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USE OF BIOMETRIC BODY VARIABLES AS INDICATORS OF ROE DEER *(CAPREOLUS CAPREOLUS)* POPULATION DENSITY CHANGES

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KEY WORDS: Roe deer, *Capreolus capreolus,* density, biometric variable, body mass, lower jaw, management, Switzerland.

ABSTRACT

The present study analyzes the variations in biometric variables measured on roe deer, Capreolus capreolus, *bagged by hunters between 1980 and 1986 in the Swiss canton of Neuchâtel, between 1984-1986 and in 1998 in the canton of Vaud, and between 1971-1982 in the eastern part of Switzerland (mostly in the canton of Thurgovie). The study's objective is to determine which of these variable variations may be used to evidence changes in population density irrespective of any physical factors (climate, habitat quality), and assess the state of balance between roe deer populations and their food resources in order to manage them. To this end the following indicators were tested: body mass of the eviscerated animals, skeleton size (according to the lower jaw length) and physical condition (measured by the residual of the regression of body mass of the eviscerated animals on lower jaw length). Three age classes (fawns, yearlings and adults) were defined by the degree of wear of their jugular teeth. For every canton, the influence on the indicators of the factors sex, year and region was studied. Body mass and lower jaw length are linked, whatever the age class, which is indicative of a convergence of these two indicators. Body mass and lower jaw length are influenced by sex (males being bigger and heavier than females), by year and region. In the canton of Neuchâtel between 1980 and 1986, the body mass and lower jaw length of fawns and yearlings were linked to roe deer density (variation: between 10 and 20 individuals per 100 ha). These indicators may therefore be used to monitor roe deer populations. For each of these indicators, long-term monitoring is indispensable to differentiate the influence of climate and that of roe deer density on the annual indicator variations. On the other hand, neither the physical condition as defined here, nor the other variables measured on adults, may be used to monitor roe deer populations.*

I. INTRODUCTION

According to the new Forestry Act in force on the territory of the Swiss Confederacy since 1991, in all cantons the wildlife managers are assigned the duty to "avoid a harmful proliferation of game and secure the conservation of the forests, in particular their natural regeneration", through the enactment of requisite regulations. In particular, all redundant ungulate populations must be reduced under the penalty of cessation of subsidy payments for forestry projects, if a forest-game equilibrium has not been attained. The directives in pursuance of the application of the law, state that such equilibrium is attained when the damages are bearable in at least 75% of the forested area. A hunting plan must be applied, based on animal counts and hunting bag controls. To mitigate the difficulties of carrying out such a census, in each canton the people in charge are authorized to require analyses of the physical condition (as measured by body mass corrected by size) and constitution (as measured by size) of all culled animals (OFFICE FÉDÉRAL DE L'ENVIRONNEMENT, DES FORÊTS ET DU PAYSAGE, 1996).

In the case of roe deer, *Capreolus capreolus*, the difficulty of censusing the animal in forested habitats is well known (STRANDGAARD, 1972). Therefore, their population management presently is being oriented towards the use of indicators of density variation. This concept is founded on the notion of density-dependence, *i.e.* on the fact that an increase in population density will cause roe deer, but also their environment, to react. Thus, when density increases, their food resources will diminish in quantity but also in quality, and the animals' physical and physiological state will deteriorate, which will delay the age at which first breeding takes place and lead to a decrease in the number of young at fawning, and greater fawn mortality GAILLARD *et al*., 1998). Former studies had already shown that it is possible to use changes in fawn body mass, the kilometric index, or the index of consumption, as indicators of density variation (CEDERLUND *et al*., 1998).

The objective of the present study is to test the variability of three potential indicators (body mass, length of the lower jaw and body condition) with respect to different factors (year, region, sex and age), an objective achieved thanks to data collected on roe deer killed during the hunting season in Switzerland. In particular, to manage these populations, we would like to establish what indicators will give the best description of density variations.

II. MATERIAL AND METHODS

II.1. STUDY AREAS

The data were collected on roe deer that were killed by hunters in the cantons of Neuchâtel, Vaud and Thurgovie (Figure 1).

The canton of Neuchâtel is entirely situated in the Jura region (altitudes 430-1 540 m) in the north-west of Switzerland. The 293-km^2 forested area covers 37% of the 803-km^2 total surface area. Hunting requires a special license by which a hunting-license holder is granted the right to hunt in the canton's entire territory. There are about 350 to 400 of such hunters. The roe deer hunting season starts in the beginning of October and, according to the year, closes between November 1 or 10.

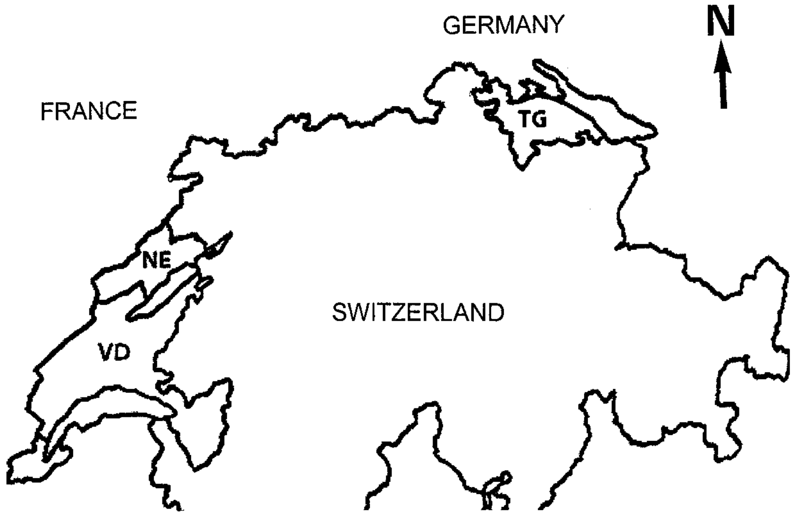

Figure 1: Location of the cantons where the study sites were located (Switzerland): NE = Neuchâtel, VD = Vaud and TG = Thurgovie.
Figure 1 : Localisation des cantons où se situaient les sites d'études en Suisse : NE = Neuchâtel, VD = Vaud et TG = Thurgovie.

