive age is 2 years, and offspring are commonly produced in the fourth year; prime age is between the 6th and 11th year of age.

Under such circumstances the optimum population structure has a species-specific ratio of SC-cohorts, but this is not necessarily generated by equal age mortality (Figs. 3, and 5A). Even with different generation longevity the SC ratio can remain within the sociobiological optimum range. The precocious disappearance of the poor generations is balanced or equalized by the presence of the longer living individuals of the optimally fit generations.

Animals who are supernumerary for social well-being must be removed forcibly by 'hard' selection, i.e. by raising the losses above the natural or 'soft' losses. It is self-evident that individuals of below normal fitness should be preferentially culled. However, in cases of extreme social disorder, the social structure must be improved as fast as possible. In that case it is necessary to ignore the basics of classical culling (Vickery 1990). One removes the requisite number from a particular class, and does not search for the "heritably undesirable" individuals.

This 'heretical' advice is based on: i) large scale experiences in different deer species culled only on the basis of SC-ratios, which within 4 years provided remarkable improvement of antler quality (von Bayern and von Bayern 1975; Pfandl 1977; Santifaller *et al.* 1978; Schwab and Messner 1986); ii) the evidence that the antlers' quality correlates with the male's well-being and social status (Bartoš 1980), and iii) on the evidence that it is the testosterone level in the rut which predetermines the antler quality of the next year (Bubenik, G. 1982). In other words, a significantly lower antler quality of well fed animals is one of the reliable indicators of social disorder.

The recently discovered "alleles for fe-

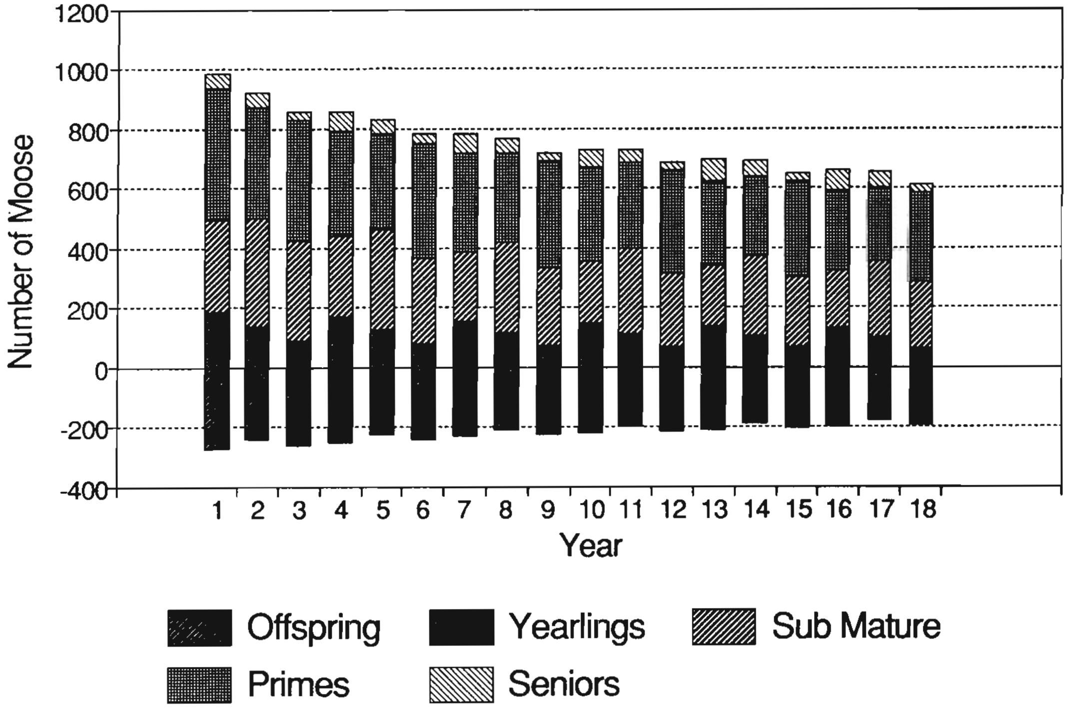


Fig. 5A. Population structure trends (**A P O A P O...**).

males' hind legs" and "for longer or shorter, less- or multi-pointed antlers" in both sexes, (Hartl *et al.* 1990), ascribed to intense culling of males with 'low quality antlers' may be the effect of a hidden factor of a non-genetic nature, e.g. individual intensity of hormonal secretion, lower density etc. The fruitless attempts throughout Europe to improve the overall quality of red deer or roe deer antlers by a similar culling strategy (Vickery 1990), and the evidence that antler-anlage is inherited over the daughters, and thus should be linked to the females sex chromosome (Harmel 1982; Vogt 1947) justifies a sceptical view of the Hartl *et al.* (1990) allele-hypothesis. The same objections apply to the simulation model of Thelen (1991), who also completely omitted the relationship between prime age, rank and antler quality (Bubenik, A. 1990). It is highly probable that more significant correlation about frequency of multi-pointed antlers would be obtained with modelling of social structure of the population and moose bulls in particular.

The social type and its adaptability to environmental conditions are of paramount importance, as has been shown in the breeding behaviour of taiga and forest-tundra moose (Bubenik A. 1987). However, in a practical model of a specific area, population size and density cannot be omitted. Then, variables like the upper and lower range of density of **individualistic**[4] species species differ from those of gregarious ones (Bubenik, A. 1984).

In moose, as representative of individualistic deer, the upper limit of density is dependent on individual distances within and between SC's, on number and acreage of preferred feeding umwelts and eventually on the seasonal clustering pattern for both sexes (Baskin 1990; Elsky 1990). The optimum density in umwelt concept is neither identical with the "carrying capacity" of Leopold (1947), nor with that of "ecological carrying capacity" of Caughley (1979). Moreover, a maximum sustained yield (Boer and Keppie 1988; Caughley1979) is a very tricky term for deer like moose. Hence, it should be investigated whether the 0.67 K (McCullough 1979) or 0.7 K (Boer and Keppie 1988; Gasaway *et al.* 1992) is a factor which limits taiga moose density, except on the screen.

In the taiga umwelt every burn or clearcut is not preferred feeding ground. Despite this the occurrence, abundance and distribution of preferred feeding grounds is permanently changing and their use is limited to a few years (Crête 1976; Hjeljord *et al.* 1990; Lundbergand Danell 1990; Saether and Andersen 1990). In individualistic species the lower limit of density seems to depend only on communicative feasibility. It can be extremely low, as is well known in moose (Revin and Volpert 1990).

THE SIMULATION MODEL

The model used here is designed to illustrate some of the ideas of presented in the introduction. It is simpler than what would be required for a complete management model incorporating these concepts. It is a prototype used to examine the impacts of i) a variety of sequences of generation-specific mortality and ii) of reproduction characteristics on the age structure and size of a moose population.

