Harcourt, A. H.; Stewart, K. J. (1978): Sexual behaviour of wild mountain gorillas. In: Recent advances in primatology Vol. 1. Ed by D. J. Chivers and J. Herberts. London: Academic Press. 611–612.
Harcourt, A. H.; Stewart, K. J.; Fossey, D. (1981): Gorilla reproduction in the wild. In: Reproductive biology of the great apes. Ed. by C. E. Graham. New York: Academic Press. 265–279.
Hess, J. P. (1973): Some observations on the sexual behaviour of captive lowland gorillas. In: Comparative ecology and behaviour of primates. Ed. by. R. P. Michael and J. H. Crook. London, New York: Academic Press. 507–581.
Hoff, M. P.; Nadler, R. D.; Maple, T. L. (1982): Control role of an adult male in a captive group of lowland gorillas. Folia Primatol. **38,** 72–85.
Johnstone-Scott, R. (1979): Notes on mother-rearing in the Western lowland gorilla. Int. Zoo News **26,** No. 161, 9–20.
Jongh, T. de (1978): Sociaal gedrag van vijf laaglandgorilla's in dierenpark Wassenaar. Doctoraalverslag, Univ. Utrecht und Leiden (unveröff.).
Keiter, M. D.; Pichette, L. P. (1979): Reproductive behavior of captive subadult lowland gorillas *(Gorilla g. gorilla).* Zool. Garten **49,** 215–237.
Kirchshofer, R. (1982): Internationales Register und Zuchtbuch für den Gorilla. Teil 3: 1. 1. 1977–31. 12. 1979. Zoologischer Garten Frankfurt/Main.
Maple, T.; Hoff, M. P. (1981): Gorilla behavior. New York: Van Nostrand Reinhold.
Meder, A. (1982): Untersuchungen zum sozialen Verhalten in einer Gruppe von Flachlandgorillas mit Schwerpunkt auf dem Grad sozialer Integration handaufgezogener Tiere. Diplomarbeit, Univ. Heidelberg, unveröff.
Nadler, R. D. (1974): Periparturitional behavior of a primiparous lowland gorilla. Primates **15,** 55–73.
— (1976): Sexual behavior of captive lowland gorillas. Archives Sex. Behav. **5,** 487–502.
— (1980): Reproductive physiology and behavior of gorillas. J. Reprod. Fert. Suppl. **28,** 79–89.
— (1982): Laboratory research on sexual behavior and reproduction of gorillas and orang-utans. Amer. J. Primatol. Suppl. **1,** 57–66.
Rowell, T. E.; Hinde, R. A. (1963): Responses of rhesus monkeys to mildly stressful situations. Anim. Behav. **11,** 235–243.
Schaller, G. B. (1963): The mountain gorilla. Chicago: Chicago Univ. Press.
Scherpner, C. (1975): Umgestaltung und Erweiterung des Menschenaffenhauses im Zoo Frankfurt/Main. Zool. Garten **45,** 168–174.
Siegel, S. (1956): Non-parametric statistics for the behavioral sciences. New York: McGraw-Hill.
Southwick, C. H. (1967): An experimental study of intragroup agonistic behavior in rhesus monkeys. Behaviour **28,** 182–209.

Anschrift der Verfasserin: Dipl.-Biol. Angela Meder, Peter-Böhm-Str. 47, D-6904 Eppelheim

Seasonal changes in the condition of Rabbits, *Oryctolagus cuniculus* (L.), in a coastal sand dune habitat

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Receipt of Ms. 8. 5. 1985

Abstract

Studied the condition of a wild rabbit population to assess whether it has reached the carrying capacity of its area. Therefore age and condition of rabbits shot from September to March, in 1977 through 1981, is determined from eye-lens weight, body weight and kidney fat. Rabbits older than one year (adults) could be separated from rabbits aged less than one year (juveniles) by eye-lens weight. Both kidney-fat weight and body weight were highly correlated with total fat content and with each other.

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Z. Säugetierkunde 51 (1986) 26–36

ISSN 0044-3468

There were no significant differences in body weight nor detectable differences in autumn or winter mortality between sexes. The overall sex ratio (♂ : ♀) was 1.14.

Adults were heavier and had larger fat reserves than juveniles. In every winter they suffered less mortality. Only in a very severe winter did weight loss together with starvation occur. Juveniles suffered more from starvation than adults. After a winter like that the population did not reach the limit set by the food resources of the area.

Introduction

Rabbits (*Oryctolagus cuniculus* L.) have been living in the Dutch coastal dunes since the 13th century (Rentenaar 1978). Their numbers were diminished by myxomatosis during 1955–58, but now the population has recovered and rabbits are abundant in a large part of the area. The sand dunes protect the low-lying country behind them from the sea. For this reason there is popular concern about the possibility that rabbits may cause erosion by burrowing or overgrazing. In this context, it is important to determine whether the rabbit population has reached the carrying capacity of the vegetation.