The canton of Vaud is situated in the three regions of the Jura, the Plateau and the Alps (at altitudes ranging between 370 and 3,210 m) in the west of Switzerland. The 1,103-km² forested area covers 34% of the 3,212-km² total surface area. As for the Neuchâtel canton, hunting with a special license is practiced by 800 to 850 hunters. The roe deer hunting season takes place at the same moment as in the canton of Neuchâtel.

The canton of Thurgovie is situated in the Prealpine Plateau and Hill regions (at altitudes between 400 and 1,000 m) in the east of Switzerland. The 195-km² forested area covers 20% of the 991-km² total surface area. The hunting system is of the « leased » type, *i.e.* the canton's territory is divided into plots of land which are administered by a tenant (hunting society or private person). On each one of such plots, each hunting license holder has the right to hunt if he is member of the society that is managing the plot. This type of hunting is practiced by 360 successful tenders in some hundred hunting territories (called "*Reviers*" in German). The roe deer hunting season goes from May to January of the following year. The data collected on roe deer data in the two territories that belong to the cantons neighbouring the one of Thurgovie (Argovie and Saint-Gall), were added to the Thurgovie sample to form a sample called « East of Switzerland ». The territory of Saint-Gall is situated in the Alpine region.

II.2. DATA COLLECTION

Data on hunter-killed roe deer were collected between 1980 and 1986 in the canton of Neuchâtel, between 1984 and 1986 and in 1998 in the canton of Vaud, and between 1971 and 1982 in the East of Switzerland (Table I).

TABLE I
Numbers (individuals) of sampled roe deer, *Capreolus capreolus,* killed during the hunting season in the cantons of Neuchâtel (NE) and Vaud (VD) and in the east of Switzerland (EAST-CH) as a function of site and the year (1971-1983, 1998) in which the samples were collected.

TABLEAU I
Effectifs (individus ; classes d'âge : < 1 an, 1 à 2 ans, > 2 ans ; mâles, femelles) des chevreuils, *Capreolus capreolus*, échantillonnés tués à la chasse dans les cantons de Neuchâtel (NE) et Vaud (VD) et dans l'est de la Suisse (EAST-CH) en fonction du site et de l'année de prélèvement des échantillons (1971-1983, 1998).

Sample	Roe deer numbers (individuals)					
	< 1 year		1 to 2 years		> 2 years	
	Males	Females	Males	Females	Males	Females
NE 1980	26	15	24	26	35	39
NE 1981	4	10	12	8	25	39
NE 1982	19	21	28	30	37	31
NE 1983	23	25	30	25	46	64
NE 1984	13	15	22	32	32	62
NE 1985	17	21	15	19	36	53
NE 1986	3	4	14	11	15	22
VD-Jura 1984	3	0	6	9	14	9
VD-Jura 1985	2	5	1	3	6	6
VD-Jura 1986	1	0	4	3	10	11
VD-Jura 1998	22	10	28	18	58	48
VD-plain 1984	9	16	19	19	38	50
VD-plain 1985	8	7	4	7	12	18
VD-plain 1986	8	8	17	13	16	26
VD-plain 1998	31	28	48	44	74	83
VD-Alps 1984	0	0	0	0	2	1
VD-Alps 1985	1	0	0	0	2	2
VD-Alps 1986	0	1	1	0	2	1
VD-Alps 1998	3	2	7	1	15	18
EAST-CH plain 1971	11	15	1	0	17	26
EAST-CH plain 1972	5	2	1	0	23	38
EAST-CH plain 1973	1	0	0	0	10	3
EAST-CH plain 1974	0	0	0	0	1	3
EAST-CH plain 1975	2	2	0	0	6	18
EAST-CH plain 1976	1	2	0	0	2	23
EAST-CH plain 1977	1	5	0	0	2	6
EAST-CH plain 1978	2	3	4	1	3	4
EAST-CH plain 1979	4	6	1	2	0	10
EAST-CH plain 1980	0	51	0	64	0	81
EAST-CH plain 1981	3	51	2	23	1	51
EAST-CH plain 1982	0	46	0	28	0	46
EAST-CH Alps 1971	0	3	1	0	13	14
EAST-CH Alps 1972	0	3	0	0	8	4
EAST-CH Alps 1973	0	0	0	0	0	9

Body mass

Body mass was measured by the body mass of the entirely eviscerated deer. However, in Neuchâtel, most (90%) of the carcasses had only been partially eviscerated (BLANT, 1987: 102). In the East of Switzerland, body mass had been measured by carcass body mass without the head. The measurements had been taken with a variable precision, certain body masses had been weighed with a precision of more or less 100 g while others had been rounded at half a kilogram, and even one kilogram. However, since these procedures did not change over time, the heterogeneity of these measure-takings did not have any consequences on the comparisons we made.

Lower jaw length (LJL)

Lower jaw length (LJL) was measured with the help of slide calipers (Figure 2). On the samples from Neuchâtel and Vaud, the mandibular distance (LJL1, between the infradental and articular extremities; STUBBE and GLEICH, 1990; ANGIBAULT *et al*., 1993) was measured. On jaw samples from East Switzerland collected between 1971 and 1977, the jugular distance (LJL2, between the infradental extremity and the extremity of the caudal gonion; EIBERLE, 1965; LANGVATN, 1977) was measured and, for the years 1978-1982, the mandibular and jugular distances. Measurement precision was 1 mm. In the East of Switzerland, the jugular distances were transformed into estimated mandibular distances by adding a +1 mm factor of correction. The choice of this value was based on the measurements' degree of precision (1 mm) and the average factors of correction calculated by A. KRÄMER (person. comm.) for two samples for which these two measures had been taken, that is LJL1 = LJL2 + 1.4 mm for adult males (n = 39, 1971-1977) and LIJ1 = LIJ2 + 0.5 mm for adult females (n = 170, 1971-1977).