The cohort-survival model has the innovation that separate reproduction and mortality parameters are applied to generations of differing degrees of fitness but similar social role. The three fitness classes: **O**, **A** and **P** are characterized by specific fecundity rates (neonates per female) and a schedule of age-specific annual mortality rates which reflect the average fitness level of the animals in a particular generation. In this model a single

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[4] The term solitary, despite its general use is a misnomer; it means not social (Allaby 1985); however, the nongegarious ungulates like moose or roe deer (*Capreolus* sp.) prefer temporarily to live in clubs of peers, a behaviour which is in accord with their individualistic way of life.

parameter (male: female ratio) for each fitness class determines the proportion of females in a given fitness class which are capable of reproduction.[5]

The heart of a cohort survival model is a table which keeps account of the moose in each age-class of each generation. A column in the table represents the population history of a single generation of moose as it ages. A single row in a column contains the number of moose of a given age in that generation. The first row contains the number of offspring born of females of reproductive age in previous generations. A cell in rows below the first row contains the number of moose in the cell above it (the previous age class in the previous year) minus the number of moose which died in that year. For example, the second row (yearlings) contains the number of offspring (row one) which survive into the second year. The population structure and total size in a particular year can be read on the diagonal from upper right to lower left; births in that year, plus the yearlings from the previous generation, plus two-year-olds of the generation before that. Table 1 illustrates a part of the population table for the first five age classes.

The reproduction component of the model calculates the number of new born offspring as the sum of the offspring produced by each age cohort of calf-bearing age, i.e., from 3

Table 1. A section of the population accounting table.

	Generation number and fitness class							
	...-4 ... P	-3 O	-2 A	-1 P	0 O	1 A	2 O	3... A...
Age Class								
Calves	...				births ⟶	*307*	257	287...
						survival		
Yearlings					185	*153*	167	143...
						S		
2 year olds				85	148	*107*	133	100...
						S		
3 year olds			80	64	126	*81*	113	75...
						S		
4 year olds		85	72	54	113	*72*	102	68...
						S		
5 year olds	65	79	65	48	105	*65*	95	61...
.	.	.	.	.	.		.	.
.	.	.	.	.	.	S	.	.
.	.	.	.	.	.	↓	.	.

Notes:
Underscored figures represent the population structure in the year in which generqation 1 is born.
Italicized figures represent the members of generation 1 as it ages.

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[5] Although variation in sex-ratios is recognized as having a significant effect on population, the sex-ratio does not enter the model at the point of determining the sex of neonates, but only in calculating the number of cow moose which may produce calves.

to15 years. The number of offspring born of a single age cohort is calculated as the product of: i) the number of moose in that age cohort, ii) the proportion of females typical of that age cohort's generation and iii) the number of live births per female typical of the age cohort's generation (Table 2A).

The number of moose in a particular age class (a+1) is the product of moose in that generation in the previous year (when the generation was one year younger) and the survival rate (1- mortality rate) for that age class and for the fitness class of that generation. This can be expressed algebraically as shown in Table 3A. The mortality component of the model removes moose from the population according to age and generation specific mortality rates (see Table 3B, and Fig. 3).

The model must start at some point in time; two options for specifying a starting population are available: i) to start the model with two moose and let the model build up a population itself (Moen and Ausenda 1987), or ii) to start with an "average" population structure and allow the model to modify the starting structure. Since the reproduction and mortality parameters are roughly in balance in this model and the Moen and Ausenda (1987) model had no mortality component, the latter method appeared to be more appropriate. The fitness history of the starting population was a three year repeating cycle of generations of average, poor and optimal fitness [**A P O**]. The starting population data are shown in Table 4. The total number of moose excluding offspring is 1,000 and a ratio of 'submature' to 'mature' moose is 50 : 50. Although any of the input parameters can be changed, for the experiments of interest in this work, the only variation between experiments is the sequence of generational fitness levels.

Cohort survival models, because of their tabular and repetitive structure, are well-suited to implementation in a spreadsheet program. Use of a spreadsheet for modelling has provided a great deal of flexibility in experimentation with different model designs and sets of parameters. It has also provided excellent graphical views of the resulting population structure and trends.

Table 2A. The reproduction equation.

$$N_{ot} = \sum_{a=3}^{16} N_{at} \cdot f_{F(t-a)} \cdot b_{F(t-a)}$$

where:

N_{ot}	is the number of calves produced in year t.
t	is the year index.
a	is the age class index.
$t-a$	is the generation index.
N_{at}	is the number of moose of age a in year t.
$f_{F(t-a)}$	is the percentage of female moose expected in fitness class F of generation (t-a).
$b_{F(t-a)}$	is the fitness class of generation (t-a); it will be Average (A), Optimal (O) or Poor (P).

Table 2B. Generation and fitness-class-specific reproduction parameters.

	Fitness class of a generation		
	Average	Poor	Optimal
Male:Female Ratio:	50:50	100:200	120:100
Fecundity (live births/female)	0.75	0.5	0.9

Table 3A. The survival equation.

$$N_{a+1,t+1} = N_{a,t} \bullet (1 - m_{F(t-a)})$$

where:

$N_{a,t}$	is the number of moose in age class a in year t.
$m_{F(t-a)}$	is the mortality rate for moose in fitness class F of generation (t-a).
$F_{(t-a)}$	is the fitness class of generation (t-a); it will be Average (A), Optimal (O) or Poor (P).

Table 3B. Generation and fitness-class-specific mortality rates.

	Fitness class of a generation		
	Average	Poor	Optimal
Age class			
Neo-natal	0.5	0.65	0.35
1	0.3	0.5	0.2
2	0.25	0.25	0.15
3	0.1	0.15	0.1
4	0.1	0.12	0.07
5	0.05	0.1	0.04
6	0.05	0.1	0.03
7	0.08	0.15	0.03
8	0.1	0.2	0.03
9	0.15	0.3	0.04
10	0.2	0.5	0.05
11	0.4	1	0.08
12	0.5	1	0.15
13	0.6	1	0.3
14	0.8	1	0.4
15	1	1	0.5
16	1	1	0.6
17	1	1	0.6
18	1	1	1

The impact of varying generational fitness on population dynamics can be followed when a selected pattern of generations (templates) will repeat in the long run (in our case a template of 6 generations is repeated three times) to give an 18 year projection. The expected number of offspring is shown as 'minus values' under the base line.

For the fitness pattern [**A P O A P O**], shown in Figs. 5A, 5B and 5C, the appearance of two poor generations within the 6 year template affects the dynamics so that within 18 years the population size drops to 600. Under the impact of P-generations the population size fluctuates in permanently descending quartets of [**A P O A P O**] from the centre of the 6 year template. This is a logical result of the high mortality and low productivity of the P-generations from which yearlings enter in the reproductive cycle every fourth year.