Wintertime seems to be the most difficult period for rabbits to get an adequate amount of good quality food. The 'duinmeiers', who used to make their living by catching and selling wild rabbits' (like the British 'warreners'), supplemented the rabbits' diet with hay in winters with much snow (Rentenaar 1978). Since the winter season seems crucial for the rabbits' survival, I studied the condition of rabbits in this season.

Whether the population has reached the limit of available food, where the survival of individuals and the growth of the population become impaired by food shortage, would be indicated by the animals' condition at this time.

It has been established that the condition of individuals is related to population dynamics. Myers and Poole (1963) as well as Gibb et al. (1978) found a positive correlation between body weight and the probability of survival in wild rabbits. Vaughan and Keith (1978) found the same correlation in another Lagomorph, the Snowshoe hare *(Lepus americanus)*.

Caughley (1970) and Martin (1977) considered the level of fat reserves as an indicator of an animal's well-being, its general state of nutrition and the favourability of its environment. They demonstrated a positive correlation between the level of fat reserves and the rate of increase of a population, while Batzli and Pitelka (1971) found a positive relation between low fat reserves and population decline.

These relations are useful in comparing animals in a single environment, although Malpas (1981) and Millar (1981), who studied African elephants *(Loxodonta africana)* and whitefooted mice *(Peromyscus leucopus)* respectively, warned that the relation between fat reserves and the well-being of an animal should be used with care when comparing individuals of populations living in different environments. The deposition of fat is an adaptation of the animal to the variability of the environment: in an environment with little variation only small reserves are formed, while large fat reserves are advantageous when foraging conditions are uncertain.

As fat deposition and body weight are influenced by age and sex (Martin 1977) body weight, fat reserves, age, and sex all had to be considered in this study.

Material and methods

This study was done in 'het Noord-Hollands Duinreservaat' (N-H D), a 4765 ha coastal dune area northwest of Amsterdam, which is used as a catchment area and managed by the provincial water company 'het Provinciaal Waterleidingbedrijf Noord-Holland' (PWN). In order to control the rabbit population, the PWN has appointed game wardens to shoot rabbits from August till December, and sometimes until March. The average hunting pressure is 1,1 rabbit per hectare per year.

Changes in body weight were studied from rabbits bagged in this way. It seems probable that there is some bias in the material, but since no data could be collected in another way, it is impossible to characterize or correct for this bias. It is assumed, however, that the direction and extent of the bias is constant throughout the season and in different years.

Altogether 2024 rabbits, shot in a selected area of ca. 1000 ha over four years, were studied. The length of the sampling period depended on the management policy of the PWN.

In the season 1980–81, 191 rabbits were collected more systematically by shooting every two weeks from August to December and every three weeks from January till March in a smaller part of the study area ('Vogelduin').

The game wardens use two methods of hunting. From August until the middle of November they customarily hunt at night, and from then until the end of the season they hunt in the daytime. When hunting at night, they use lights mounted on their guns to spot the rabbits. In the daytime, they or their dogs flush the rabbits from above-ground hiding places.

Possible differences in the data collected through these two methods were checked by comparing the results of hunts that were near to each other in time.

Sex, age and body weight were assessed. Age was determined from eye-lens weight, which has been shown to be a reliable measure of age till the age of 24 months (Myers and Gilbert 1968). The fresh lens was kept in 10 % formol for three weeks, dried at 80 °C for a week and weighed on a Mettler electronic balance to 10 mg.

Body weight was measured to 10 g. Because the variation in body size was small, a correction for body size was not considered necessary.

From the 'Vogelduin' samples kidney fat (= abdominal fat deposit) and stage of moulting were also determined. These measures depend on Martin's (1977) observation that 'the abdominal fat index appears to be a consistent measure of relative changes in fast reserves in rabbits'. Kidney fat was taken as the total fat deposit which lies in the abdominal cavity, after removing mesenteric fat and fat adhering to testes. Since moulting could influence body weight, the time of moulting was assessed by noting how many rabbits in a sample had broad black patches or stripes on the inner side of the fur.

From a sample of 12 rabbits the relation between body weight, kidney fat, and total body fat was examined. Total body fat was determined by extraction of all fat from the dried carcass with petroleum ether in a Soxhlet apparatus.

Results

Sex ratio

The effects of daytime and nighttime hunting on the sample were evaluated by comparing the results of the two kinds of hunt that took place close together in time.