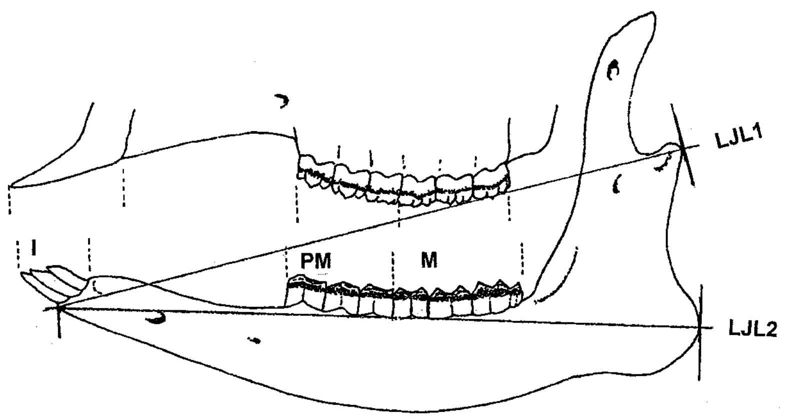

Figure 2: Lateral view of a lower jaw of a roe deer, *Capreolus capreolus*, with indication of the measured lengths: LJL1 between the infradental and articular extremities, LJL2 between the infradental extremity and the extremity of the caudal gonion. I: incisors, PM: premolars, M: molars.
Figure 2 : Vue latérale d'une mâchoire inférieure de chevreuil, *Capreolus capreolus*, montrant les longueurs mesurées : LJL1 entre les extrémités infradentale et articulaire, LJL2 entre l'extrémité infradentale et celle du gonion caudal. I : incisives, PM : prémolaires, M : molaires.

Data correction and transformation

For the data collected in the east of Switzerland, the data had to be corrected since the roe deer were shot between May and January. For fawns and yearlings linear regressions of the LJL on the date of shooting were made, and their values were corrected for a shot on October 15. Regarding the LJL in the adult class and the body mass in all age classes, the linear regressions did not show any significant variation requiring a re-calculation of the values obtained. Only the body mass values of a few bucks shot in the month of June were not used for the analysis, because the deer shot at that period of the year had been killed selectively.

The measures of body mass (kg) or length (mm) were log-tranformed since the relationship between two biometrical measures is an exponential relationship (allometric relationship of the $M = aL^b$ type where M = the body mass, L = length, a = the allometric coefficient and b = the allometric exponent).

Physical condition

Physical condition was defined as the residue of the regression of body mass on LJL (LOISON and LANGVATN, 1998). It represents the part of the body mass independent of skeleton size and may either be positive (individuals heavier than the expected value for their size), or negative (individuals lighter than the expected value for their size).

Age

Age was determined by jugular teeth wear, according to a synthesis of the descriptions by KERSCHAGL (1952), RIECK (1965), SÄGESSER (1969) and BOISAUBERT and BOUTIN (1988). For this work, we considered the determination to be reliable for the age classes of male fawns (< 1 year), yearlings (1 to 2 years) and adults (≥ 2 years). For this last class, only estimates of actual ages can be given, with a precision of +1 to 3 years (VAN LAERE *et al.*, 1989; CEDERLUND *et al*., 1992), or even a precision of 6 years or more for very old animals (HEWISON *et al.*, 1999). If all authors agree upon the unquestionable recognition of fawns, thanks to their three-cusped PM3 (BOISAUBERT and BOUTIN, 1988; VAN LAERE *et al*., 1989; HEWISON *et al*., 1999), this is not the case for the class of yearlings, for which age is often overestimated (VAN LAERE *et al*., 1989; HEWISON *et al*., 1999). Nevertheless, according to our experience, the 16- to 18-month-old yearlings differ from adults because their permanent teeth that had just appeared (PM2, PM3, M3) did not show any traces of wear. This distinction and the final distinction between three age classes, have also been proposed by LARSON and TABER (1980) for the white-tailed deer, *Odocoileus virginianus*, whose chronology of dental eruption is very similar to that of the European roe deer.

Since in the East of Switzerland, yearlings may be shot from May to December, their age could not be determined with the same reliability. Nevertheless, the method of age evaluation based on tooth wear allowed some well-trained people to determine their age classes with greater reliability than by other methods (methods of RIECK, 1965, and UECKERMANN and SCHOLTZ, 1986, based on certain criteria; cementum-ring counts used by CEDERLUND *et al*., 1992). Except for the fawn class, for which the age is correctly obtained, the yearling class represents the age class for which the tooth-wear method gives the least erroneous results (CEDERLUND *et al*., 1991), then the imprecision will increase with age and the degree of dental wear.

Roe deer density

In the Neuchâtel canton, roe deer were culled between 1980 and 1984 to reduce their population (BLANT, 1987: 10). In fact, the numbers to be shot according to the hunting plan had been increased under the pressure of the forestry services, which declared the ever-increasing damages to be the reason for this. As a consequence, their density did greatly decrease (BLANT, 1987: 27). Thus we benefited of an almost experimental manipulation of their density. Since in the other cantons no shooting plan had been applied, we only analyzed the changes in the biometric variables in reaction to the change in density in the canton of Neuchâtel. Roe deer densities were measured by drive counts on sampling areas (BLANT, 1987).

II.3. DATA ANALYSIS

First of all we estimated the animals' physical condition by adjusting a simple regression between the body mass of hunter-killed animals (dependent variable) and their LJL (independent variable). The physical condition of the individuals killed by the hunters corresponds to the residuals of this regression.

