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A field study on seasonal changes in the circadian activity of rabbits

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Abstract

Investigated the circadian activity of wild rabbits during the year. Wild rabbits are more nocturnal than their domestic relatives. Their emergence and disappearance times do not vary with the time of sunset and sunrise, but stay about the same during the whole year. When activity is defined as the presence above ground, then wild rabbits show one activity period with irregular fluctuations during the night. When comparing the average periods spent above ground by individuals there appear large differences between the activity during November to February and the rest of the year. Reasons for this are discussed. The highest percentage of the population above ground at one time during these winter months is lower than in the rest of the year. One should take this into account when trying to assess population size by sight counts.

Introduction

The rabbit is a prominent inhabitant of the coastal sand dunes of The Netherlands. Despite being of Mediterranean origin (Feen 1963; Zeuner 1963) it thrives at this latitude.

There are no published data on the circadian activity rhythm in wild rabbits under natural conditions at our latitude as there are from New Zealand (Gibb et al. 1978) and Australia (Mykytowycz and Rowley 1958; Myers and Poole 1961). First impressions (Southern 1940) indicate a much lower level of activity in western Europe.

Sight counts are generally used to assess the trend and size of the fluctuations in rabbit populations. Knowledge on the activity rhythm of rabbits is necessary when trying to assess population fluctuations from sight counts. Crucial aspects are: at what time of the day can one expect the highest and/or least variable proportion above ground. So this paper has two objectives: to describe the circadian rhythm and its seasonal change in a temperate climate and to give information that is useful in the interpretation of sight counts.

Material and method

The study site covered a 1.4 ha area within the reserve 'Het Noord-Hollands Duinreservaat', about 15 km northwest of Amsterdam (52.35° N; 4.37° E). Rabbits were caught in baited live-traps and earmarked. From September 1979, when a large part of the population (36 out of 41) was earmarked, monthly population size was assessed by constructing live-calendars from sightings and recaptures. Because it took some time to capture and tag the young, population size could not be calculated in all months. This accounts for the absence of data for May, June, July and August in table 1 and 2 and in figure 4. The population's area was confined on two sides by canals and on the third by a field of high grass not used by the rabbits.

Observations were recorded over 24 hours, once a month from August 1979 till April 1982. They were made from a pit with a shelter behind and above. From there about 70 % of the (hilly) area could be covered. The unseen part had the same type of vegetation. Therefore, to relate counts to total population size above ground, counts are multiplied by 100/70. There were always 2 observers, who were changed every three hours. Every 15 min it was noted which rabbits were visible. In all calculations the first observation after changing the observers was substituted by the average of the

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immediately previous and subsequent observation. At dark a red spotlight was used. The rabbits' eyes, and earmarks, lighted up in the beam. As a result of the insensitivity of their retina for this long wave stimulation (NUBOER 1971) the rabbits were not disturbed by this red illumination.

One use of activity rhythm data is to aid interpretation of sight counts. The Ministry of Agriculture, Fisheries and Food (England and Wales) has long experience in conducting rabbit counts. Counts are taken during several consecutive days at dawn and dusk along transects (TITTENSOR et al. 1978). As an index of population size the maximum count is taken. The average is a less reliable measure as it is influenced strongly by incidental low values caused by disturbances (pers. comm. A. M. TITTENSOR). The index is adopted in this study.

In this article the word 'activity' means any presence above ground.

Results

Timing of start and end of activity

Figure 1 shows the times of the start and end of activity within the population. Activity is arbitrarily said to begin at the start of the first half hour in which at least 2 percent of the total activity of that day occurred and to cease at the end of the last half hour in which at least two percent of the total activity of that day occurred. For an example see Fig. 2.