With regard to sex ratio, age class distribution and mean body weight, no consistent difference was found between samples from the same period taken with different methods. Consequently the data from both hunting methods are pooled.

The overall sex ratio (♂ : ♀) was 1,14. Comparing Aug. + Sept. + Oct. to Jan. + Feb. + March of all years together there is no change in the ratio.

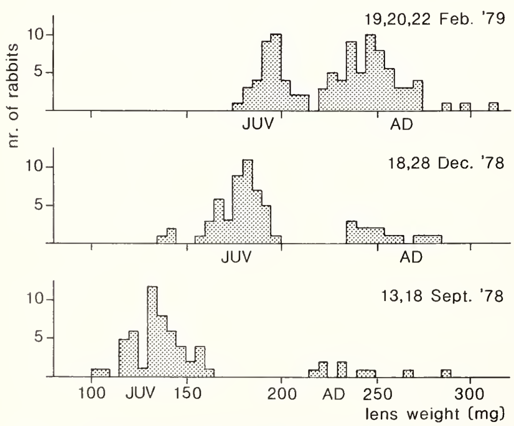

Fig. 1. Frequency distribution of eye-lens weight in a few samples from 1978–1979

Age classes

Fig. 1 gives the frequency distribution of eye-lens weights for a few dates in 1978–79. There are two distinct age groups recognizable: juveniles, less than one year old, and adults, more than one year old, separated by a gap caused by the pause in reproduction from August to February. From this graph the discriminating lens weight for the different months is derived.

Table 1 shows how the percentage of adults in the game bagged

Tabelle 1

Percentage adults in sample

Month	1978–1979		1980–1981	
	n	% ad.	n	% ad.
Aug.	–		153	14
Sept.	93	12	103	13
Oct.	45	18	48	21
Nov.	72	35	102	27
Dec.	95	24	84	31
Jan.	16	64	19	47
Feb.	170	60	11	27
March	–		8	63

Aug. + Sept. + Oct. vs. Jan. + Feb. + March 1978–79: $\chi^2 = 81$ $p < 0.001$
1980–81: $\chi^2 = 23$ $p < 0.001$

increase during the course of the season. This indicates a higher mortality among juveniles than in adults. The highest percentage of adults is found in winter 1979.

Fat reserves

Table 2 gives the total fat content of the carcass and two other parameters frequently used to determine fat reserves: kidney fat (KF) and body weight (BW). Both these parameters have a high positive correlation with total body fat (TBF).

Tabelle 2

The relation between total body fat (g), kidney fat (g) and body weight (g)
n = 12

Sex	Age	Month	Total body fat	Kidney fat	Body weight
♀	juv	Oct.	2	0	1320
♀	juv	Oct.	7	0	1240
♂	juv	Jan.	6	0	1250
♂	juv	Jan.	41	2	1400
♂	juv	Jan.	95	17	1500
♂	juv	Jan.	61	11	1450
♂	ad	Jan.	87	8	1630
♂	ad	Jan.	141	46	1760
♀	ad	Jan.	88	11	1600
♀	ad	March	90	18	1550
♀	ad	March	80	19	1600
♀	ad	March	91	14	1610

Body weight and total body fat are linearly related as follows:

$$BW = 1270 + 3.4\ TBF,\ n = 12,\ r = 0.90.$$

This means that after reaching a body weight of 1270 g, 1.0/3.4, i.e. about 1/3 of the additional weight increase is laid down as fat.

The relation between TBF and KF is best expressed as a logaritmic function:

$$TBF = 7 + 31 \ln (KF),\ n = 12,\ r = 0.96.$$

As overall body weight increases, the kidney fat deposit becomes an ever greater part of the fat reserves.

In Fig. 2 the relation is shown between the total body weight and the amount of kidney fat for the rabbits from the 'Vogelduin' sample.

The mean weight of the kidney fat in adults was 21 + 2 g (n = 33) in juveniles 7 + 1 g (n = 147).

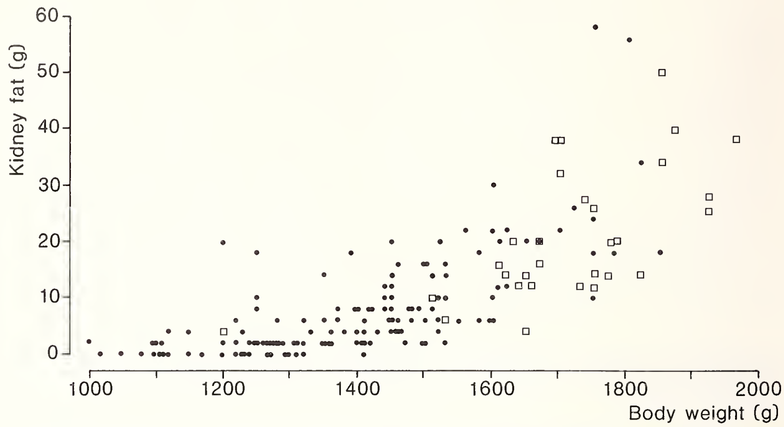

Fig. 2. Kidney fat weight in relation to body weight. 'Vogelduin' sample, 1980–1981. Legend: □ = adults ; ● = juveniles