Then a global analysis of the values taken by the « indicator » parameters was carried out with the help of an analysis of variance and covariance on factors that might be variable (the factors sex, year and region). The samples from the three cantons were treated separately. An ANOVA3 procedure was carried out with the help of GLIM software (FRANCIS *et al.*, 1993). The models obtained by this software made it possible to show and interpret the effect of the variables that had been tested and recognized to have a significant influence, by excluding the disturbance effects of other factors. We used a retrieval procedure (SEARLE, 1971) whereby, first, the most complex model is adjusted to the data, then successively the higher-order interactions are tested, then the double interactions, and finally the factors' main effects. The level of significance taken into account for the comparisons of the means obtained by the models, was 0.05.

Then, the response of the studied biometric variables (body mass, LJL and physical condition) with respect to the variation in roe deer population density in the Neuchâtel canton, was analysed by adjusting a linear regression between the annual averages of the biometric variable considered and the density over these same years.

Finally, regression analyses were made for each cohort (defined as the total number of roe deer born in the same year). The only cohorts that are exactly known are those formed by the fawns (killed in year x) and the yearlings of the following year (killed in year x+1). These analyses were used to investigate whether, with respect to body mass and LJL, the low values obtained for fawns will also stay low for the yearlings the following year (hypothesis of the impossibility to catch up on delays in growth), or whether the differences observed in fawns in the beginning do no longer occur in yearlings (hypothesis that these fawns will catch up with their delayed growth). For these analyses the adults were not taken into account, because, for this age class, only an approximate evaluation of age had been made. For these last analyses on cohorts, a "Jura" sample was composed by the addition to the data from Neuchâtel, of other data from the nearby cantons of Vaud and Jura (JU) belonging to the biogeographical region of the Jura chain.

III. RESULTS

III.1. RELATION BETWEEN BODY MASS AND JAW LENGTH

Body mass and jaw length (Table II) are linked (since all P's were less than 0.0001), but this relation is particularly strong in the age class of fawns (between 37 to 52% of the variability observed in body mass is accounted for by the variations in LJL), the values of the slopes observed for these relations being close to 3 (in accordance with the allometric relation linking a measure of length with a measure of volume). This demonstrates that, in this age class,

TABLE II
Linear regression results of body mass (after log-transformation) on the lower jaw length of roe deer, *Capreolus capreolus*, killed during the hunting season in the cantons of Neuchâtel (NE) and Vaud (VD), and in the east of Switzerland (EAST-CH), in 1971-1983 and 1998. All regressions are significant at the threshold of $P < 0.0001$.

TABLEAU II
Résultats des régressions linéaires de la masse corporelle (après transformation en logarithmes) sur la longueur de la mâchoire inférieure des chevreuils, *Capreolus capreolus*, tués à la chasse dans les cantons de Neuchâtel (NE) et de Vaud (VD), et dans l'est de la Suisse (EAST-CH) de 1971 à 1983 et en 1998. Toutes les régressions sont significatives au seuil de $P < 0,0001$.

Sample			Linear regression			
Place, year	Age (year)	*n*	Constant	Slope	*r*	r^2
NE 1980-1986	< 1	211	-11.63	2.888	0.686	0.471
VD 1984-1986; 1998	< 1	161	-8.455	2.233	0.610	0.372
EAST-CH 1971-1983	< 1	298	-11.895	2.910	0.721	0.519
NE 1980-1986	1 to 2	294	-8.334	2.224	0.507	0.257
VD 1984-1986;1998	1 to 2	244	-5.624	1.678	0.427	0.183
EAST-CH 1971-1983	1 to 2	128	-3.537	1.269	0.386	0.149
NE 1980-1986	> 2	515	-5.930	1.747	0.441	0.195
VD 1984-1986;1998	> 2	492	-5.763	1.711	0.442	0.195
EAST-CH 1971-1983	> 2	400	-4.065	1.353	0.389	0.151

body mass is first of all a function of size. This relationship is not so strong in yearlings (only 15 to 26% of the variability observed in body mass is taken into account by variations in LJL). Likewise, in adults, one deviates from the expected allometric coefficient of 3, and only between 15 and 20% of the variability observed for weight is taken into account by variations in LJL.

III.2. ANALYSIS OF THE FACTORS OF VARIATION OF BIOMETRIC VARIABLES

Body mass (Table III)

In the canton of Neuchâtel, in all age classes, body mass greatly varied between years and according to sex. The maximum range of variation (between 1980 and 1986) was 2.82 kg for fawns, 2.30 kg for yearlings, and 1.38 kg for adults. Among the fawns, males were 0.63 kg heavier than the females, among the yearlings 0.78 kg and among the adults 0.93 kg.

In the canton of Vaud, body mass was significantly higher in the Alps than in the Jura (more than 1.61 kg for fawns and 1.00 kg for adults). Only the body mass of yearlings varied between years (a maximum difference of 1.68 kg between 1984 and 1998). Males were heavier than females but only among the yearlings (0.97 kg more) and the adults (1.61 kg more). Finally in the east of Switzerland, body mass of the adults only varied according to sex, the males being 0.49 kg heavier than the females.

Lower jaw length (Table III)

In the canton of Neuchâtel, the LJL of all age classes varied from one year to another. The maximum amplitude of these variations (between 1980 and 1985) was 6.98 mm in fawns, 4.53 mm (between 1980 and 1986) in yearlings, and 2.73 mm (between 1980 and 1982) in adults. Males had longer jaws than the females, *i.e.* 2.02 mm longer in fawns, but the difference obtained in adults (showing the same tendency) was just at the limit of the level of significance. In the canton of Vaud, the fawn LJL was significantly greater in the plain than in the Alps or in the Jura (a 2.32-mm maximum difference between the Plain and the Jura). The yearlings and adults in the Plain also had longer jaws than those in the Jura and the Alps (yearlings: a 2.43 mm maximum difference between the Plain and the Jura, adults: a maximum difference of 2.05 mm between the Alps and the Jura). The LJL of fawns and yearlings also varied between years (fawn: a 4.33-mm maximum difference between 1984 et 1998, yearlings: a 3.04-mm maximum difference between 1984 and 1986). The jaws of male adults were 1.63 mm longer than those of the females. Finally, in the East of Switzerland, the adult roe deer that were living in the plain had a 4.38-mm longer LJL length than those living in the Alps. It should be added that in the Alpine region only one hunting territory is concerned (Grabs *Revier* in the Saint-Gall canton) and that it is still necessary to confirm this result with data from other territories. For the yearlings, the LJL obtained in 1980 was 8.19 mm longer than the one obtained in 1979 whereas for adults, the LJL obtained in 1981 was 6.05-mm less long than the length recorded in 1973. In this region the LJL did not differ between sexes.

