

Factors determining the onset of sexual maturity in New Zealand chamois (*Rupicapra rupicapra* L.)

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Abstract

During a study on the dynamics of New Zealand chamois populations, subadult animals (less than two years) were examined for evidence of sexual maturity and reproduction. High incidence of sexual maturity in yearlings was found. This phenomenon seems to be restricted in European chamois to introduced populations found in low altitudes. Furthermore sexual maturity (gonad development, follicle maturation, ovulation) and actual reproduction (presence of embryo) was found in 7 month old females.

It could be shown, that sexual maturation within this age class in both sexes is being determined by critical body weight and daylight values, both acting as synergistic double stimuli.

Daylength, being a fixed parameter acts hereby as primary stimulus, which depends on a critical body weight for activation. Should the animal fail to reach this critical weight before the sensitive phase passes, sexual maturity is delayed for at least one year. Comparison of two regions with different plane of nutrition and final adult body size showed, that this critical body weight does not appear to be an absolute value, but seems more likely to be a specific percentage of the final adult body weight. Implications of these results for the rate of increase of populations are discussed briefly.

Introduction

The age of sexual maturity in different species of artiodactyls appears to be rather uniform; variability within one species being larger than between species. Under optimal conditions females of all Caprinae species can give birth at the age of two years. The beginning of reproduction at the age of one year, known from pronghorn antilopes (*Antilocapra americana*; MCKEAN 1954; WRIGHT and DOW 1962; MITCHELL 1967), Sika deer (*Cervus nippon*; KIDDIE 1972; CHAPMAN and HORWOOD 1968), Mule deer (*Odocoileus hemionius*; COWAN 1956), White-tailed deer (*Odocoileus virginianus*; CHEATUM and MORTON 1946; MORTON and CHEATUM 1946; CHEATUM 1942), Reindeer (*Rangifer tarandus*; KLEIN 1968) and Saiga (*Saiga tatarica*; HEPTMER et al. 1966), is less common amongst the Caprinae and seems to be confined to domesticated forms like *Ovis ammon* f. *aries* (JEWELL and GRUBB 1974) or Feral goats (*Capra aegagrus* f. *hircus*; RUDGE 1969) or breeds living in captivity. Typically, both species show high incidence of twinning when adult. In the majority of wild living populations of Caprinae however, females do not give birth before their third or fourth year of age, Alpine ibex (*Capra ibex*) may fail to bear offspring until five to six years of age (NIEVERGELT 1966). Sexual maturity in chamois is reached between the ages of 3½–4½ years (COUTOURIER 1938; SCHRÖDER 1971). The start of reproduction at the age of 1½ years, formerly believed to be confined to odd individuals (TRATZ 1957; KNAUS 1960; COUTOURIER 1938; KRÄMER 1969) was shown in later investigations to be quite common in populations of good condition. CAUGHLEY (1970) showed for New Zealand chamois from the Rangitata/Copland area, that 39 % of the yearling females gave birth for

the first time (LAMBERT and BARTHGATE 1977). In the Wanaka area the fecundity of yearling females (100%; $N = 10$) was even higher (BAUER 1982; BAUER 1983a, 1985).

European, colonizing populations of chamois show similar fecundity patterns. SALZMANN (1977), analyzing corpora albicantia from six 2½ year old females from the Swiss Jura, found that four of them had given birth previously. In the Black Forest (BAUER in prep.) and the Vosges (BAUER in prep.) it has also been observed, that a certain number of 1½ year old females may already conceive and give birth the following spring.

Consequences of the variability of sexual maturity on the rate of growth of populations are considerable. COLE (1954) and LEWONTIN (1965) pointed out, that in faster growing populations the age of sexual maturity is being reduced to the physiological minimum of the species. This phenomena to increase the growth rate of the population should be of particular importance in species which are colonizing readily under suitable conditions, however are not capable of varying their number of offspring, as is the case in chamois (BAUER in prep.). Populations living under colonizing conditions like the Wanaka chamois in New Zealand (BAUER 1982) are ideal objects for the investigation of factors determining the sexual maturity of this species and of local populations, respectively.