In Jan.–March ♀♀ deposit slightly more fat than ♂♂. Mean body weight of ♀♀ in Jan.–March is 1500 ± 50 g, of ♂♂ : 1530 ± 40 g, while mean weight of the kidney fat was for ♀♀ : 20 ± 3 g and for ♂♂ : 11 ± 2 g.

Body weight

♂♂ and ♀♀

To analyze whether ♂♂ and ♀♀ differ in the ralation of body weight to age the regression of body weight on lens weight is calculated. The regression of body weight (g) on lens weight (mg) is (with 90 % confidence limits):

$$BW = 802 + 3.5 \text{ lens} \qquad n = 153 \quad r = 0.97$$

For ♂♂ only:

$$BW = 802 + 3.6 \text{ lens} \qquad n = 79 \quad r = 0.98$$

This indicates that the group of ♂♂ can be considered a sample from a statistically identical population. In the following calculations the data from the two sexes are pooled.

Fig. 3 gives the relation between body weight and lens weight for the juveniles bagged in 1980–81. The amount of scattering increases with lens weight. If one calculates a linear regression the standard error of estimate (145 g) is about the same size as the SD of 11 % given by Myers and Gilbert (1968) for the estimation of age from eye-lens weight.

Nonetheless the concentration of values on the top-left side in the scattergram suggests maximal growth, while the zone on the lower right suggests impaired survival. I hypothesize that the curve represents the optimal growth. This curve seems to be logistic in shape. The formula is:

$$BW = 1900 / 1 + e\ (0.28\text{–}0.0068 * \text{Lens}),\ n = 82,\ r = 0.81.$$

Rabbits below this weight are in suboptimal condition. Individuals from both autumn and winter are found below the curve.

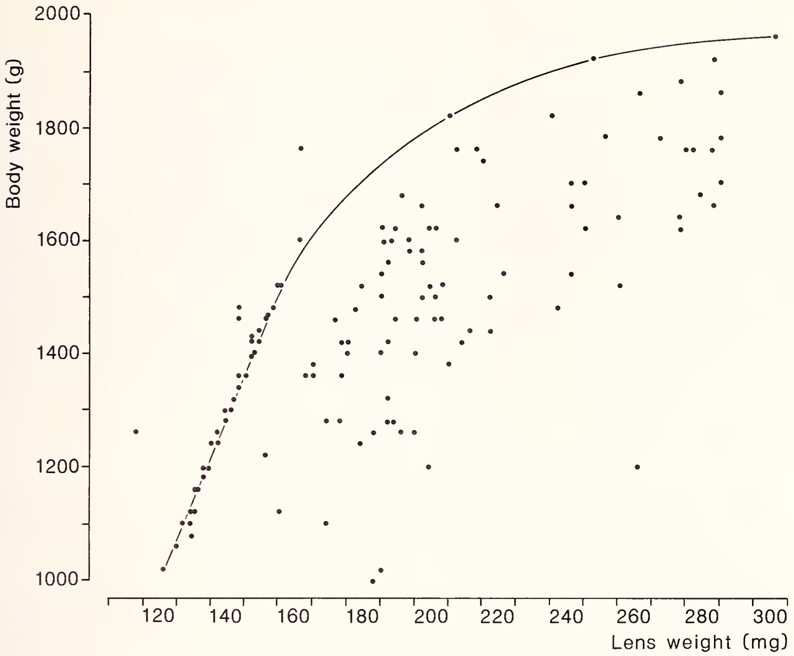

Fig. 3. Body weight in relation to eye-lens weight. 'Vogelduin' sample, 1980–1981, juveniles only

Trend during the season

Fig. 4 shows the mean body weight of adult and juvenile rabbits in the game bagged during the hunting season of 1977–81. To reach sample sizes of at least 5, sometimes results from hunts are combined and represented by a weighted mean.

The average weight of the adults is consistently higher than that of the juveniles. Between the mean weight of the juveniles in February and that of the adults in September there is a difference of ca. 300 g, which indicates a weight increase in spring and summer.

It is impossible to calculate this more precisely, as the composition of the adult age class is not known and may vary from year to year.