Despite the consistent population decline, the sub-mature to mature ratio fluctuates only between 46 : 54 and 50 : 50, i.e. within the optimum range for social balance. However, the age class ratio undergoes dramatic changes, as shown by the comparison between the starting population Fig. 5B, and its nadir in year 18 (Fig. 5C), when three year classes (13th, 26th and 17th) are absent but the SC-ratio of 46 : 54 is still within the social optimum.

The impact of P-generations becomes more dramatic if two successive **P**-generations and only one **O**-generation are born [**A A O A P P**] (Fig. 6A). Within 18 years the population drops to 50%. The nadirs repeat now in seven-year intervals, due to the cumulative effect of the low number of primiparous females of the two P-generations on number of yearlings. When these generations enter into the reproductive cycle, the class of sub-matures drops below the social optimum, as happens in year 9 when the ratio is 42 : 58. However, the SC-ratio starts to be balanced again, due to the consecutive pair of **A**-generations, and the following **O**-generation.

By years 9 and 18 the age classes vary even more than in the previous case. In year 9 (Fig. 6B) three age classes (13, 16, 17) are absent and the 14th has almost disappeared. In year 18 (Fig. 6C), four age classes have disappeared (12, 13, 16, 17) and age class 14 has almost died out. Fortunately, none of these age classes is individually of social and reproductive importance. Nonetheless, this case shows how important it is to watch over the fitness of each generation, or eventually over 'hard' losses in offspring, which may reduce the number of yearlings below the range of social optimum.

Finally, we selected a template with three **A**-, two **O**- and only one **P**-generation [**A A O O A P**] (Fig. 7A). The population rises and falls less regularly. The impact of the P-generations is clearly visible. In the 7th year 3 classes 14, 17, 18 are absent, the 15th is practically non-existent. In year 12 the classes 13, 16, 17 are absent and the 14th and 18th are markedly under-represented. The SC-ratio oscillates within a narrow range between 53 to 47 and 48 to 52. It is noteworthy that the

Fig. 5B. Infrastructure, year 1 for fitness sequence (**A P O A P O**...).

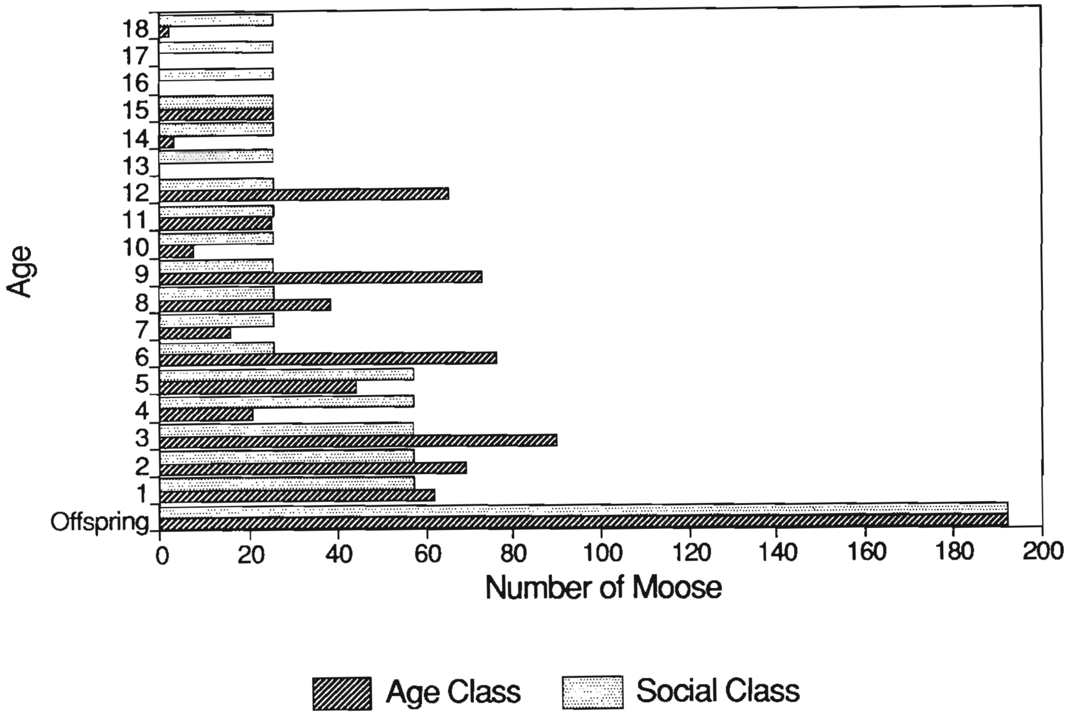

Fig. 5C. Infrastructure, year 18 for fitness sequence (**A P O A P O**...).

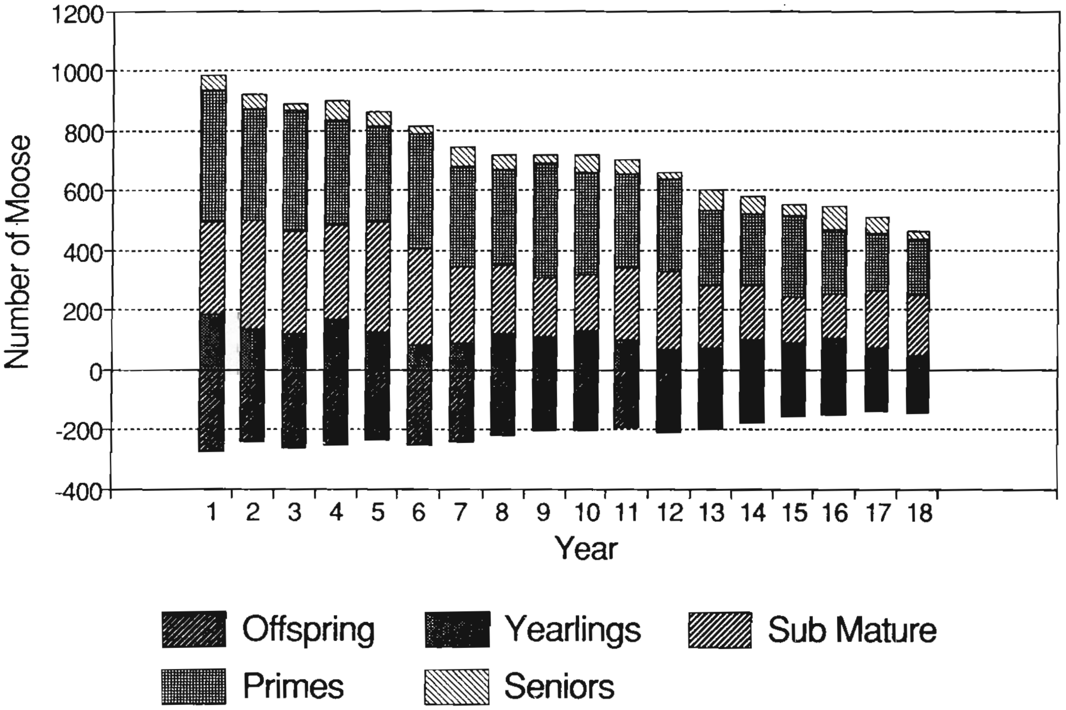

Fig. 6A. Population structure trends (**A A O A P P** ...).