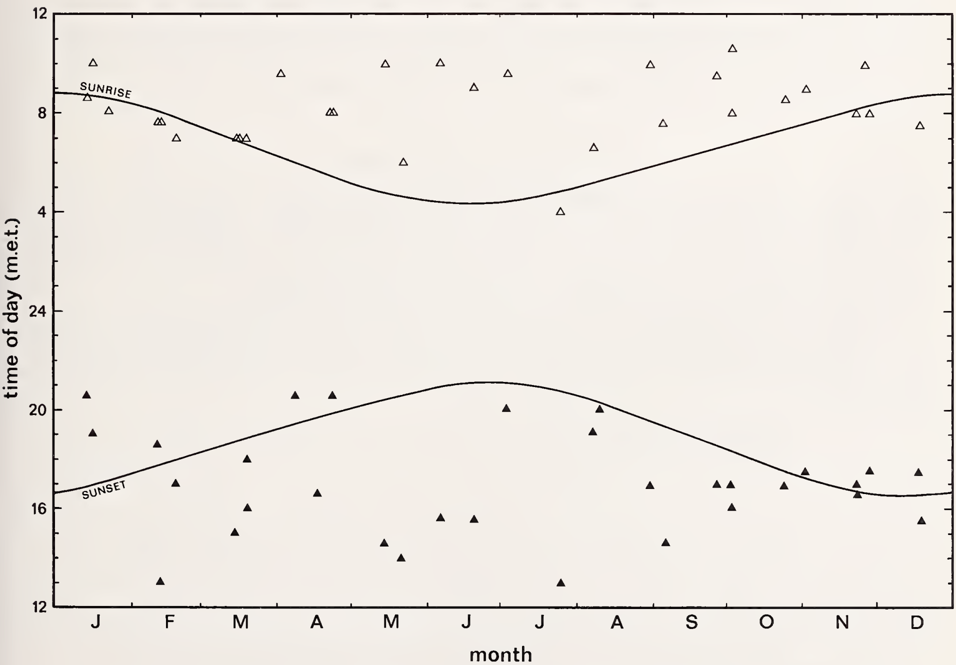

Fig. 1. Times of emergence (▲) and disappearance (△). Times of sunset and sunrise are indicated

Sometimes, in the winter, there were periods during the night with no rabbit above ground. These periods could not be taken into account in Fig. 1, but are included in calculations in the tables and Figs. 2 and 3.

In the same way, incidental activity during the daytime separated by at least an hour from the main activity period, is not taken into account in Fig. 1.

A close relation between activity period and times of sunset or sunrise may have been expected. HOF et al. (1963) showed that in domestic rabbits the time of light-on (sunrise) is

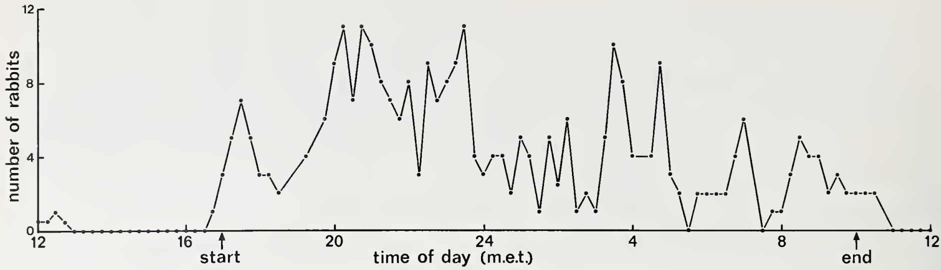

Fig. 2. Activity pattern (number of rabbits/30 min) on 2 October 1979. Arrows indicate times of emergence and disappearance as they are calculated in this paper

the trigger that determines emergence time. So one would expect a correlation between time of sunrise and start of activity. In this study, however, correlation coefficients are not significant (sunrise-start of activity, r = 0.08, n = 32, p = 0.3; and sunrise-end of activity, r = −0.06, n = 31, p = 0.4).

Holley and Greenwood (1984), studying the brown hare found the absence of this relationship to be characteristic of the summer. So I calculated sunrise-start of activity for autumn, winter and spring together, but did not find a significant correlation (Sept.–April, r = −0.07, n = 23, p = 0.4). There are large, apparently irregular fluctuations. The mean times of emergence and disappearance are 16.50 ± 2.10 h and 8.20 ± 1.30 h, respectively.

The circadian activity pattern

Figure 2 shows an example of the activity pattern during one observation period of 24 h. The numbers sighted were registered every 15 min. The evident irregularities are quite typical of rabbit emergence in this site and consistent with our observations of individual rabbits re-entering and re-emerging from burrows during the night.

To determine the existence of short-term periodicities, sample autocorrelations (Chatfield 1975) were calculated for 3 series of observations over 24 h. Fig. 3 shows that the only significant correlations are between one observation and the subsequent one to five observations.