Fig. 5 gives an example of the distribution of the weights on a few hunts. It is clear that there is a considerable overlap in weights of adults and juveniles as determined by lens weight, and that weight can not be used as a reliable indicator of age. The overlap becomes larger during the season.

The adults show a weight decrease during the season in two out of four years (fig. 4).

For the juvenile age class there is a general increase in body weight until December, but growth is interfered with by the winter. To separate the simultaneous effects of aging and time, the partial correlations of these two factors with body weight are calculated (see table 3). The results show that in juveniles growth is adversely affected by the progress of time, i.e. by the winter season, even in the favourable circumstances of 1981.

Moulting takes place mainly in September and October. In November only 2 out of 24 rabbits showed signs of moulting. So decrease in growth is not caused by moulting.

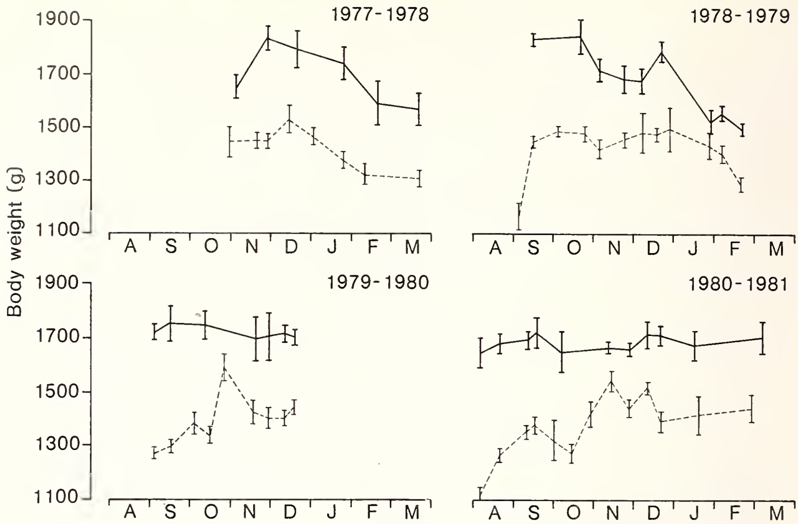

Fig. 4. Mean body weight of rabbits per hunt. Vertical bars indicate standard error. Legend: —— = adults (more than 1 year old); – – – = juveniles (less than 1 year old)

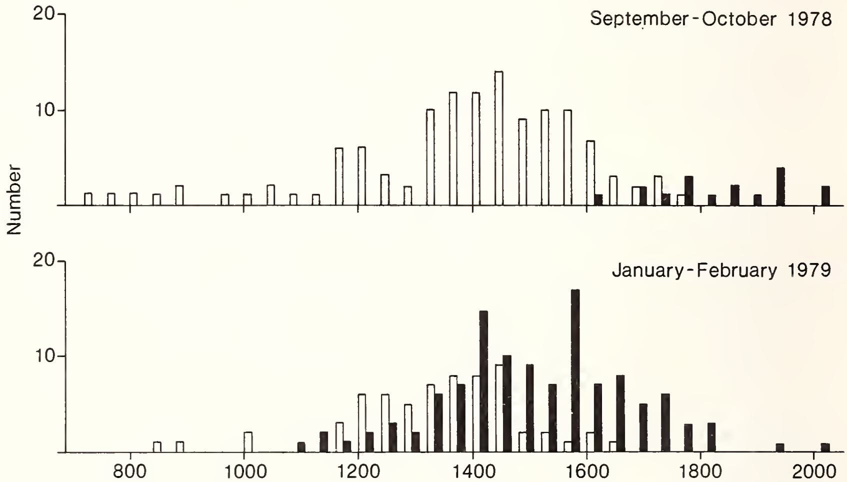

Fig. 5. Distribution of specimens by body weight. Legend: ▮ = adults; ▯ = juveniles

Tabelle 3

Influence of age and time of the year on body weight of juveniles

Data 'Vogelduin', Aug. 1980–March 1981

	Constant	Partial r	n
BW-Age	(Time)	0.77	124
BW-Time	(Age)	−0.60	124

BW = Body weight. Time-Day of the year, continually increasing from August to March. – Age is calculated from eye-lens weight according to Myers and Gilbert (1968).

Comparison between years

In 1978–79 there were a relatively great number of snowy days in January and February (36 days on which the soil was snow-covered), and mean monthly maximum temperatures were below 0 °C, while the other years were normal compared with the previous 30 years, with just a few days of snowfall and mean monthly temperatures a few degrees above 0 °C (data from the Royal Netherlands Meteorological Institute KNMI).

Fig. 4 shows that the body weights of the adult rabbits were lower in January and February 1979 (mean: 1510 g) than in 1978 (mean: 1660 g) or 1981 (mean: 1700 g).