Material and methods

During a study, comparing the condition of colonizing (Wanaka region – high plane of nutrition, Fig. 1) and stable (Harper-Avooca region – low plane of nutrition, Fig. 1) chamois populations in New Zealand (BAUER 1977; BAUER and GOSSOW 1978; BAUER 1982, 1983a, 1983b, 1983c, 1985; BAUER and GOSSOW 1983), considerable differences were found in adult body weights, fecundity and sexual maturity. Differences in growth rates of fawns were equally high. Whereas in stable populations 10–12 months old fawns averaged 9.9 kg ($N = 15$), six to eight months old fawns of peripheral (colonizing) populations had mean body weights of 15.2 kg ($N = 40$). Equally dissimilar fecundity and maturity patterns between the populations suggested some correlation between growth rate and sexual maturity as it has been found in rats (WIDDOWSON 1968), hare (FLUX 1967), cattle (JOUBERT 1954, 1963; HANSSON 1956), roe deer (ELLENBERG 1978), and red deer (MOORE 1982). As uterus, and testis development are strongly accelerated during puberty (AMIR et al. 1968), they served as indicators of sexual maturity during the study. Gonads were taken from animals 20–120 min after their death and stored in 5% formalin. Testis were dried and weighed, after removal of the tunica albuginea, (with the epididymis). Uteri were trimmed at the cervix, dried, weighed to the nearest 0.01 g, dissected and searched for blastocysts or embryos. Mean testis weights were obtained by averaging the weights of both testes. Mean weight differences in gonads of strong/weak kids were tested with Students t-test for sig-

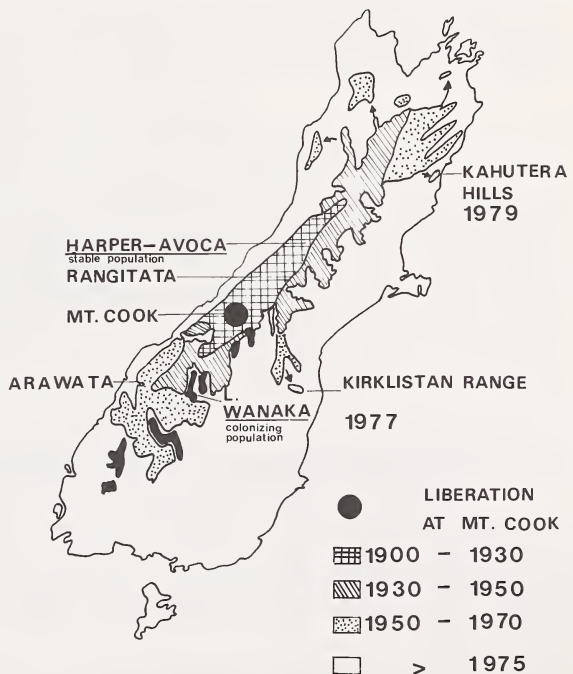


Fig. 1. Distribution and history of colonization of chamois in New Zealand (N.Z.) regions mentioned in the text are indicated. (A distribution map of the New Zealand Forest service was modified according to own observations)

nificance, assuming normal distribution. The number of examined males less than two years of age was 27, the number of females, less than two years, was 56. In both regions, high incidence of sexual maturity in yearlings was found (BAUER 1982, 1982a, 1983a, 1983b, 1985). Furthermore, sexual maturity at the age of 7 months was recorded in the Wanaka region as well as in the Rangitata/Copland region (CAUGHLEY 1970). The location of these areas is shown in Fig. 1.

As maturity at the age of 7–8 months is physiologically possible, the study on which factors determine sexual maturity in chamois, was concentrated on kids. In the Wanaka region data were collected from May–June (rut), in the Harper-Avoca region from October–February (parturition).

Results

Establishment of the hypothesis

According to the investigations of HAMMOND (1949), HAFEZ (1952) and WATSON and GAMBLE (1961), stimulation of gonad growth by diminishing daylight is only effective in animals which have reached a critical body size. Uterus growth (which is mainly stimulated by estrogen and progesterone produced by the ovaries; HEAP 1972) is fastest during puberty. Relatively faster uterus growth (in relation to body growth) shows therefore maturation of sexual organs (AMIR et al. 1968). If this also applies to chamois of the Wanaka region, New Zealand, the following testable hypotheses can be established.

1. Uterus weights of weak and strong kids should not differ significantly before a daylight stimulus becomes effective.
2. During a period of diminishing daylight, uterus weights of heavy kids should increase proportionally more to those of weak kids.

These relationships should also hold for the testis growth of male kids.

Female kids were considered as weak, if their body weights were less than 13 kg (eviscerated), they were considered as strong, if they exceeded 15 kg. The corresponding weight classification in male kids was 13.5 and 15.5 kg, respectively.