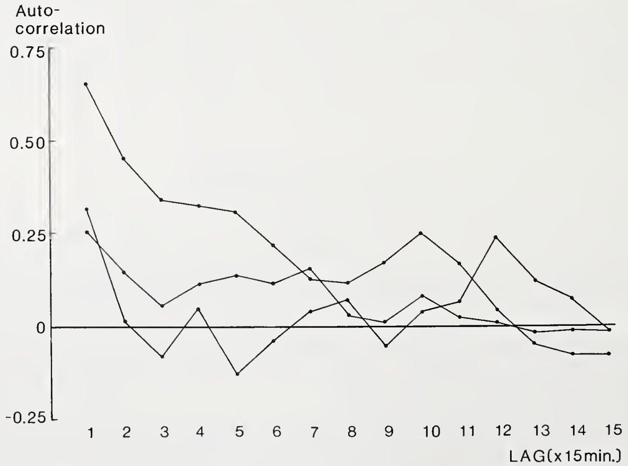

Fig. 3. Autocorrelation function for activity per 15 min on 3 dates (Oct. 1979, Oct. 1980, Dec. 1980). Only the period that the rabbits are active is used. n = 74. 90 % confidence limits = ± 0.23

Seasonal changes in the percentage of rabbits active

Figure 4 is constructed by averaging the monthly observations from the three years (only for those months for which assessments of population size were available). For each year the mean number of rabbits for the observation sessions (in each 2 hour period) is converted to a percentage of the population by dividing by the population size for that particular month. The percentages of rabbits active in corresponding time periods are then averaged for the three years. The figure illustrates the trend in activity over the year. Activity is low in wintertime and increases at the beginning of March.

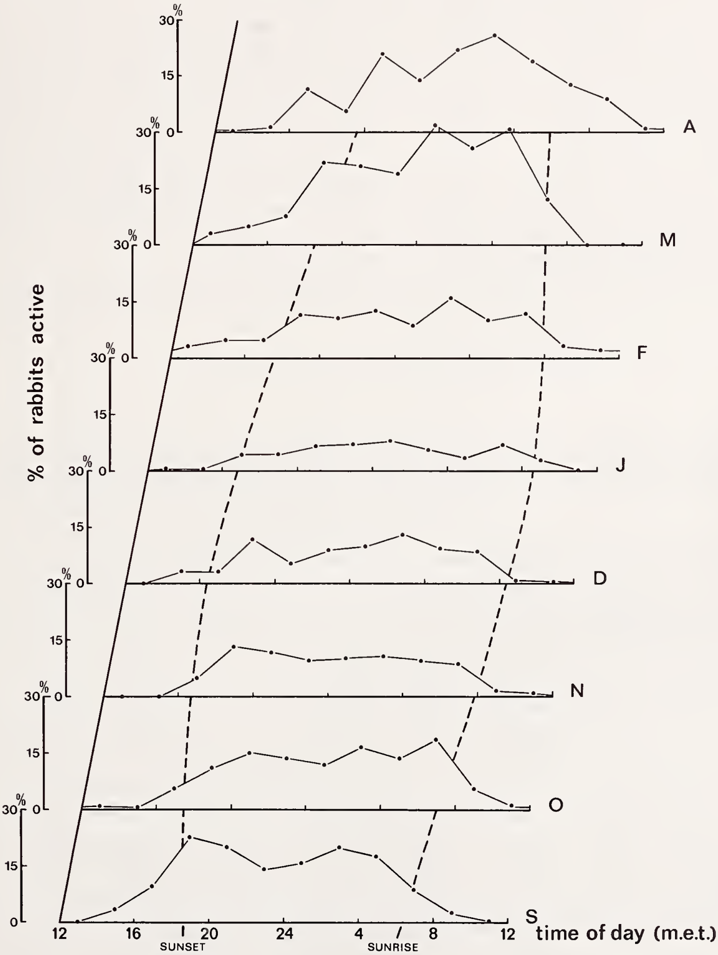

Fig. 4. Average activity patterns for each month between September and April. Each point is the mean of 3 observations made in different years

A homogeneous distribution of activity between 18.00–6.00 h can be confirmed or refuted by dividing this period into three equal parts (per day) and comparing the first and second part with Wilcoxon matched-pairs signed-ranks (Siegel 1956). This statistic does not require that the rabbits behave independently of each other. It is computed both for the whole series and for the separate seasons. In all cases $p > 0.05$, so there is no significant tendency to bimodality.