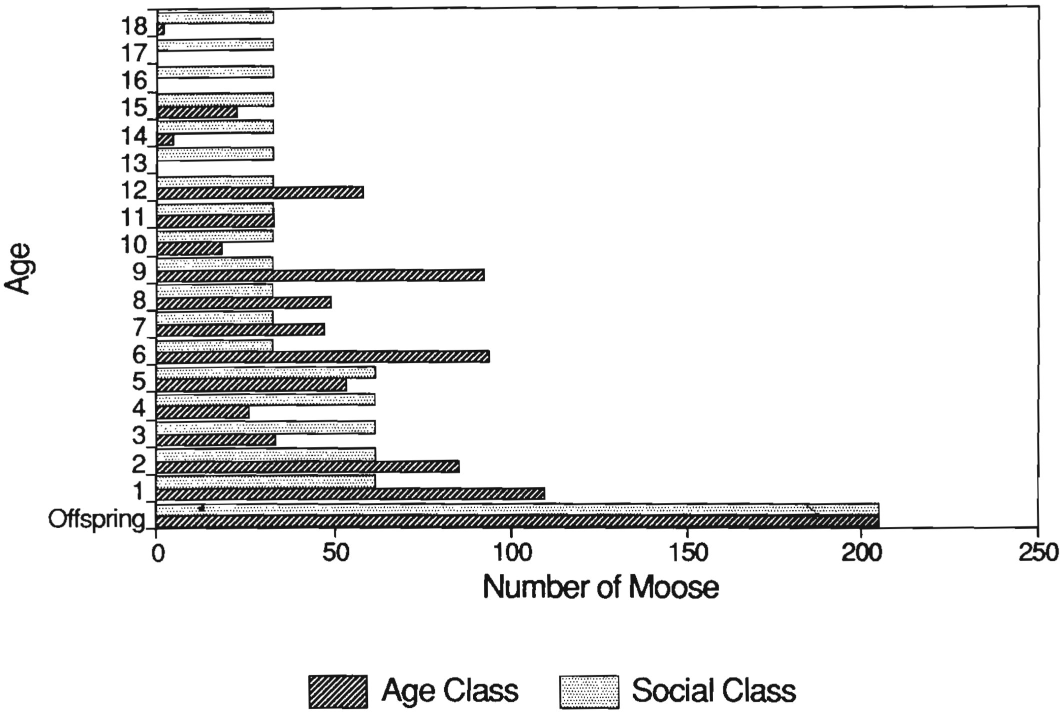

Fig. 6B: Infrastructure, year 9 for fitness sequence (**A A O A P P**...).

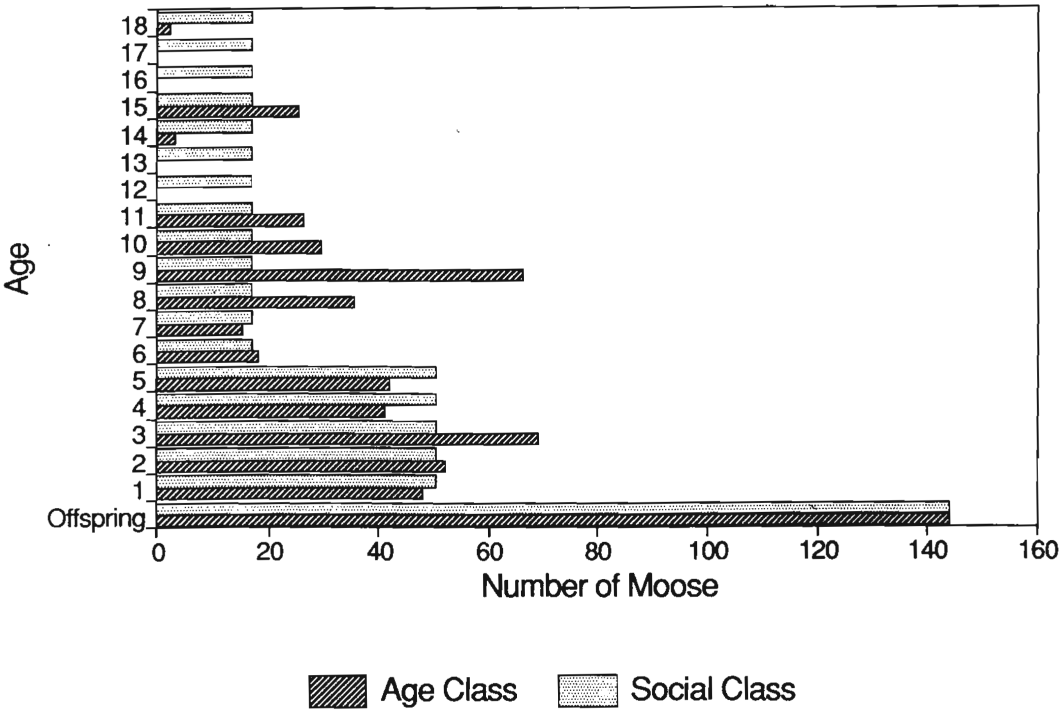

Fig. 6C: Infrastructure, year 18 for fitness sequence (**A A O A P P**...).

Table 4. Starting population structure.

Age Class	Number of moose	Fitness class
1	185	O-ptimal
2	85	P-oor
3	80	A-verage
4	85	O-ptimal
5	65	P-oor
6	70	A-verage
7	80	O-ptimal
8	60	P-oor
9	70	A-verage
10	75	O-ptimal
11	55	P-oor
12	40	A-verage
13	45	O-ptimal
14	0	P-oor
15	0	A-verage
16	5	O-ptimal