Testing of the hypothesis

Sexual maturation in female kids from the Wanaka region

The average weights of female kids between the two sampling dates (18. 5. and 24. 7.) increased by 7 % and the uterus weights by 30 % (Tab. 1). Although both increases are not significant, the proportionally larger increase of the gonads during this period, indicates that already in their first year gonads mature during the rut. Plotting uterus weights against body weights of female kids (N = 18), shows a rather high linear correlation which holds especially well within weight ranges of 12–16 kg. From 16 kg onwards, the uterus growth seems to be accelerated (Fig. 2).

Table 1

Body weight and uterus weight increase of chamois kids (absolute and relative) in the Wanaka region, New Zealand, between the 18. 5. 1977 and the 24. 7. 1977 (N = 17)

	N	18.5	N	24.7	Increase (%)
Body weight (kg)	9	15.2 ± 1.64	8	16.1 ± 0.7*	+ 7
Uterus weight (g)	8	3.09 ± 0.68	5	4.00 ± 1.28**	+30
* Differences in body weights not significant. ** Differences in uterus weights: FG = 11, t = 1.91, p < 0.10					

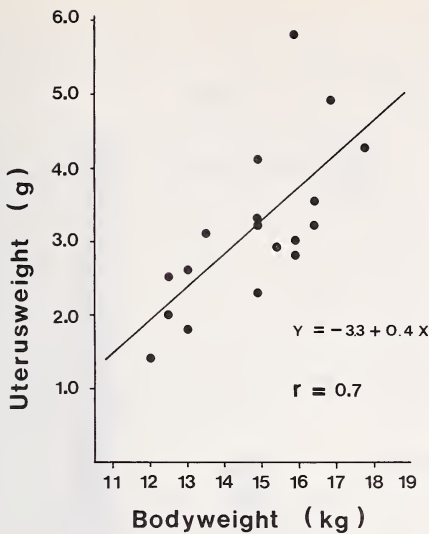


Fig. 2. Uterus weights of 7 month old chamois kids ($N = 18$) which have not yet ovulated, in the Wanaka region, (N.Z.), as a function of body weight ($y = -3.3 + 0.4x$; $r = 0.70$)

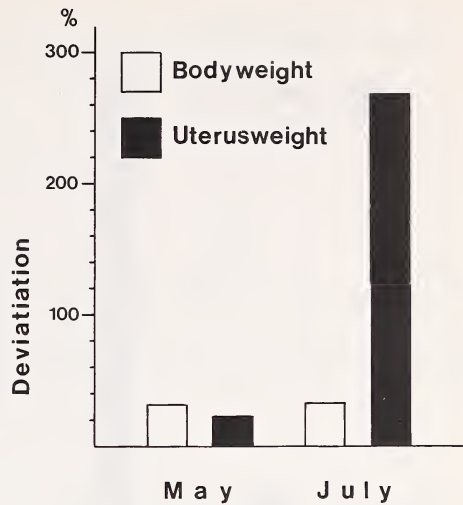


Fig. 3. Mean body weight (kg) and mean uterus weight (g) of strong chamois kids (≥ 15 kg) in the Wanaka region, N. Z. in May/July, expressed as positive deviation (%) from the mean body weight (uterus weight) of weak kids (< 13 kg), ($N = 13$)

Table 2

Mean uterus weights and mean body weights of female chamois kids from the Wanaka region, New Zealand ($N = 13$)

		Weak kids			Strong kids			
		N	Body weight (kg)	Uterus weight (g)	N	Body weight (kg)	Uterus weight (g)	
			mean $\pm$ SD	mean $\pm$ SD		mean $\pm$ SD	mean $\pm$ SD	
May	A	3	13.0 $\pm$ 0.5	2.73 $\pm$ 0.32	B	4	16.5 $\pm$ 0.9	3.30 $\pm$ 0.53
July	C	3	12.5 $\pm$ 0.5	1.73 $\pm$ 0.31	D	3	16.4 $\pm$ 0.5	4.63 $\pm$ 1.32

In Tab. 2 average body weights and uterus weights in May and July are shown. Despite small sample size ($N = 13$) differences in weight proportions of uteri and body weights of weak and strong kids (Tab. 2) are evident in July ($FG = 4$, $t = 3.02$, $p < 0.05$), whereas in May, strong and weak kids do not differ ($FG = 5$, $t = 1.49$, not significant). Whereas the gonads of weak kids decrease between May and July significantly by about 40% ($FG = 4$, $t = 3.16$, $p < 0.05$), the gonads of strong kids increase during the rut by 40% ($FG = 5$, $t = 1.23$, not significant). The relative deviations (positive) of uterus weights (g) and body weights (kg) of strong kids and those of weak kids are comparable in May, whereas in July the relative deviation of uterus weights exceeds by far the deviation in body weights (Fig. 3).