Table 1. **Average activity (hours above ground) per rabbit in 24 hours**

Full-grown rabbits only

year	1979	1980	1981	1982	average
January		–	0.9	1,4	1,2
February		3,1	1,3	1,2	1,9
March		2,9	4,5	2,6	3,3
April		3,3	2,9	2,4	2,9
May		4,8	–		4,8
June		5,0	–		5,0
July		–	–		
August	–	–	–		
September	–	3,2	2,3		2,8
October	2,9	1,9	1,9		2,2
November	1,6	1,5	2,1		1,7
December	–	1,8	0,5		1,2

Sept. + Oct. versus Nov. to Feb.: $p = 0.02$; March + April versus Nov. to Febr.: $p = 0.02$ (Mann-Whitney-U-test)

The average period spent above ground per individual is calculated for each month by summing the mean number of active rabbits per hour and dividing this total by the known population size for that month (Tab. 1). From November to February it is only 1.5 h, in March and April 3.1 h. It may be even higher during the summer months.

Maximum number of active rabbits

To calculate the theoretical results of the sight count method, I have taken the maximum value of 5 consecutive 15 min sightings starting or ending with at 1 h after sunset or 1 h before sunrise, respectively, and divided it by the population size and multiplied it by 100/70 to get the percentage of the population above ground (Table 2).

The data in Table 2 show that the rabbits were never all above ground at the same time. Generally, the percentages in January are lower than in either September or March.

Fluctuations are smaller just after sunset (from 5–57 %) than just before sunrise (from 0–77 %).

Table 2. **The percentage of the total population which is active, one hour after sunset and one hour before sunrise. The highest value of five consecutive observations is given**

Full-grown rabbits only

	Highest percentage of the population observed							
	at 1 hour after sunset				at 1 hour before sunrise			
year	1979	1980	1981	1982	1979	1980	1981	1982
January		5	8	24		5	8	24
February		20	27	34		31	45	34
March		48	48	24		34	76	–
April		48	55	27		16	77	27
May		57	–	–		48	–	–
June		44	–	–		–	–	
July		–	–			–	–	
August		–	–			–	–	
September	35	38	22		–	24	29	
October	40	35	16		33	22	29	
November	30	28	28		8	28	9	
December	–	34	11		–	27	0	

Discussion

Start of activity

Our results show that emergence time varies, but does not correlate with the time of sunset as would be expected from experiments and observations on synchronization of activity periods of wild rabbits with daily variations in colour and light intensity of the sky (Nuboer et al. 1983). This 'non-synchrony' was also found in summertime in the hare (Holley and Greenwood 1984).

This is partly due to the fact that in my study area foraging areas were adjacent to the burrows. Nuboer et al. (1983) recorded the movement from hutch to food supply (indoors) or between the warren in the dune and feeding site on the floodplain. I took emergence out of the burrow to be 'start of activity'. In my study site we saw rabbits re-enter or re-emerge from their burrows during the night. This has also been noted by Mykytowycz and Rowley (1958) and Kraft (1978).

Another reason for the lack of synchrony may be the influence of weather. Rowley (1957) found a late emergence during strong winds and/or rain. Kolb (1986) mentions an extremely variable onset of activity for rabbits in a small enclosure. He found a negative correlation with the maximum temperature during the previous day.

In particular a change in the type of weather is expected to influence emergence time. An example is the influence of changes in cloud cover on suckling behaviour of hares (*Lepus europaeus*, Pallas) (Broekhuizen and Maaskamp 1980). The influence of the period of the moon has been analysed only by Lord (1964) on *Sylvilagus*. He did not find any effect on activity pattern.

I did not find a significant correlation between either emergence time or maximum percentage active with temperature, wind speed or length of showers. However, the data collected were not sufficient for a detailed analysis of the influence of weather conditions. During the fieldwork I did notice that directly after snowfall rabbits stayed underground at night and that during prolonged snow periods the entire population may be above ground in the afternoon.

The circadian activity pattern

The rabbits' eyesight is good at low light intensity. Their sensitivity to the "blue" and "green" parts of the spectrum and their "blue-green" dichromacy seems an adaptation to the light environment during twilight (Nuboer et al. 1983). One would expect the highest activity in twilight, and therefore a bimodal activity pattern.