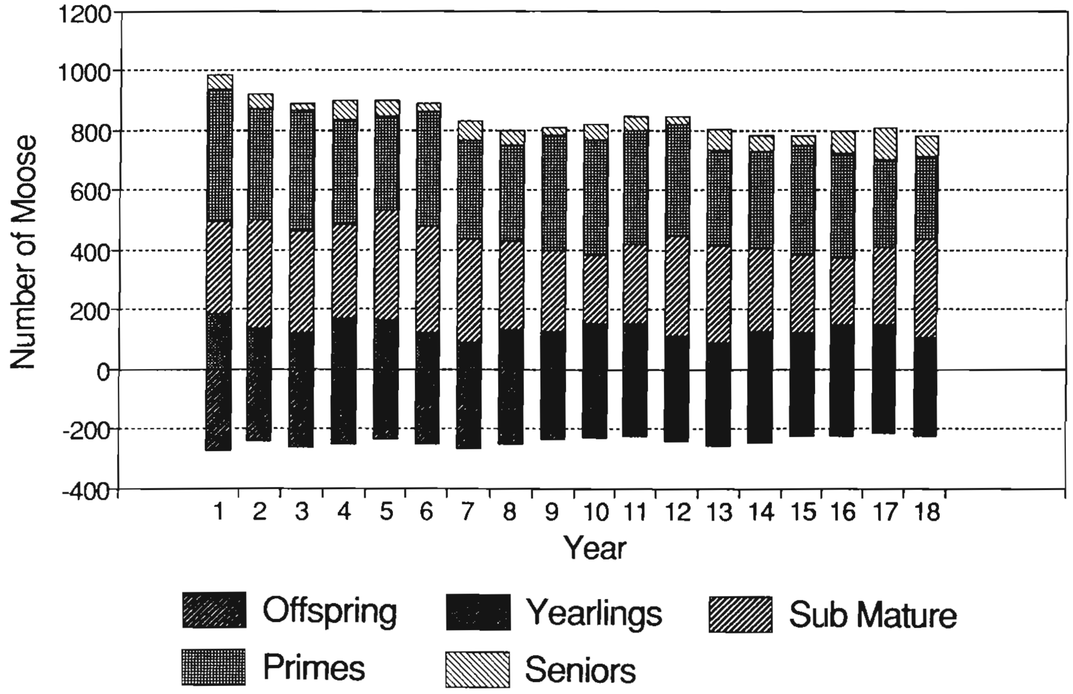

Fig. 7A. Population structure trends (**A A O O A P**...).

bulk of mature individuals remain in the best reproductive age, and that bulls between prime and postprime class (ages 10 to 12) are well represented. The relative stability of the population must be ascribed to the fitness of the **A**- and **O**-generations, which produce a slight surplus of sub-mature individuals.

These simulations show that the reported

Fig. 7B. Infrastructure, year 7 for fitness sequence (**A A O O A P**...).

Fig. 7C. Infrastructure, year 12 for fitness sequence (**A A O O A P**...).

absence of some age classes in harvest or census (Bubenik, A. *et al.* 1975; Bubenik, A. and Schwab 1975; Bubenik, A. and Bellhouse 1980), may be due to the appearance of **P**-generations and must not be ascribed to chance events or recording errors.

CONCLUSION - PRACTICAL ASPECTS

Sociobiological modelling has the advantage that the manager can effectively control population well-being under the presumption that the preferred feeding grounds are not overused. The generation fitness is then the leading indicator for the direction towards which the SC-ratio and sex-ratio should be monitored and how high the harvest could be set.

In the model the hunter serves as controller of the population welfare and the manager is no longer a 'game producer' but a 'game protector.' Simultaneously, the harvest by hunters must be considered a reward for the expensive hunting of supernumerary classes and not as an inhuman killing or shooting of living targets.

The few models used as examples show how flexible the population behaviour of moose is, and how it depends on the frequency of generations of poor, average and optimal fitness. Whether the population remains stable, declines or eventually rises depends on the overall losses and whether or not they remain within the range of generations' longevity. It is the manager's role to assess which SC is over- or under-represented and approximately how high the soft losses are to be. The modelling of harvest according to the SC-ratios has many practical advantages. In North America, due to the hunting system and frequent inaccessibility of hunting grounds, it is relatively difficult to predict losses of offspring. Hence, it is more useful to watch over the generation fitness and model the population development according of the fitness and relative number of yearlings on the one hand and the behaviour of SC-ratios on the other.

The annual harvest is the number of animals per SC which are supernumerary, either because the natural mortality is too low, or because the classes are over-represented and have supernumerary individuals. The recommendation to harvest according to SC-features and not age classes is of practical importance because these features are more easily assessed than age. Nonetheless, from a behavioral view, the supernumerary age class are almost always more vulnerable and thus preferentially removed. This can be facilitated by choosing an opening date which corresponds to a period of highest activity of the supernumerary classes. For example, in the case of over abundant teenagers, setting the opening date after the peak of the rut will be effective in reducing their numbers (Child and Aitken 1989; Crête 1982; Timmermann and Gollat 1982). The control of yearlings should be easy because they are readily identified both for assessment and for harvest by hunters with low biological knowledge.

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REFERENCES

ALLABY, M. 1985. The Oxford Dictionary of Natural History. Oxford University Press, NewYork.

ALLEN, A.W., J.W. TERELL and P.A. JORDAN. 1988. An overview of a habitat suitability index model for moose: Lake Superior region. Alces 24:118-125.

ALTMANN, M. 1961. "Teenager" problems in the wilderness. Animal Kingdom 64:41-

44.

_______. 1963. Seniors of the wilderness. Animal Kingdom 66:181-183.

ARNOLD, G.W., D.E. STEVEN and A. GRASSIA. 1990. Association between individualsand classes in groups of different size in population of western grey kangaroos, *Macropusfuliginosus*. 17:551-562.

BAJOHR, W.A. 1988. Brauchen wir Trophäenolympiaden der Eitelkeit? Der Anblick March:92-96.

BAKER, R. 1985. The American hunting myth. Vantage Press, New York..

BALČIAUSKAS, L. 1990. Modelling of moose hunting: protection effect of cows with twins. Page 180 *in* Abstracts of Papers and Posters. Third. Inter. Moose Sympos. N.E. Kochanov (ed.) AN USSR,Ural Div.Syktyvkar.

BALLARD, W.B., S.D. MILLER, and J.S. WHITMAN. 1986. Modeling a south - central Alaskan moose population. Alces 22:201-243.

BARTECKI, R. and Z. JACZEWSKI. 1983. Seasonal variation in the plasma androgens concentrations of red deer. Acta Theriol. 28:333-336.

BARTOŠ, L. 1980. The data of antler casting, age and social hierarchy relationship in the red deer stag. Behav. Proc. 5:293-301.

______ and V. PERNER. 1985. Integrity of a red deer stag group during velvet period,association of individuals, and timing of antler cleaning. Behav. 95:314-323.

BASKIN, L.M. 1990. Population Ecology of the Moose in the Russian Southern Taiga. Page 99 *in* Abstracts of Papers and Posters. Third Inter. Moose Symp. N.E. Kochanov (ed.): AN USSR Ural Div. Syktyvkar, USSR.

B EJŠOVEC, J. 1955. Špatý vývoj parůžkú u scrnčí zvěře. (Kümmerliche Geweihentwicklung beim Rehwild.) Acta Soc. Bohemoslov. 19:119-137.

BOBEK, B., K. PERZANOWSKI and J. WEINER. 1990. Energy expenditure for reproductionin male red deer. J. Mammal. 71:230-2323.

BOER, A.H., and D.M. KEPPIE. 1988. Modelling a hunted moose population in New Brunswick. Alces 24:201-217.

BOWER, B. 1991. Questions of mind over immunity. Science News 139:216-217.

BROWN, J. S. and T.L. VINCENT. 1987. Coevolution as an evolutionary game. Evolution 41:66-79.