The adult cohort lost, on average, 225 g between December 1978 and February 1979, which is far more than their fat reserve (ca. 90 g, see table 4).

The juvenile class had a light average weight in September 1979. This last fact can be explained by a mean younger age, caused by a later start of the breeding season in '79 than in other years (table 4 and Wallage-Drees 1983).

Tabelle 4

Mean age of juveniles in game bag in September

	n	Lens Weight ± s.e	Age
Sept. '78	82	135 ± 2	158
Sept. '79	146	127 ± 1	143
Sept. '80	91	132 ± 1	152

Age (days) estimated according to the formula of Myers and Gilbert (1968): Age = −57 + 181.4/ln (314/lens [mg])

The body weight of the juveniles in January and February 1978 and 1979 is plotted against lens weight and the regression line drawn (fig. 6). The line of 1979 is significantly below the one in 1978 (more than ± 1.96* s.e., $p < 0.05$).

Discussion

In this study no difference was found between males and females in body weight (fig. 3) and mortality rate (table 1). There is a difference between the sexes in the seasonal pattern of fat deposition. Females store slightly more fat in January and February than males. This may be a preparation for the breeding season, which starts in this area in March (Wallage-Drees 1983). The same was shown by Gibb et al. (1978), Myers and Poole (1963), Parer (1977) and Shira (1980), where different fat deposition was accompanied by distinctly different trends in body weight.

This study shows that rabbits in a temperate zone increase in weight even after reaching maturity. Weight increase stops or is reversed during wintertime, but continues in spring and summer. Consequently the weight of individual rabbits studied here shows an upward oscillating trend much like that described for hares in Poland (Pielowski 1971), and different from the more asymptotic weight curve of rabbits living in less variable circumstances in Spain (Soriguer 1980) and New Zealand (Watson 1957; Wodzicki and Roberts 1960).

In all years of the study period, the mean body weight of the juveniles stayed below that of the adults (fig. 4). The proportion of the adults in the game bag increased during the winter season (table 1), indicating a higher mortality rate in juveniles compared to adults. This is probably the result of a higher vulnerability to predation and hunting due to less experience and to myxomatosis (Wallage-Drees in prep.).

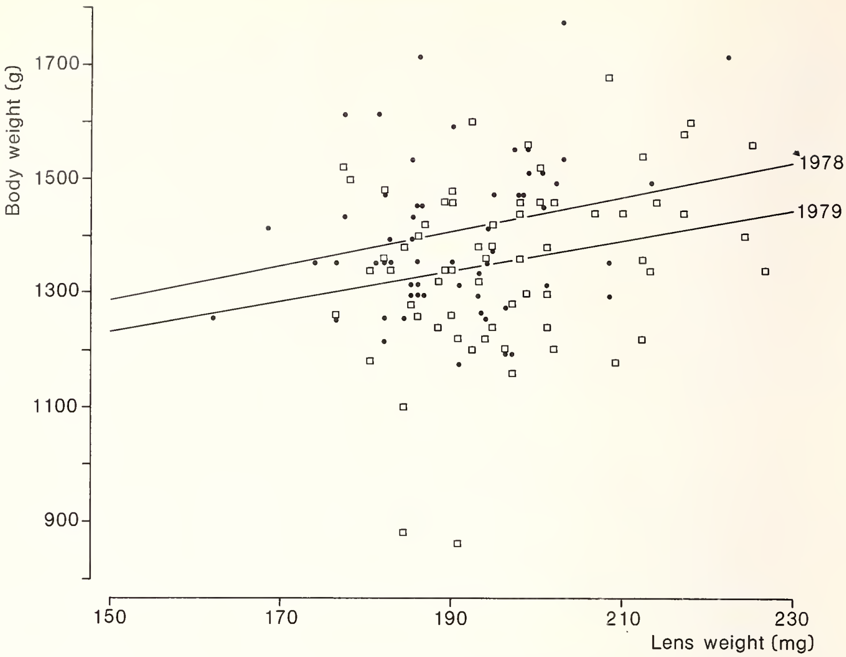

Fig. 6. Body weight in relation to eye-lens weight of juveniles in January and February. Legend: ● = 1978; □ = 1979. Regression formulae: 1978 BW (g) = 829 + 3.02 Lens (mg) S.e. b = 0.09 n = 57, r = 0.30; 1979 BW (g) = 829 + 2.66 Lens (mg) S.e. b = 0.09 n + 64, r=0.30

In the winter 1978–79, with many days of snow, juveniles suffered a higher mortality than in other years (table 1). These findings parallel the data of other studies on Lagomorphs (Gibb et al. 1978; Myers and Poole 1963; Mykytowycz 1961; Vaughan and Keith 1981) which show that adults have a higher rate of survival than juveniles when starvation occurs. It is an advantage to have had time to grow and lay down reserves. Kleiber (1975) formulated the general rule that the basal metabolic rate of mammals is 293 × $BW^{3/4}$ Joule/day (BW in kg). Accordingly, when a rabbit increases its weight by 1 g, its basal metabolic rate increases by 2 J and its fat reserves by 1.0/3.4 g = 11 J (this study, table 3).