Hof et al. (1963) did indeed find this pattern for locomotor activity in domestic rabbits. Rietveld et al. (1964) showed that changing the irradiance abruptly gave more pronounced activity peaks. Prud'hon and Goussopoulos (1976) measured locomotor and foraging activity in indoor cages and Kraft (1978) 'total activity' and foraging activity in small outdoor enclosures. Both compared wild to domestic rabbits in this respect. Wild rabbits showed one phase of nearly uninterrupted activity, with more (Kraft) or less (Prud'hon and Goussopoulos) pronounced bimodal foraging peaks. Domestic rabbits changed phases of rest and activity a few times during 24 hours. Broekmeyer and Lunen (1986) saw that they kept this pattern after release in the wild. It is thus not advisable to study the behaviour of domestic rabbits to get more insight into that of their wild relatives.

When, in experiments under controlled light conditions, a bimodal pattern for either locomotor or foraging activity is not obvious, it does not surprise us that workers studying overall activity of (more or less) free-living rabbits report no peaks. Generally they find rabbits to be equally active the whole night (Stodart and Myers 1964; Myers and Poole 1961, this study). A similar unimodal activity period is also found in the related *Sylvilagus* (Lord 1964) and *Lepus timidus* (Lemnell and Lindlöf 1981).

Interpretation of sight counts

Data on activity levels can be useful to people monitoring rabbit populations by sight counts. Fig. 4 can be used to choose the best time for counting.

People wishing to count rabbits on their land often start at either 1 h after sunset or 1 h before sunrise. Table 2 gives the proportion of rabbits active at these times.

One will have to correct for the proportion of the terrain that is visible, especially when comparing counts done in different areas. Here I will only consider the influence of the circadian and yearly activity patterns on the chance that a rabbit is above ground.

Different figures have been given for the maximum proportion above ground at any one time: Dunnet (1957) 55–60 %, Lésel (1968) 50 %, Myers (1957) 90 %, Mykytowycz and Rowley (1958) 66 %, Schantz and Liberg (1982) 57 %, Southern (1940) 'usually' 30 % and in this study 5–57 %.

Gibb et al. (1978) found a large effect due to population density: at a high density with food shortage 90–95 % were above ground, at a low density only 45 %. This is, however, different from the situation in our dunes, where a possible food shortage coincides with the coldest time of the year and being above ground costs energy.

The influence of the weather on short-term fluctuations in the maximum percentage active is probably not as strong as its influence on time of emergence. Gibb et al. (1978) found that only wind speeds higher than 6 Bf had an influence on numbers above ground.

For the same population as described here, Geut and Jansen (1980) made 4 series of at least 9 consecutive morning and evening observations. They found that highest daily maxima occurred where there was no or very little rain and low wind speed, and lowest maxima occurred after rainfall. Temperature and wind direction seemed to have no effect.

Seasonal changes in activity

The level of activity varies strongly with the seasons. Activity reachs a nadir in wintertime, followed by a strong increase in March. The increase corresponds with the onset of reproduction in the study area (Wallage-Drees 1983: 50 % of does pregnant in the first week of March, so 50 % lactating in the first week of April). Lactating requires a lot of energy (2 to 3 times the demands for maintenance, Reyne et al. 1977). Thus does need more food at that time and, consequently, will forage longer. Lloyd (1964) mentions a longer feeding period in pregnant does compared to other rabbits active at the same time.

The short activity period in winter is a surprise, the more so since domestic rabbits (3 kg) who had access to food for only 4 h a day, lost weight. The coldest night during this study was in December 1981. The temperature dropped from 0 to −8 °C. The associated activity pattern, with hardly a rabbit above ground after 23.00 h, was the most extreme. This means that foraging time was short where one would have expected rabbits to need more time to gather a sufficient quantity of good quality food (Wallage-Drees and Deinum 1986).

The demand for food in winter is determined by diametrically opposed factors. Rabbits do not have a large fat reserve (mean: 7–21 g, Wallage-Drees 1986). The energy requirement in winter is less than in other seasons because there is hardly any sexual, aggressive or burrowing behaviour. On the other hand energy is needed to keep the body temperature stable. In domestic rabbits basal metabolism increases 1,5 times when outdoor temperature drops from 14 °C to 4 °C (Kleiber 1975). Wild animals that have had time to adapt compensate partly by enhancing their fur thickness (insulation, Hart et al. 1965). Also keeping the fur dry, avoiding strong winds and staying in their burrows will help to reduce heat losses. The burrow presents an environment of moderate, stable temperatures (Hayward 1961). In this dilemma the Dutch rabbits choose to stay underground for many hours a day.