BUBENIK, A.B. 1971. Social well-being as a special aspect of animal sociology. Paper presented at the Intern. Conf. on the Behaviour of Ungulates and its Relation to Management. Calgary, Nov. 2-5. Mimeo.

_______. 1980. On demographic factors and neurohumoral substrates. Comments to "human ethology" - concepts and implications for the sciences. Behav. and Brain Sci. 4:524-615.

_______. 1982. Physiology of wapiti. Pages 125-179 *in* J.W. Thomas and D.E. Toweill, (eds). Elk of North America. Stackpole Books, Harrisburg, PA.

_______. 1984. Ernährung, Verhalten und Umwelt des Schalenwildes. BLV Landwirtschaftsverlag München.

_______. 1985. Reproductive strategies in cervids. Pages 363-373 *in* Biology of Deer Production. P.F. Fennessy and K.R. Drew (eds). Roy. Soc. N.Z. Bull. 22.

_______. 1987. Behaviour of moose (*Alces alces* ssp.) of North America. Swedish Wildlife Research Suppl. 1:333-365.

_______. 1989. Coevolution of forest ecosystems, as a basis for coexistence. page 21. Algonquin Region: Forest/Wildlife Workshop. Febr.15-16. 1989. Hidden Valley, Ont.Min.Nat.Res. Toronto, Ontario.

_______. 1990. Epigenetical, morphological, physiological, and behavioral aspects of evolution of horns, pronghorns and antlers. *in* Horns, Pronghorns and Antlers.

G.A.Bubenik, and A.B. Bubenik eds. Springer Verlag, New York.

_______. 1991. The wildlife resources-mine, ours or whose? *in* Proceeding of the 2nd Intern. Wildlife Ranching Symposium 1990. L.A. Renecker (ed.) Calgary. in press.

_______, J. LOCHMAN and J. PRÚŠEK. 1956. Biostatistische Untersuchung einer Hirschbrunft. Z.Jagdwiss. 2:142-148.

________, and P. SCHWAB. 1974. Populationsstruktur des Gamswildes, ihre Simulierung und Bedeutung für die Regulierung des Bestandes. Pages *in* 117-123. Tagungsbericht - 1. Intern. Gamswild-Treffen. Instit. f. Wildforsch. Oberammergau, Germany.

_______, H.R. TIMMERMANN and B. SAUNDERS. 1975. Simulation of population structure and size in moose on behalf of age and structure of harvested animals. Proc. N. Am. Moose Conf. Workshop. 11:391-463.

________, O. WILLIAMS and H.R. TIMMERMANN. 1977. Visual estimation of sex and social class in moose (*Alces alces*) from the ground and the plane - A preliminary report. Proc. N. Am. Moose Conf. Workshop. 13:157-176.

________, O. WILLIAMS and H.R. TIMMERMANN. 1978. The significance of hooves in moose management - Preliminary report. Proc. N. Am. Moose Conf. Workshop. 14:209-226.

_______, and T.J. BELLHOUSE. 1980. Brain volume of taiga moose (*Alces alces* sp.) in relation to skull parameters - a pilot study. Proc. N. Am. Moose Conf. Workshop. 16:11-34.

_______, and H.R. TIMMERMANN. 1982. Spermatogenesis in the taiga moose of North Central Ontario. Alces 18:54-93.

BUBENIK, G.A. 1982. The endocrine regulation of the antler cycle. Pages *in* 73-106. R.D.Brown (ed). Antler Development in Cervidae. C. Kleberg Wildl. Res. Institute,Kingsville, TX.

_______. 1986. Regulation of seasonal endocrine rhythms in male boreal cervids. Pages 461-474 *in* I. Assenmacher, and J. Boissin (eds). Endocrine regulations as adaptive Mechanism to the environment. Intern. Coloq. CEBAS-CNRS, Paris.

_______, and A.B. BUBENIK. 1985. Seasonal variations in hair pigmentation of white-tailed deer and their relationship to sexual activity and plasma testosterone. J.Exp.Biol.235:387-395.

_______, and D. SCHAMS. 1986. Relationship of age to seasonal levels of LH, FSH,prolactin and testosterone in male, white-tailed deer. Comp. Biochem. Physiol. 85A:179-183.

_______, D. SCHAMS, and A.J. SEMPÉRÈ. 1987. Assessment of the sexual and antler· potential of the male white-tailed deer (*Odocoileus virginianus*) by Gn/ stimulation test. Comp. Biochem. Physiol. 86A:767-771.

BURSCHEL, P. 1979. Der Wald als Gesellschaft von Bäumen (The forest as society of trees). Pages 74-93 *in* pp.74-93. Rettet den Wald (Save the forest). H. Stern (ed.) Kindler Verlag. Munich.

CALHOUN, J.B. 1962. A "behavioral sink". Chapter 22. *in* pp. 29515. Roots of behavior.E.L. Bliss (ed.) Harper & Brothers - Hoeber Medical Division, New York.

CARLEY, J.S. 1990. UniPOP: A universal population and harvest dynamics model. Unpublished manual.

CAUGHLEY, G. 1970. Population statistics of chamois. Mammalia 34. Part. 2:194-199.

_______. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York.

_______. 1979. What is this "thing" called carrying capacity? Pages 2-5 *in* M.S. Boyce and L.D. Heyden· ·ng (eds). University of Wyoming Press. Laramie, WY

CHILD, K.N. and D.A. AITKEN. 1989. Selective harvests, hunters, and moose in Central British Columbia. Alces 25:81-97.

CLUTTON-BROCK, T.H. 1985. Reproductive success in red deer. Scient. Amer. 252:86-92.

_______. 1988. Reproductive success. Ethol. and Sociobiol. 11:141-143.

_______,S.D. ALBON and F.E. GUINNESS. 1982. Competition between female relatives in a matrilocal mammal. Nature 300:178180.

CRÊTE, M. 1982. Le pourqoui du retardement des saisons de chasse. Sentier Chasse-Pêche 11:53+55-59.

BECKER, D.J. 1990. Wildlife management - for whom and for what? Wildlife managers' use· of social values indicators. Pages 713-721 *in* Trans. 19th IUGB Congress, Trondheim 1989.

DEEVEY, E.S. 1947. Life tables for natural populations of animals. Quarter. Rev. Biol.22:283-314.

DIETRICH, H. 1979. Die Saisonveränderungen der Hoden und Nebenhoden von Gamsböcken verschiedener Altersstufen in der Vor-, Haupt- und Nachbrunft. Dr. Th., Vienna,Veter. Univ

DOBZHANSKY, T. 1968. Adaptedness and fitness. Pages 109-122 *in* Chapter 8. Population Biology and Evolution. R. Lewontin (ed.) Syracuse University Press, Syracuse, NY.

DODDS, D.G. 1990. Hearing our voices - what do they say? Thoughts concerning game biologists and natural systems. Pages 367-372 *in*: Trans. 19th IUGB Congress, Trondheim 1989.