Sexual maturation in male kids from the Wanaka region

The development of testis weights of male kids is consistent with the previous findings in females. The growth acceleration between the first period of decreasing daylength between May and July is distinct (Fig. 4). Whereas body weight increases only slightly (12%), the



Fig. 4. Relative increase (%) in body weights and testis weights of male kids of the Wanaka region, N. Z. between the 15.-20. May and 10.-25. July (N = 10)

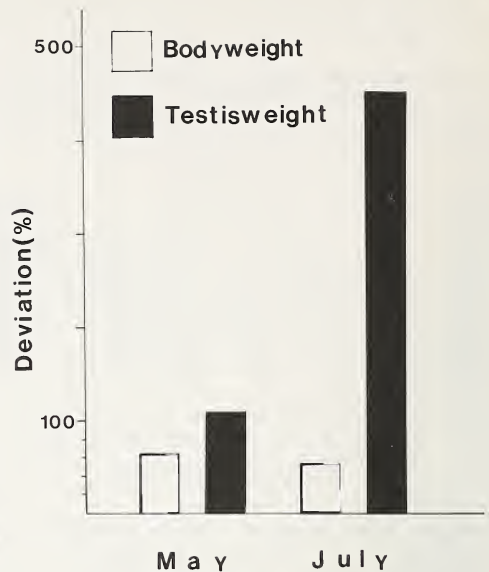


Fig. 5. Mean body weight (kg) and mean testis weight (g) of strong (≥ 15.5 kg) chamois kids of the Wanaka area N. Z. in May and July, expressed as percentual deviation from mean body weights (testis weights) of weak kids (≤ 13.5 kg). (N = 14)

increase in testis weight is very high (544 %). Here, a differentiation of gonad development in contrast to body weight growth is evident, too.

Differences in growth acceleration of the testis between weak and strong kids indicate, that stimulation of testis development is dependent on a critical body weight. Fig. 5 shows the relative deviation of body and testis weights in May and July of strong kids from the respective weights in weak kids.

Sexual maturation in juvenile females from the Harper-Avoca region

In female kids of the Harper-Avoca region there is no evidence of accelerated uterus development or follicle maturation at the age of 12–15 months. However 43 % (N = 7) of 24–27 months old females had given birth and must therefore have conceived as yearlings. The weights of nine 22–36 month old females averaged only 13.3 ± 3.1 kg.

Sexual maturation in juvenile males from the Harper-Avoca region

Males show also very low weights as kids and yearlings. Four 12–15 month old males weighed on the average 11.6 ± 1.7 kg. The largest yearlings shot had testis weights of 2.3 ± 0.43 g (N = 3). The mean testis weight of four male kids weighing 9 kg was 1.34 g. Accelerated testis development between November and February was found in all age classes but was highest in yearlings (Tab. 3). Whereas testis weights of yearlings increased significantly (+ 414 %) in this time period (FG = 5, $t = 2.99$, $p < 0.05$), increase in other animals is less pronounced. Testis weight of yearlings in November differed highly

Table 3

Mean average testes weights of different chamois age classes from the Harper-Avoca region in November and May (N = 17)

Age	N	November		N	February		Increase (%)
		Mean $\pm$ SD	testis weight (g)		Mean $\pm$ SD	testis weight (g)	
1	4	2.1	0.60	3	10.8	4.10	414
2	1	8.0		2	16.8	4.63	110
3	4	13.1	2.34	3	20.3	5.91	55

significantly from respective weights of adult males (FG = 6, $t = 8.14$, $p < 0.001$). In February however, the testis weights of yearlings did not differ significantly from the testis weights of older animals.