The rabbit originates from the Mediterranean. They have been extensively studied in Australia, where they are very successful in areas with climates resembling that of the Mediterranean (Myers 1971). Rabbits are also successful in coastal dunes. It looks as if they have adapted to our climate by showing low activity in winter and becoming diurnal on the coldest days.

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Zusammenfassung

Eine Feldstudie über saisonale Änderungen der circadianen Aktivität von Kaninchen

Wilde Kaninchen sind in der Nacht aktiver als Hauskaninchen. Der Zeitpunkt ihres Erscheinens und Verschwindens ändert sich nicht mit Sonnenuntergang und Sonnenaufgang; er bleibt während des Jahres ungefähr gleich.

Definieren wir ‚aktiv‘ als die oberirdische Anwesenheit, dann haben wilde Kaninchen nur *eine* aktive Periode mit unregelmäßigen Schwankungen während der Nacht.

Vergleichen wir die durchschnittliche Zeit, die ein Kaninchen während des Jahres oberirdisch verbringt, dann zeigen sich große Unterschiede zwischen dem Zeitabschnitt November/Februar und den anderen Monaten. Die Ursachen dafür werden besprochen.

Das Maximum im Anteil aktiver Kaninchen während eines Tages ist im Winter niedriger als in den übrigen Monaten. Dem muß man Rechnung tragen, wenn man die Größe der Population abschätzt.

References

Broekhuizen, S.; Maaskamp, F. (1980): Behaviour of does and leverets of the European hare *(Lepus europaeus)* whilst nursing. J. Zool. (Lond.) **191**, 487–501.

Broekmeyer, M.; Lunen, K. van (1986): Een onderzoek naar het effect van konijnen op de vegetatie van de Derde Duintjes, Boschplaat, Terschelling. Hugo de Vrieslab., Univ. Amst., intern. rep. **206.**

Chatfield, C. (1975): The analysis of time series: theory and practice. London: Chapman and Hall.

Dunnet, G. M. (1957): Notes on emergence behaviour of the rabbit *Oryctolagus cuniculus* (L.) and its bearing on the validity of sight counts for population estimates. CSIRO Wildl. Res. **2**, 85–89.

Feen, P. J. van der (1963). Hoe en wanneer zijn wilde konijnen in Europa verspreid geraakt? Biologisch Jaarboek **31**, 237–243.

Geut, G.; Jansen, M. (1980): Enkele aspecten van de oecologie van het wilde konijn (*Oryctolagus cuniculus* (L.)). Intern. rep., Univ., Groningen.

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

Hart, J. S.; Pohl, H.; Tener, J. S. (1965): Seasonal acclimatization in Varying Hare *(Lepus americanus).* Can. J. Zool. **43**, 731–744.

Hayward, J. S. (1961): The ability of the wild rabbit to survive conditions of water restriction. CSIRO Wild. Res. **6**, 160–175.

Hof, M. W. van; Rietveld, W. J.; Tordoir, W. E. M. (1963): Influence of illumination on locomotor activity of rabbits. Acta Physiol. Pharmacol. Neerl. **12**, 266–274.

Holley, A. J. F.; Greenwood, P. J. (1984): The myth of the mad March hare. Nature, Lond. **309**, 549–550.

Hörnicke, H.; Dietzel, F.; Aigner, E.; Schulte, R. (1976): Alimentary behaviour in rabbits under different influences. 1er Congr. Int. cunicole, Dyon, commun. **13**,.

Kleiber, M. (1975): The fire of life. Huntington, New York: R. E. Krieger.

Kline, P. D. (1965): Factors influencing roadside counts of cottontails. J. Wildl. Manage. **29**, 65–671.

Kolb, H. H. (1986): Circadian activity in the wild Rabbit *(Oryctolagus cuniculus).* Mammal Rev. **16**, 145–151.

Kraft, R. (1978): Beobachtungen zur Tagesperiodik von Wild- und Hauskaninchen. Z. Säugetierkunde **43**, 155–166.

Lemnell, P. A.; Lindlöf, B. (1981): Diurnal and seasonal activity pattern in the mountain hare. Ed. by K. Myers and C. D. MacInnes. Proc. First World Lagomorph Conf., Guelph, Ontario. pp. 349–356.