DONAUBAUER, E., H. GOSSOW and F. REIMOSER. 1990. "Natürliche" Wilddichten oder forstliche Unverträglichkeitsprüfung für Waldschäden. Österr. Forstztg. 101:6-9.

EABRY, S. 1970. A glossary of deer terminology. Northeastern Deer Study Group.(ed.)Wildl. Res. Lab. Delmar, NY.

ELSKY, G.M. 1990. Dynamics of moose populations in transformed forests of the middle· Siberia. Page 64 *in* Abstracts of Papers and Posters. Third. Intern. Moose Symp. N.E.Kochanov (ed.). AN USSR, Ural Division. Syktyvkar, USSR.

FRANCO, N. 1991. Recommendations of the European and Asian Big Game Commission (Palearctic region). Annual Assembly of C.I.C., Quebec City, May 1991. C.I.C. Paris, in press

GARNER, D. L., M.L. WILTON, and K.A. GUSTAFSON. 1990. Importance of moose immigration into a heavily hunted area from an unhunted area. Alces 26:30-36

GASAWAY, W.C., R.D. BOERTJE, D.V. GRANGAAERD, D.G. KELLEYHOUSE, R.O.STEPHENSON and D.G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildl.Monogr.120:1-54.

GEIST, V. 1968a. On the interrelation of external appearance of social behaviour and social structure of mountain sheep. Z. Tierpsychol. 25:199-215.

_______. 1968b. On delayed social and physical maturation in mountain sheep. Can. J. Zool.46:899-904.

_______. 1985. Game ranching: threat to wildlife conservation in North America. Wild. Soc.Bull. 13:594-598.

GOMENDIO, M., T.H. CLUTTONEOCK, S.D. ALBON, F.E. GUINNESS and M.J.SIMPSON. 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. Nature 343:261-263.

GREENWOOD, C.E. and R.E.A. CRAIG. 1987. Dietary influences on brain function: Implications during periods of neuronal maturation. Current Topics in Nutrition and Disease 16:159-216.

GUINNESS, F.E, G.A. LINCOLN and V.R.

SHORT. 1971. The reproductive cycle of the female red deer, *Cervus elaphus* L. J.Reprod. Fert. 27:427-438.

HAINES, C.J. and A.L. EMES. 1991. The relationships between follicle diameter, fertilization· rate, and microscopic embryo quality. Fertility and Sterility 55:205 - 207.

HARMEL, D.E. 1982. Effects of genetics on antler quality and body size in white-tailed deer. Pages 339-348 *in* R.D.Brown. Antler development in Cervidae. C. Kleberg Institute. Kingsville, TX.

HARRISON, G.A. 1990. Life styles, health, well-being, and natural selection. Primate Life History and Evolution 14:221-228.

HARTL, G.A., G. LANG, F. KLEIN and R. WILLING. 1991. Relationships between allozymes, heterozygosity and morphological characters in red deer (*Cervus elaphus*),and the influence of selective hunting on allele frequency distributions Heredity 66:343-350.

HEIMER, W.E. 1987. Publication of dall sheep findings and development of future research direction. Alaska Dept. Fish & Game, Div. Game. Project W"G Mimeo.

_______, A.M. WATSON. 1986. Comparative dynamics of dissimilar dall sheep populations. Final Report. Alaska Dept. F&G, Juneau AK.

HENNIG, R. 1988. Zur Darstellung von Bestandesstrukturen beim Schalenwild. Z. Jagdwiss.34:69-73.

HJELJORD, O., N. HOVIK and H.B. PEDERSEN. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Holarctic Ecology 13:281-292.

JOHNSON, B.C. 1990. Analogy 1.0 A wildlife population model. Manitoba Department of Natural Resources Wildlife Branch -Biological Services, Winnipeg, Manitoba.

KANSAS, J.L. and R.M. RAINE. 1990. Habitat modeling in the wildlife sector. Pages *in* 128-134. Forest Modeling Symposium. Beak Assoc. Cons. Ltd. Calgary, Alberta.

LEARY, R.F. and F.W. ALLENDORF. 1989. Fluctuating asymmetry as an indicator of stress - implications for conservation biology. Trend in Ecology & Evolution. 4:214-217.

LEOPOLD, A. 1947. Game management. Charles Scribner's Sons, New York.

LINCOLN, G.A. 1971. Puberty in a seasonally breeding male, the red deer stag (*Cervus elaphus L.*). J. Reprod. Fertil 25:41-54.

LOMNICKI, A. 1988. Population ecology of individuals. Princeton University Press,Princeton, NJ.

LORENZ, K. 1974. Analogy as a source of knowledge. Science 185:229-234.

LUNDBERG, P. and K. DANELL. 1990. Functional response of browsers - tree exploitation by moose. Oikos 58:378-384.

McCULLOUGH, D.R. 1979. The George Reserve deer herd. The University of Michigan Press, Ann Arbor, MI.

MEILE, P. and A.B. BUBENIK. 1979. Zur Bedeutung sozialer Auslöser für das Sozialverhalten der Gemse *Rupicapra rupicapra* (Linné, 1758). Säugetierkdl. Mitt.,Sonderheft Gemse.

MITCHELL, B. and J.M. CRISP. 1981. Some properties of red deer (*Cervus elaphus*) at exceptionally high population density in Scotland. J.Zool. 183:157169.

MOEN, A.N. and F. AUSENDA. 1987. Sensitive population parameters in modeling long-lived species such as moose. Alces 23:33-48.

NIINI, T.R. 1982. Zur Morphologie des Hodens und Nebenhodens vom Rehbock (*Capreolus capreolus* L.). Histologische und histochemische Untersuchungen an der Gonade aus der Vor-, Haupt und Nachbrunft. Dr.Th., Vienna Vet. University.

ÖSTERR. FORSTVEREIN 1990. Die Jagd

braucht eine Neuorientierung [Hunting needs to be reoriented].Österr. Forstztg. 101:10-12.

OWEN, D.F. 1990. The language of attack and defence. Oikos 57:133-135.

OZOGA, J.J. 1987. Behavior and deer herd dynamics. Michigan Out of Doors, March:50-51+53.

PAGEL, M.D. and P.H. HARVEY. 1990. Diversity in the brain sizes of newborn mammals.Biosicence 40:116-122.

PALO, R.T. and C.T. ROBBINS. 1991. Plant defenses against mammalian herbivory. CRC Press Inc., Boca Raton, FL.

PARSONS, M.G. 1987. Era of land management planning and resource modeling: Changing times for habitat managers. Alces 23:1-32.

PAYNE, P.R. and E.F. WHEELER. 1968. Comparative nutrition in pregnancy and lactation.Proc. Nutr. Soc. 27:129-138.

PEMBERTON, J.M., S.D. ALBON, F.E. GUINNESS, T.H. CLUTTONEOCK and R.J.BERRY. 1988. Genetic variation and juvenile survival in red deer. Evolution 42:921-934.