Physical condition (Table III)

In the canton of Neuchâtel, the physical condition varied from one year to another but only in adults (a maximum difference of 0.08 between 1985 and 1980). Among yearlings and adults, males were in better condition than females (a 0.32 difference for yearlings and a 0.04 one for adults).

In the canton of Vaud, the physical condition of fawns in the Alps was much better than in the Jura and in the Plain (a 1.88 maximum difference between the Alps and the Jura). Only among yearlings did the physical condition vary between years with extremely high values in 1985 and 1998 in comparison to 1984. Also in this canton, were males in better condition than females among yearlings (a 0.50 difference) and adults (a 0.07 one).

In the East of Switzerland, only among fawns did physical condition vary between years and with values for 1979 to 1982 that differed from those of 1971, indicating a tendency towards a decrease over this period, while all values together are showing the existence of random variations. The maximum range was 0.13. Like in other cantons, it is among the adults that the males were in better condition than the females (a difference of 0.029).

TABLE III

Results (*P* values or ns with *P* > 0.10) of analysis of variance (ANOVA) between three biometric variables measured on roe deer, *Capreolus capreolus*, of different ages killed during the hunting season in the cantons of Neuchâtel (NE, 1980-1986) and Vaud (VD, 1984-1986, 1998) as well as in the east of Switzerland (EAST-CH, 1971-1982), and three factors (year, sex and region).

TABLEAU III

Résultats (valeurs de *P* ou ns quand *P* > 0.10) des analyses de variance entre trois variables biométriques (masse corporelle, longueur de la mâchoire inférieure et condition physique) mesurées sur des chevreuils, *Capreolus capreolus*, d'âges différents (chevrillards, yearlings et adultes) tués à la chasse dans les cantons de Neuchâtel (NE, 1980-1986) et de Vaud (VD, 1984-1986, 1998) et dans l'est de la Suisse (EAST-CH, 1971-1982), et trois facteurs (année, sexe et région).

Sample (place, age of roe deer)	*P* value in variance analyses between biometric variables (MC, LJL, PC) and factors (year, sex, region)								
	Body mass (MC)			Lower jaw length (LJL)			Physical condition (PC)		
	Year	Sex	Region	Year	Sex	Région	Year	Sex	Region
NE fawns	0.002	0.019		<0.001	0.007		ns	ns	
NE yearlings	0.005	0.002		0.002	ns		ns	0.026	
NE adults	0.001	<0.001		0.019	0.063		0.002	<0.001	
VD fawns	ns	ns	0.039	0.007	ns	0.067	ns	ns	0.016
VD yearlings	0.004	0.002	ns	0.013	ns	0.002	0.017	<0.001	ns
VD adults	ns	<0.001	0.038	ns	<0.001	0.001	ns	<0.001	ns
EAST-CH fawns	ns	ns	ns	ns	ns	ns	ns	ns	ns
EAST-CH yearlings	ns	ns	ns	0.013	ns	ns	ns	ns	ns
EAST-CH adults	ns	0.047	ns	0.019	ns	<0.001	<0.001	0.022	ns

III. 3. RELATIONSHIP WITH RESPECT TO DENSITY

In the canton of Neuchâtel roe deer density dropped markedly between 1980 (density of more than 20 roe deer per 100 ha) and 1986 (less than 10 roe deer per 100 ha). As a reaction to this great variation, the body mass of fawns and yearlings of both sexes increased (Figure 3). The equations of the relations are: $y = -0.014x + 2.679$ ($r^2 = 0.565$) for male fawns $y = -0.014x + 2.620$ ($r^2 = 0.568$) for female fawns, $y = -0.008x + 2.961$ ($r^2 = 0.594$) for male yearlings and $y = -0.008x + 2.912$ ($r^2 = 0.594$) for female yearlings, where y is the logarithm of weight (in kg) and x the roe deer density (in individuals per 100 ha). Among the adults, on the contrary, no relation was detected between body mass and density.