Discussion

The differences in uterus weights between sexually immature kids (mean uterus weight 3.13 ± 1.06 g, N = 18), one ovulating (uterus weight: 18 g) and one pregnant kid (uterus weight: 50 g, at gestation period of about 30 days) are due to the role of hormones activated during sexual maturation. Uterus growth, stimulated by estrogen and to a smaller extent progesterone, is due to the highly increased production of theca cells in the ovaries. This can lead to pronounced uterus growth during the course of a few days (HEAP 1972). In the case of female chamois kids of the Wanaka region this suggests that sexual maturity and successive pregnancy is not only due to overproportionally developed uteri of few animals. Other animals with comparable body weights might have reached sexual maturity as well, possibly only several days later. This possibility is further suggested by the incidence of mature graafian follicles in the ovaries of most strong kids. Similarly, further evidence for weight and daylight dependant sexual maturation is found in male kids. The heaviest male kid which was shot, weighed 19.7 kg and was shot in May. Although its mean testis weight of 2.7 g exceeded the mean testis weight of weaker animals (mean body weight: 12.15 ± 1.2 kg; N = 4), shot at the same time (mean testis weight: 1.3 ± 0.55 g; N = 4), the difference is not great, which might suggest, that body weight itself could not stimulate testis growth, but that another stimulus (daylength?!) was necessary. No evidence of sexual maturation of male and female kids (11–13 months) of the Harper-Avoca region was found. This is not surprising as kids gain weight during their first year of life continuously (SCHRÖDER 1971) and it is highly improbable that any of these animals reached a body weight of more than 12 kg by the age of 6–8 months (rut). As expected, testis weights of 12 month old animals from the Harper-Avoca region do not show any differences to testis weights of Wanaka kids before puberty.

This critical weight seems to be equally important for sexual maturation in $1\frac{1}{2}$ year old males. As in the Wanaka region all 18 months old males are well above this limit (21.4 kg, N = 11), weight as critical factor for the development of testis is not crucial.

In Harper-Avoca animals, however, variation around this critical weight indicates further delay of sexual maturation in some animals. Whereas yearlings within the range of the critical weight show strong acceleration of testis growth (mean testis weight = 14.6 g), one weak animal, shot in February showed much less developed testes (6.4 g). Although chamois of the Harper-Avoca region do not reach 15 kg at their second period of sensitivity to diminishing daylight conditions, they do become sexually mature.

This is less surprising, if adult body size is being considered. Whereas adult males and females of the Wanaka region weigh on the average 24–29 kg, Harper-Avoca animals weigh

between 13–20 kg (BAUER 1982a). If body size at the time when all (Wanaka) or two thirds (Harper-Avoca) of the animals reach sexual maturity (18 months) is expressed as the fraction of body weight in comparison to adult animals, values of 0.90 for Wanaka animals and 0.74 for Harper-Avoca animals can be determined.

SADLER (1969) assumes that four main factors influence or determine sexual maturation in mammals. These are nutrition, temperature, population density and light regime. Temperature, nutrition and population density (the latter does not only increase intraspecific competition for food, but also causes stress induced endocrine changes which influence puberty; CHITTY 1962; CHRISTIAN 1956) having effect upon puberty mainly by changes in growth rate (FLUX 1967; AMIR et al. 1968; JOUBERT 1954; 1963; HAMMOND 1949; HANSSON 1956; DAVIS 1951; MOUSTGAARD 1959).

Experimental research on domesticated species of ungulates shows, that although final adult size seems to be genetically fixed (GALL 1969, HANSSON 1956), rate of growth (HANSSON 1956) and sexual maturity (REID 1960) are determined by the plane of nutrition. Whereas in cattle (HANSSON 1956, JOUBERT 1954, 1963), as well as in hare (FLUX 1967) or in rats (DAVIS 1951, 1953); WIDDOWSON 1968) a strong correlation between nutrition, growth rate and body size on the one hand, and sexual maturity on the other hand, was observed, similar experiments in sheep show somewhat inconclusive results (HAMMOND 1949), although THOMSON and AITKEN (1959) found cues, that food supply during winter influenced fertility of female sheep. High plane of nutrition increases the relative number of breeding females at 1½ years of age, as has been shown in thar (CAUGHLEY 1970), chamois (BAUER 1982, 1983, 1985), red deer (ALBON et al. 1983; MOORE 1982), white-tailed deer (CHEATUM and MORTON 1946) or roe deer (ELLENBERG 1978). A protein as well as phosphorous deficient diet is also known to delay sexual maturity (MOUSTGAARD 1959; NEHRING 1972).

The influence of the light regime on the time of ovulation in mammals is described by several authors (HAMMOND J. 1944; CAUGHLEY 1971; HART 1950; Marshall 1937) and seems to be of major importance to the onset of puberty, at least in sheep (HAMMOND J. 1944; WATSON and GAMBLE 1961; SADLER 1969) and in Whitetailed deer (BUDDE 1983).

Analysis of chamois, presumably living under optimal conditions in the Wanaka area, New Zealand, show, that the physiological minimum of sexual maturity of this species is six months. This seems to apply for both sexes. The onset of sexual maturity being determined by critical body weight and daylength values, both acting as synergistic double stimuli.