Lesel, R. (1968): Essai d'estimation de la population d'*Oryctolagus cuniculus* L. sur la Peninsula Courbet (Iles Kerguelen). Mammalia **32,** 612–620.
Lloyd, H. G. (1964): Influences of environmental factors on some aspects of breeding in the wild rabbit, *Oryctolagus cuniculus* (L.). MSc thesis, University of Wales.
Lockley, R. M. (1964): The private life of the rabbit. Worcester, London: Baylis and Son.
Lord, R. D. (1964): Seasonal changes in the activity of penned cottontail rabbits. Anim. Behav. **12,** 38–41.
Myers, K. (1957): Some observations on the use of sight counts in estimating populations of the rabbits, *Oryctolagus cuniculus* (L.). CSIRO Wildl. Res. **2,** 170–171.
— (1971): The rabbit in Australia. In: Proc. adv. study inst. 'Dynamics of Numbers in Populations'. Oosterbeek, The Netherlands. Ed. by P. J. den Boer and G. R. Gradwell. pp. 478–507.
Myers, K.; Poole, W. E. (1961): The effects of season and population increase on behaviour. CSIRO Wildl. Res. **4,** 14–26.
Mykytowycz, R.; Rowley, I. (1958): Continuous observations of the activity of the wild rabbit, *Oryctolagus cuniculus* (L.), during 24-hour periods. CSIRO Wildl. Res. **3,** 26–31.
Niethammer, G. (1938). Ergebnisse von Markierungsversuchen an Wildkaninchen. Z. Morphol. Ökol. Tiere **33,** 297–312.
Nuboer, J. F. W. (1971): Visual acuity measurements in a rabbit. PhD thesis, Univ. Utrecht.
Nuboer, J. F. W.; Nuys, W. M. van; Steenberger, J. C. van (1983): Colour changes in a light regimen as synchronizers of circadian activity. J. comp. physiol. **151,** 359–366.
Prud'hon, M.; Goussopoulos, J. (1976): Comportement alimentaire du lapin de garenne en captivité. Ann. Zootech. **25,** 407–410.
Reyne, Y.; Prud'hon, M.; Debicki, A. M.; Goussopoulos, J. (1977): Caracteristiques des consommations d'aliments solide et liquide chez la Lapine gestante puis allaitante nourrie ad libitum. Ann. Zootech. **27,** 211–223.
Rietveld, W. J.; Tordoir, W. E. M.; Hof, M. W. van (1964): Influence of light to dark ratio, for a 24-hour cycle, on locomotor activity of rabbits. Acta Physiol. Pharmac. Neerl. **13,** 87–95.
Rowley, I. (1957): Observations on evening rabbit activity in relation to weather and sunset. CSIRO Wildl. Res. **2,** 168–169.
Sanderson, J.; Vanderweele, D. (1975): Analysis of feeding patterns in normal and vagotomized rabbits. Physiol. Behav. **15,** 357–364.
Schantz, T. von; Liberg, O. (1982): Censusing numbers of medium-sized nocturnal mammals in open landscapes. Proc. XIV Int. Wildl. Congr., Dublin, 1979. pp. 409–417.
Siegel, S. (1956): Nonparametric statistics for the behavioral sciences. Kogakusha: McGraw-Hill.
Snyder, W. I. (1978): Feed constituent digestibility by adult and juvenile cottontail rabbits. PhD thesis, Department of Natural Resources, Univ. Cornell, Cornell.
Southern, H. N. (1940): The ecology and population dynamics of the wild rabbit *(Oryctolagus cuniculus).* Ann. appl. biol. **27,** 509–526.
Stodart, E.; Myers, K. (1964): A comparison of behavior, reproduction and mortality of wild and domestic rabbits in confined populations. CSIRO Wildl. Res. **9,** 144–159.
Tittensor, A. M.; Woods, J. A.; Fox, A. P. (1978): Ecology of farmland rabbit populations. Pest Infestation Control Laboratory Report 1974–76, pp. 155–157. London: HMSO.
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.
— (1986): Seasonal changes in the condition of rabbits, *Oryctolagus cuniculus* (L.), in a coastal sand dune habitat. Z. Säugetierkunde **51,** 26–36.
Wallage-Drees, J. M.; Deinum, B. (1986): Quality of the diet selected by wild rabbits [*Oryctolagus cuniculus* (L.)] in autumn and winter. Neth. J. Zool. **36,** 438–448.
Zeuner, F. E. (1963): A history of domesticated animals. London: Hutchinson. pp. 409–415.

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