In times of severe food shortage, body weight decreases by more than the weight of the fat reserves. Obviously other body tissue is degraded as well.

Body weights of individuals in a population can indicate whether the population suffers from food shortage. In the sand dune area where this study was done, a general decrease in body weight with accompanying mortality occurred only in a year with severe weather conditions, in 1978–79. The limit set by the food resources was exceeded not because of fluctuations in population density, but because of fluctuations in this limit.

In the 'normal' winter 1977–78 there was a weight decrease, but not in 1980–81. This suggests that in 1978 the population had reached the limit of the carrying capacity of the area, while in 1980–81 it had not yet recovered from the reduction in numbers caused by the severe winter of 1978–79. This confirms observations from people working in the area and the results of seasonal hunting (PWN, 1984), both of which indicate an increase in population density from 1980 onward. Hunting could have promoted this situation. I do, however, consider the hunting pressure to be small and did observe the same population fluctuations in an experimental area where no hunting was done (Wallage-Drees unpubl.).

In conclusion: data on the condition of wild rabbits in the study area indicate that the population density was limited by the available food in a year with a severe winter.

Acknowledgements

The support of the PWN, the manager of the dune reserve, made it possible to carry out this study. I thank the game wardens for their cooperation: P. Woudsma, J. Verdwaald, A. A. de Witte, K. Postma, G. Smit, H. Zonneveld. The students J. van Genderen, E. Nijssen, M. Rutz, M. Scholten, H. v. d. Water and ir. E. M. Drees assisted in the collecting of data. I thank Dr. Broekhuizen (Research Institute for Nature Management) and Prof. Dr. K. Bakker, Dr. N. Croin Michielsen and Dr. E. v. d. Meijden (University of Leiden) for their interest during the study and the advice on the presentation of the data.

Zusammenfassung

Jahreszeitliche Änderungen von Gewicht und Fettreserven bei Kaninchen (Oryctolagus cuniculus L.) in einem Dünengebiet an der niederländischen Küste

Der Zustand einer Population von Wildkaninchen wurde untersucht, um festzustellen, wie weit sie ihre maximale Dichte erreicht hat. Von im September bis März in den Jahren 1977 bis 1981 geschossenen Kaninchen wurden dazu das Körpergewicht, das Gewicht des Nierenfettes und zur Altersschätzung das Gewicht der Augenlinse bestimmt.

Weniger als ein Jahr alte Jungtiere und über ein Jahr alte Adulte konnten auf Grund des Linsengewichtes unterschieden werden. Nierenfett, Gesamtfett und Körpergewicht sind eng miteinander korreliert. Das Geschlechterverhältnis (♂♂ : ♀♀) war 1,14. Zwischen den Geschlechtern gab es weder im Körpergewicht noch in der Sterblichkeit im Herbst und Winter signifikante Unterschiede. Die adulten Kaninchen waren schwerer und hatten größere Fettreserven als die jungen. Ihre Sterblichkeit war im Winter geringer. Nur in strengen Wintern nahm das Gewicht infolge Hungerns ab. Die Jungen litten stärker unter dem Nahrungsmangel als die Adulten. Nach einem solchen strengen Winter erreichte die Population nicht ihre maximale Dichte.

Literature

Provinciaal Waterleidingbedrijf Noord-Holland (1984): Beheersnota '85–'90 Noord-Hollands Duinreservaat, Provinciale landgoederen en overige Provinciale natuurgebieden. Bloemendaal, PWN.

Batzli, G. O.; Pitelka, F. A. (1971): Condition and diet of cycling populations of the California vole, *Microtus californicus*. J. Mammalogy **52**, 141–163.

Caughley, G. (1970): Fat reserves of the Himalayan Thar in New Zealand by season, sex, area and age. N. Z. Jl. Sci. **13**, 233–248.

Gibb, J. A.; Ward, C. P.; Ward, G. D. (1978): Natural control of a population of rabbits, *Oryctolagus cuniculus* (L.), for ten years in the Kourarau enclosure. N. Z. Dep. Sci. Ind. Res., DSIR Bulletin 223.

Kleiber, M. (1975) The fire of life. An introduction to animal energetics. Huntington: R. E. Krieger Publ. Co.