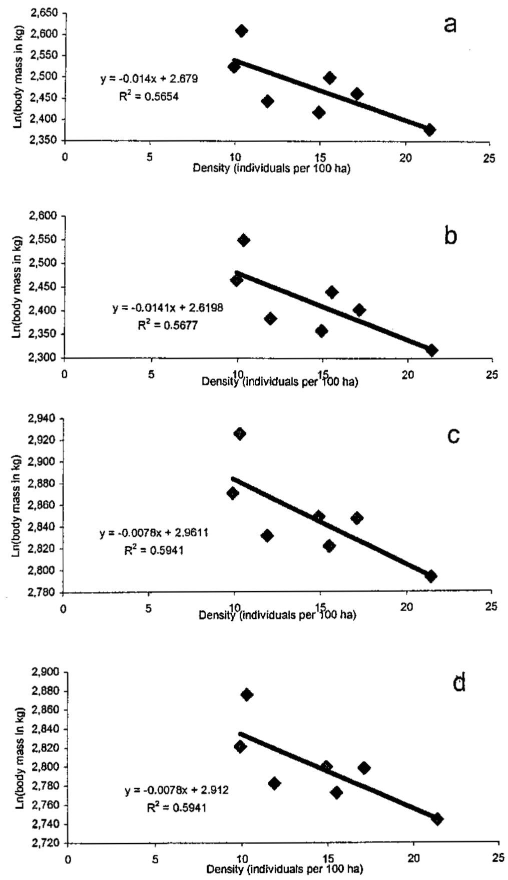

Figure 3: Linear regression of the body mass (in kg after log-transformation) of a) male fawns, b) female fawns, c) male yearlings and d) female yearlings on the density (individuals per 100 ha) of a roe deer, *Capreolus capreolus*, population in the canton of Neuchâtel, Switzerland, between 1980 and 1986.
Figure 3 : Régression linéaire de la masse corporelle (en kg après transformation en logarithmes) des a) chevrillards mâles, b) chevrillards femelles, c) yearlings mâles et d) yearlings femelles sur la densité (individus pour 100 ha) dans une population de chevreuils, *Capreolus capreolus*, du canton de Neuchâtel, Suisse, entre 1980 et 1986.

In the same way, between 1980 and 1986 the LJL increased for the roe deer fawns of each sex and the yearlings of both sexes in the absence of any sex-dependent effect (Figure 4). The equations of these relations are: y = -0.004x + 4.936 (r^2 = 0.642) for male fawns, y = -0.004x + 4.92 (r^2 = 0.642) for female fawns and y = -0.002x + 5.044 (r^2 = 0.706) for yearlings of both sexes. Like for body mass, no relation was detected between LJL and density in adults. The absence of any difference in their physical condition between years, as had been found among fawns and yearlings, is an indication that the physical condition of these age classes did not respond to the variations in roe deer density in the canton of Neuchâtel.

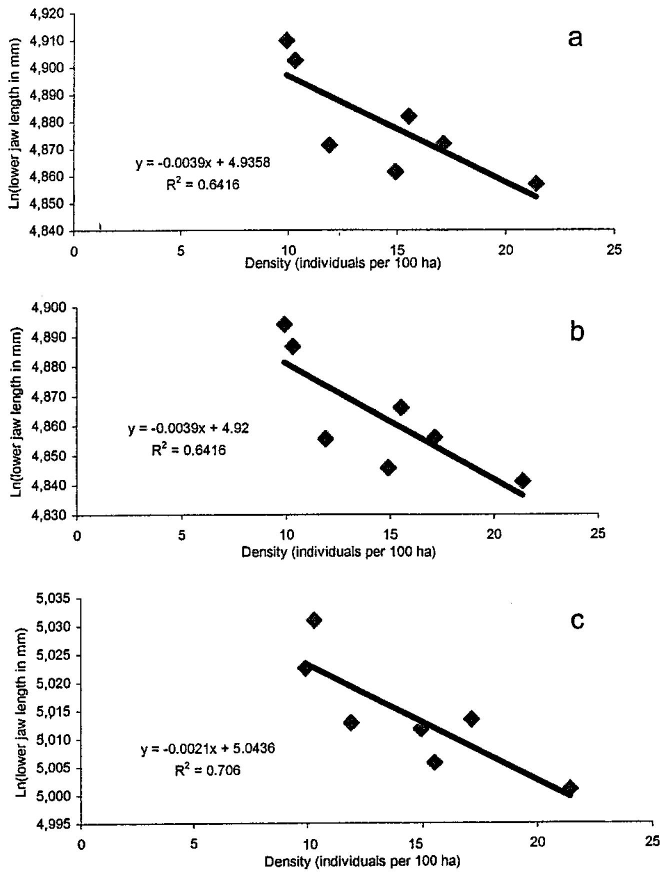

Figure 4: Linear regression of the lower jaw length (in mm after log-transformation) of a) male fawns, b) female fawns and c) male and female yearlings on the density (individuals per 100 ha) of a roe deer, *Capreolus capreolus*, population in the canton of Neuchâtel, Switzerland, between 1980 and 1986.
Figure 4 : Régression linéaire de la longueur de la mâchoire inférieure en mm après transformation en logarithmes) de a) chevrillards mâles, b) chevrillards femelles et c) yearlings mâles et femelles sur la densité (individus pour 100 ha) dans une population de chevreuils, *Capreolus capreolus*, du canton de Neuchâtel, Suisse, entre 1980 et 1986.

III.4. ANALYSIS PER COHORT

For both sexes, the regression of body mass of the yearlings killed in year (x+1) on that of the fawns killed in year x (Table IV) is significant for the sample from the Jura mountains. For each sex separately, this relation is not significant. The relation is at the limit of the level of significance for the canton of Neuchâtel alone. For the canton of Thurgovie, the regression is not significant.

In the same way, the regression of the LJL of the yearlings killed in year (x+1) on that of the fawns killed in year x (Table V) is significant for the mixed sample collected in the canton of Neuchâtel. The same relation is close to the level of significance for the data collected in the whole Jura mountain chain, while the relations for the samples of each sex were not significant. For the canton of Thurgovie, the regression is not significant.

TABLE IV
Results of the linear regressions of the body mass of roe deer, *Capreolus capreolus*, yearlings killed in year (x+1) on the one of fawns killed in year x, in the cantons of Neuchâtel (NE) and Thurgovie (TG) and in the Jura, Switzerland. The « Jura » samples contain those collected in the cantons of Neuchâtel, Vaud (VD) and Jura (JU) situated in the Jura-mountain region.
TABLE IV
Résultats des régressions linéaires de la masse corporelle des yearlings de chevreuil, *Capreolus capreolus*, tués l'année (x+1) sur celle des chevrillards tués l'année x dans les cantons de Neuchâtel (NE) et de Thurgovie (TG) et dans le Jura, Suisse. Les échantillons « Jura » regroupent ceux des cantons de Neuchâtel, de Vaud (VD) et du Jura (JU) situés dans la région de la chaîne du Jura.