Daylength, being a fixed parameter acts hereby as primary stimulus, which is dependent on a critical body weight for activation. Should the animal fail to reach this critical weight, before this sensitive phase passes, sexual maturity is delayed for at least one year.

Results from the Wanaka and Harper-Avoca regions further suggest, that this critical body weight, required to reach sexual maturity, differs between populations.

Whereas it could be seen that sexual maturation is physiologically possible at a very early age, there are few studies which allow estimation of actual reproductive success of age classes, which have not reached their final body size and are socially immature. Reproductive success of male immature animals is mainly affected by dominance relationships to other males. In the absence of older males or within populations of imbalanced sex ratio however, even yearling males of 2½ year old males can participate substantially at reproduction as has been shown in chamois (BAUER, in prep.) and roe deer (BAUER et al. in prep.).

Reduced reproductive success in very young females will be due to physiological as well as behavioural and social factors. The size of the birth channel will not be optimal in not fully grown females, leading to birth complications as has been suggested in mountain sheep (GEIST 1971) and observed in chamois yearling females (BAUER in prep.). Appropriate behavioural responses to the newborn offspring will affect survival of the young. This

has been shown in roe deer (KURT 1968; ELLENBERG 1978) and red deer (CLUTTON-BROCK et al. 1982). Actual contribution of females reproducing for the first time, to the rate of increase of a population will therefore be substantially lower as expected.

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Zusammenfassung

Geschlechtsreifebestimmende Faktoren bei neuseeländischen Gamsen (Rupicapra rupicapra L.)

Im Verlauf einer Studie zur Dynamik neuseeländischer Gamsenpopulationen wurden die Gonaden von 27 männlichen und 56 weiblichen subadulten (weniger als zwei Jahre) Tieren auf Geschlechtsreife bzw. Fortpflanzung untersucht. Innerhalb beider Vergleichspopulationen wurde ein hoher Anteil geschlechtsreifer Tiere innerhalb dieser Altersgruppe festgestellt. Dieses Phänomen scheint bei europäischen Gamsen nahezu ausschließlich bei Populationen in Mittelgebirgen nach Einbürgerungen aufzutreten.

Weiterhin jedoch wurde in Neuseeland bei Gamsen, die ein neues Areal kolonisierten, Geschlechtsreife (Follikelreifung, Gelbkörperentwicklung) bei sieben Monate alten weiblichen Kitzen festgestellt. Nicht nur Geschlechtsreife, sondern auch tatsächliche Fortpflanzung (Embryo) konnte weiterhin bei einer Kitzgeiß nachgewiesen werden. Es konnte gezeigt werden, daß innerhalb der Kitzaltersklasse sexuelle Reifung in beiden Geschlechtern sowohl durch ein kritisches Körpergewicht als auch durch bestimmte Tageslängenwerte eingeleitet wird. Hierbei wirken beide als synergistische Stimulanten. Tageslänge, als unabhängiger Parameter, wirkt hierbei als Primärauslöser, der jedoch der Erreichung eines kritischen Körpergewichts zur Aktivierung bedarf. Erreicht ein Kitz dieses kritische Gewicht nicht, bevor die sensitive Lichtphase vorüber ist, wird der Eintritt der Geschlechtsreife wenigstens für ein Jahr verschoben. Der Vergleich zweier Regionen mit unterschiedlichen Ernährungsgrundlagen, Wachstumsraten und Körpergrößen der adulten Tiere zeigte, daß dieses Schwellengewicht keinen absoluten artspezifischen Wert darstellt. Vielmehr scheint er mit den Wuchsverhältnissen jeweiliger Populationen in Zusammenhang zu stehen. Schlußfolgerungen dieser Ergebnisse für die Soziobiologie der Gamsen werden kurz besprochen.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Hair brush organs in Viscachas, *Lagostomus maximus*

By I. RIEGER and DORIS WALZTHÖNY

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Viscachas are rare zoo animals and not of great economic importance. This is probably one of the main reasons why the amount of scientific data of the species is rather small. Only four zoos in the world are breeding this species (OLNEY 1982). Recently, the Zurich Zoo viscacha females started to abandon their offspring. Therefore, the head keeper of the Small Mammals Section, Mr. HEINZ KOHLER, was obliged to hand-raise them.

Viscachas of all ages have a rather unexpected and striking morphology of their hind feet: the dorso-medial fleshy part of the longest, i.e. second toe is, compared to the

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