Knmi (1978–81): Dagelijks weerbericht. Daily publication Royal Netherlands Meteorological Inst., de Bilt.

Malpas, R. C. (1977): Diet and the condition and growth of elephants in Uganda. J. app. Ecol. **14**, 489–504.

Martin, J. T. (1977): Fat reserves of the wild rabbit, *Orycotolagus cuniculus* (L.). Aust. J. Zool. **25**, 631–639.

Millar, J. S. (1981): Body composition and energy reserves of the northern *Peromyscus leucopus*. J. Mammalogy **62**, 786–794.

Myers, K.; Gilbert, N. (1968): Determination of age of wild rabbits in Australia. J. Wildl. Manage. **32**, 841–849.

Myers, K.; Poole, W. E. (1963): A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations V. Population dynamics. CSIRO Wildl. Res. **8**, 166–203.

Mykytowycz, R. (1961): Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.) IV. Conclusion: outbreak of Myxomatosis, third breeding season, and starvation. CSIRO Wildl. Res. **6**, 142–156.

Parer, I. (1977): The population ecology of the wild rabbit, *Oryctolagus cuniculus* (L.), in a Mediterranean-type climate in New South Wales. Aust. Wildl. Res. **4**, 171–205.

Pielowski, Z. (1971): The individual growth curve of the Hare. Acta theriol. **16**, 79–88.

Rentenaar, R. (1978): De vroegste geschiedenis van het konijn in Holland en Zeeland. Holland: reg.-hist.ÿdschr. 10, 2–16.
Skira, I. J. (1980): Some population parameters and seasonal changes in the weights of internal organs of rabbits *Oryctolagus cuniculus* (L.) at Macquarie Island. Aust. Wildl. Res. **7**, 235–245.
Soriguer, R. C. (1980): El conejo, *Oryctolagus cuniculus* (L.), en Andalucia Occidental: Parámetros corporales y curva de creciemento. Doñana Acta Vert. **7**, 83–90.
Vaughan, M. R.; Keith, L. B. (1981): Demographic response of experimental Snowshoe Hare populations to overwinter food shortage. J. Wildl. Mange. **45**, 354–381.
Wallage-Drees, J. M. (1983): Effects of food on onset of breeding in rabbits, *Oryctolagus cuniculus* (L.), in a sand dune habitat. Acta zool. fenn. **174**, 57–59.
Watson, J. S. (1957): Reproduction of the Wild Rabbit in Hawke's Bay, New Zealand. N. Z. Jl. Sci. Techn. B **38**, 451–482.
Wodzicki, K.; Roberts, H. S. (1960): Influence of population density on the adrenal and body weights of the wild rabbit *Oryctolagus cuniculus* (L.) in New Zealand. N. Z. Jl. Sci. **3**, 103–120.

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Karyotype differentiation in the endemic subterranean Mole rats of South Africa (Rodentia, Bathyergidae)

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Receipt of Ms. 1. 8. 1985

Abstract

Analyzed karyotype differentiation in 3 genera and 4 currently accepted species of African mole rats, Bathyergidae. The species and subspecies examined and in parenthesis the sample size (N) and the diploid chromosome numbers (2n) are: *Cryptomys hottentotus hottentotus* (N = 5, 2n = 54), *Cryptomys hottentotus natalensis* (N = 8, 2n = 54), *Cryptomys hottentotus damarensis* (N = 2, 2n = 74 and 78), *Georychus capensis* (N = 7, 2n = 54), *Bathyergus suillus* (N = 1, 2n = 56) and *Bathyergus janetta* (N = 1, 2n = 54). The results suggest that karyotypically, 2n = 54 is shared by all species except *C. h. damarensis* and *B. suillus* and karyotypic evolution is distinct in both diploid numbers and in karyotype morphology. We conclude that bathyergids are not karyotypically conservative, and display prolific speciation involving chromosomal evolution.

Introduction

Prolific speciation of subterranean rodents has occurred over all major continents and has given rise to an unusually large number of species. Chromosomal differences are frequently associated with different species, a common pattern in rodents (Patton and Sherwood 1983) including subterranean rodents (Nevo 1979). However, while karyotypic differentiation is well documented for most families of subterranean rodents, little is known about the Bathyergidae, an endemic family of subterranean rodents in Africa (Matthey 1956; George 1979; Capanna and Merani 1980; William et al. 1983). Based on the karyotypic analysis of two bathyergids, George (1979) suggested chromosomal conservatism for the Bathyergidae in contrast to other subterranean rodents, such as the genera *Ctenomys*,

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Z. Säugetierkunde 51 (1986) 36–49

ISSN 0044-3468