Sample			Linear regression				
Place, year	Sex	*n*	Constant	Slope	*r*	r^2	*P*
NE 1980-1986	Males and females	6	10.51	0.574	0.548	0.300	0.0649
Jura (NE/VD/JU)	Males and females	10	9.028	0.687	0.568	0.323	0.0173
Jura (NE/VD/JU)	Males	10	9.203	0.690	0.505	0.255	0.1653
Jura (NE/VD/JU)	Females	10	9.6	0.617	0.641	0.411	0.0865
TG 1971-1983	Males and females	11	7.429	0.688	0.370	0.137	0.2627

TABLE V
Results of the linear regressions of the lower jaw length of roe deer, *Capreolus capreolus*, yearlings killed in year (x+1) on the one of fawns killed in year x, in the cantons of Neuchâtel (NE) and Thurgovie (TH) and in the Jura, Switzerland. The « Jura » samples contain those collected in the cantons of Neuchâtel, Vaud (VD) and Jura (JU) situated in the Jura-mountain region.
TABLEAU V
Résultats des régressions linéaires de la longueur de la mâchoire inférieure des yearlings de chevreuil, *Capreolus capreolus*, tués l'année (x+1) sur celle des chevrillards tués l'année x dans les cantons de Neuchâtel (NE) et de Thurgovie (TG) et dans le Jura, Suisse. Les échantillons « Jura » regroupent ceux des cantons de Neuchâtel, de Vaud (VD) et du Jura (JU) situés dans la région de la chaîne du Jura.

Sample			Linear regression				
Place, year	Sex	*n*	Constant	Slope	*r*	r^2	*P*
NE 1980-1986	Males and females	6	99.783	0.385	0.685	0.469	0.0139
Jura (NE/VD/JU)	Males and females	10	107.043	0.332	0.466	0.217	0.0692
Jura (NE/VD/JU)	Males	10	110.446	0.310	0.400	0.160	0.3260
Jura (NE/VD/JU)	Females	10	109.288	0.310	0.567	0.321	0.1431
TG 1971-1983	Males and females	10	48.035	0.776	0.392	0.154	0.2622

IV. DISCUSSION

IV.1. RELATION BETWEEN BODY MASS AND JAW LENGTH

As expected, there is a very strong relation between body mass and LJL in the class of roe deer fawns, which reflects the existence of differences in growth between individuals rather than differences in physical condition. In yearlings and adults, the relationship between body mass and LJL will become less close, and so may be replaced by variations in mass for a given size, generally interpreted as variations in physical condition (LOISON and LANGVATN, 1998). Variations in fat reserves could be implicated in this variation in mass for a constant size. These variations, however, are of little importance in roe deer, in comparison to other ungulates, and throughout the year body mass will stay relatively constant in the individuals of this species (HOLAND, 1992; HEWISON *et al*., 1996b; ANDERSEN *et al*., 1998). Then, factors other than fat reserves should be found: a thicker skin at higher altitudes, variable muscle mass, variable mass of other organs, etc. Variable correlations between body mass and LJL in adult roe bucks and does have also been found by EIBERLE (1965), and STUBBE and GLEICH (1990).

IV.2. VALUE OF BODY MASS AS INDICATOR

Fawn body mass is very sensitive to any increase in population density (GAILLARD *et al*., 1996, 1998; LINNELL *et al*., 1998) but is secondarily influenced by climate (BLANT, 1987; GAILLARD *et al*., 1993a; in red deer, *Cervus elaphus*: POST *et al*., 1997; LOISON and LANGVATN, 1998) and habitat quality (HEWISON, 1996; PETTORELLI *et al*., 2001). A variability in fawn body mass in autumn as a function of habitat quality, has also been shown to exist in red deer (DE CROMBRUGGHE *et al*., 1989; BIRTLES *et al*., 1998). In that case the body mass of young may be considered a good indicator of population productivity (ANDERSEN *et al*., 1998 ; BIRTLES *et al*., 1998) and was validated as a monitoring method for roe deer populations in France (GAILLARD *et al*., 1996; GROUPE CHEVREUIL, 1996). Our analysis shows that this is equally true in Switzerland.

Although used less often to monitor roe deer populations, yearling body mass also strongly reacts to variations in density. Therefore this measure could be used more often. Adult body mass, on the contrary, only reacts little to variations in density and, in the first place, seems to react to regional differences. Although in the Alps where density is low, body mass is greater (DURAND, 1992) than in the plain and Jura (BLANT *et al*., 1998) where density is higher, adult roe deer body mass variability in Switzerland rather seems to be due to climate variability (BLANT, 1987).

In the Jura mountain massif, the significant positive relationship between fawn and yearling body mass obtained indicates that a retarded growth may not be recovered. Therefore we demonstrate the existence of a cohort effect in certain years, whereby the male fawns with a low body weight correspond to the yearlings with a low body weight in the following year. In the plateaus of the East of Switzerland, such a correlation, but weaker, between fawn and yearling body mass had been found, which gives food for thought that, regarding their growth rate, a phenomenon of catch-up might exists on these plateaus. Then, one could consider this type of habitat to be the optimum one whereas the Jura habitat appears to be a rather limited one (GAILLARD *et al*., 1998). This line of argument might be taken into account to explain the difference in the breeding rates observed between Thurgovie (high and constant rate, KRÄMER, 1994) and the canton of Neuchâtel (where this rate may vary from one year to another, BLANT, 1987).

IV.3. IMPORTANCE OF LOWER JAW LENGTH AS INDICATOR

The lower jaw length (LJL) of male roe deer fawns strongly reacts to variations in population density although, secondarily, it may be influenced by climate (case of the red deer: POST *et al*., 1997), and even habitat quality (case of the red deer: DE CROMBRUGGHE *et al*., 1989). Because of the fact that sex has only little influence, this index may be used for mixed samples. Since a “region” effect cannot be excluded, the LJL should be applied within a homogeneous geographic unity.