PETERSON, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S.. Nat. Park Serv. Scien. Monogr. Ser. No 11. U.S. Gov. Printing office, Wash., D.C. 210pp.

PFANDL, E. 1977. Ergebnisee aus den Achentaler Revieren. Jagd in Tirol 10:10-14.

PINSKER, W. 1978. Die Saisonveränderungen der Hoden und Nebenhoden von Hirschenverschiedener Altersstuffen in der Vor-, Haupt- und Nachbrunft. Dr.Th. Vienna, Veter. University.

PROTHERO, W.L., J.J. SPILETT and D.F. BALPH. 1980. Rutting behavior of yearling and mature bull elk: from some implications for open bull hunting. Pages 160-165 *in* North American Elk: Ecology, Behavior and Management. M.S. Boyce and L.D.Hayden (eds). The University of Wyoming Press, Laramie, WY.

REVIN, Yu.V. and Ya.L. VOLPERT. 1990. Spatial distribution and moose numbers in Yakutia. Page 90 *in* Abstracts of Papers and Posters. Third Intern. Moose Symposium.N.E. Kochanov (ed.). AN USSR, Ural Division. Syktyvkar USSR.

ROUGHGARDEN, J. 1983. Coevolution between competitors. Chapter 17 Pages 383-403 *in* Coevolution. D.J. Futuyma, and M. Slatkin, (ed.) Sinauer Assoc. Incorp., Sunderland,MA.

RYDER, M.S. 1989. Animal revolution - changing attitudes towards speciesism. Basil Blackwell, London.

SAETHER, B.E. and R. ANDERSEN. 1990. Resource limitation in a generalist herbivore, the moose *alces alces* -ecological constraints on behavioural decisions. Can.J.Zool. 68:993-999.

SANTIFALLER, K., K. SCHMIDT, K. WEISS and H. RINNER. 1978. Festschrift 15 Jahre Rotwild-Heggemeinschaft Karwendel 1963. Bezirkstelle Schwaz, Tirol, Austria.

SCANLON, P.F. 1990. Introduced species in the United States as damage causing species. Pages 543-548 *in* Trans. 19th IUGB Congress, Trondheim 1989

SCHWAB, P. 1979. Waldgerechte Schalenwildhege im Hochgebirge (Sylviculture adapted to Ungulate Management in Alpine Zone). Allg.Forstztg. 17/18:445-455.

__________. and L. MESSNER 1986. Sozialklassen, Infrastruktur und Bejagung von Gamswild,Jagd in Tirol 38:June 16-20; Jul-Aug. 18-21; Sept. 18-23.

SCRIBNER, K.T., M.H. SMITH and P.E. JOHNS. 1984. Age, condition and genetic effect onincidence of spike bucks. Proc.Ann. Conf.Southeast Assoc. Fish & Wildl. Agencies(SEAFWA):23-32.

SHACKELTON, D.M. 1991. Social maturation and productivity in bighorn sheep: are young males incompetent? Applied

Anim.Behav.Sci. 29:173-184.

SINGER, F.J., E.C MURPHY, B.A. COOPER and K.K. LAING. 1991. Activity in a hunted and unhunted herd of dall sheep. Applied Anim. Behav. Sci 29:185-193.

SMITH, H.L. 1976. Identification of social classes by physical features and management implications for white-tailed deer (*Odocoileus virginianus*). MSc Thesis, Department of Zoology, University of Guelph, Ontario. 103 pp.

STRINGHAM, S.F. and A.B. BUBENIK. 1974. Physical condition and survival rate of chamois (*Rupicapra rupicapra·*) as a function of maturity-sex class ratios in the population: Implications for ungulate harvest plan. Pages i*n* 123-160. Tagungsber. 1.Intern. Gamswildtreffen. W. Schröder (ed.). Inst. f. Wildforsch. u. Jagdkunde,Oberammergau, Germany.

TAYLOR, M.K. and J.S. CARLEY. 1988. Life table analysis of age-structured populations in seasonal environments. J.Wildl. Manage. 66:234-249.

THELEN, T.H. 1991. Effects of harvest on antlers of simulated populations of elk. J.Wildl.Manage. 66:234-249.

THOMAS, J.W. (ed). 1979. Wildlife habitats in managed forests - the Blue Mountains of Oregon and Washington. Handbook No. 533. U.S. Dept. Agric. Washington, D.C.

THOMPSON, I.D. 1988. Moose damage to pre-commercially thinned balsam fir stands in Newfoundland. Alces 24:56-61.

TIMMERMANN, H.R. and R. GOLLAT. 1982. Age and sex structure of harvested moose related to season manipulation and access. Proc. N. Am. Moose Conf. Workshop. 18:301-3228.

_______, and M.W. LANKESTER. 1978. Joint disease in ungulates with special reference to moose. Proc N. Am. Moose Conf. Workshop. 14:89-108.

VARIĆAK, V. 1991. Declaration of the commission of exposition and trophies. Mimeo, *In*: C.I.C. General Assembly Quebec City. May 1991. C.I.C. Paris, in press.

VERME, L.J. 1991. Decline in doe fawn fertility in southern Michigan deer. Can.J.Zool.69:25-28.

VICKERY, P. 1990. German deer management: practice and recept. Deer 8:44-46.

VITAKOVA, A.N. 1990. Content and milk productivity of female moose being domesticated. Page 176 *in* Abstracts of Papers and Posters. Third Inter. Moose Symp. N.E.Kochanov (ed.). AN USSR, Ural Divis. Syktyvkar, USSR.

VOGT, F. 1947. Das Rotwild. Österr. Jagd- u. Fischereiverlag. Vienna.

VON BAYERN, A. and J. VON BAYERN 1975. Über Rehe in einem Steierischen Gebirgsrevier. Johannes Bauer Verlag, Hamburg.

VON UEXKÜLL, J. 1937. Umweltforschung. Z.Tierpsychol. 1:33-34.

_______. J. 1957. A stroll through the world of animals and men; a picture book of invisible world. Pages 5-80 *in* Instinctive behavior: the development of a modern concept. Schiller, C.H. (ed.) Transl. Schiller, C. H. International Universities Press, New York..

WALLACE, B. 1975. Hard and soft selection revisited. Evolution 29:465-473.

_______. 1977. Automatic culling and population fitness. Evol. Biol. 10:265-276.

WEBER, R.J. and A. PERT. 1989. The periaqueducal gray matter mediates opiate-induced immunosuppression. Science 245:188-189.

WEBSTER, N. 1983. Webster's new twentieth century dictionary. 2nd ed. Simon and Schuster, New York.

WILSON, E.O. 1975. Sociobiology - The new synthesis. Belknapp Press of Harvard University Press, Cambridge, MA..

WRIGHT, S. 1978. Evolution and genetics of populations. Vol.4. Variability within and among natural populations. Chicago University Press, Chicago, IL.