The LJL of yearlings also reacts to density variations and only secondarily is it influenced by region. A slowdown in their growth rate due to social stress because of high population density has been demonstrated for yearling hinds in enclosures (BLANC and THERIEZ, 1998; BLANC *et al*., 1999). Since in the first two years of life the skull is essentially growing in length (HRABE and KOUBEK, 1991; ARAGON *et al*., 1997), a slowdown in length growth may be a particular tell-tale sign of density increase for the class of yearlings that are 18 months old.

The LJL of adults shows an important variability between years, with a variability of secondary importance between regions and sexes, but does not react to variations in density contrary to the results obtained for the other age classes. The LJL of adults first of all depends on environmental factors (WAHLSTRÖM and KJELLANDER, 1995; HEWISON *et al*., 1996a; ARAGON *et al*., 1998; BLANT *et al*., 1998).

In Neuchâtel, the positive relationship obtained between the LJL of roe deer fawns killed in year x and that of yearlings killed in year (x+1) shows that in the case of a delayed growth no compensatory catch-up takes place. This demonstrates the existence of a cohort effect whereby fawns with a small LJL in certain years, would correspond to yearlings with a small LJL the year after. A similar result has been reported for the red deer in Norway (POST *et al*., 1997), while here a similar tendency is observed for Thurgovie.

IV.4. PHYSICAL CONDITION AND ITS VALUE AS INDICATOR

In spite of the fact that roe deer density was greatly reduced in the canton of Neuchâtel between 1980 and 1986, for the adults no improvement of their physical condition was found. Physical condition of fawns did not vary much, probably because in this age class body mass and LJL are very closely related. Contrary to body mass or LJL, physical condition apparently does not seem to be of any practical interest for the monitoring of roe deer populations.

In yearlings and adults, sex has an influence on physical condition, which is better in males. The weight of their trophy certainly contributes to this result. Only for a few samples are year and region significant factors of variability. In our series of data the variability of their physical condition thus seems to occur only rather randomly.

V. PRATICAL CONSEQUENCES FOR THE MANAGEMENT OF ROE DEER POPULATIONS

The biometric variables “body mass and LJL of fawns and yearlings” may be used as basic data to monitor roe deer populations in a homogeneous geographic unit. Given their spatial variation only local longitudinal (over time) measurements of these indicators must be carried out (CEDERLUND *et al*., 1998). On the contrary, not all the same variables measured on adults are adapted to be used for population monitoring. The variability in body mass of the adults is, above all, an expression of the variability of the quality of the habitat (HEWISON, 1996; PUTMAN *et al*., 1996; ANDERSEN *et al*., 1998).

A yearly control of the biometric variables and the densities of two successive cohorts, *i.e.* the fawns and yearlings, should be generalized. This would allow to differentiate between the influence of climate and that of density. In fact, stochastic variations of weather are clearly shown when they appear by oscillations, one year among the fawns and the following year among the yearlings. For a population in a given habitat, one may also bring to the fore the roe deer’s capacity to compensate a slowdown in development when oscillations are noted in fawns, and not in yearlings. Then, it is possible to establish whether a habitat is optimal or limited, according to the definition given by GAILLARD *et al*. (1998). This differentiation is of major importance for their management, since it allows to know whether, in a given territory, the breeding rates are varying, or not, as a function of density and/or climate (GAILLARD *et al*., 1993b).

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UTILISATION DE VARIABLES BIOMÉTRIQUES CORPORELLES COMME INDICATEURS DES VARIATIONS DE DENSITÉ DE POPULATION DE CHEVREUILS *(CAPREOLUS CAPREOLUS)*

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MOTS-CLÉS : Chevreuil, *Capreolus capreolus*, densité, variable biométrique, masse corporelle, mâchoire inférieure, gestion, Suisse.

RÉSUMÉ

La présente étude analyse les variations de variables biométriques mesurées sur des chevreuils, Capreolus capreolus*, tués à la chasse de 1980 à 1986 dans le canton suisse de Neuchâtel, de 1984 à 1986 et en 1998 dans celui de Vaud et de 1971 à 1982 dans l'est de la Suisse (surtout canton de Thurgovie). Son but est de rechercher lesquelles permettent une mise en évidence des variations de la densité indépendamment des facteurs physiques (climat, biotope), afin d'évaluer le niveau d'équilibre entre population de chevreuils et ressources alimentaires pour la gestion de ces populations. Les indicateurs testés ont été : la masse corporelle des animaux vidés, la taille du squelette (représentée par la* *longueur de la mâchoire inférieure ou LMI) et la condition physique (mesurée par le résidu de la régression de la masse corporelle des animaux vidés sur la LMI). Trois classes d'âge (chevrillards, yearlings et adultes) ont été définies d'après l'usure des dents jugales. Pour chaque canton, l'influence des facteurs suivants sur les indicateurs a été étudiée : le sexe, l'année et la région. La masse corporelle et la LMI sont liées quelle que soit la classe d'âge, ce qui indique une convergence de ces deux indicateurs. La masse corporelle et la LMI sont influencées par le sexe (mâles plus grands et plus lourds que les femelles), l'année et la région considérés. Sur le canton de Neuchâtel entre 1980 et 1986, la masse corporelle des chevrillards, celle des yearlings, la LMI des chevrillards et celle des yearlings étaient liées à la densité de chevreuils (variation : de 10 à 20 individus pour 100 ha). Ces indicateurs peuvent donc être utilisés pour le suivi des populations de chevreuils. Pour chacun de ces indicateurs, un suivi sur le long terme est indispensable afin de distinguer l'influence du climat de celle de la densité dans l'interprétation des variations annuelles. En revanche, ni la condition physique telle que définie ici, ni les autres variables mesurées sur les adultes, ne sont utilisables pour le suivi des populations de chevreuils.*

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