Weather Effects on Reproduction, Survival, and Body Mass of European Rabbits in a Temperate Zone Habitat

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Introduction

Understanding the effects of environmental factors on the dynamics of animal populations is one of the major challenges for population biologists. In particular, the impact of climate and weather has been the focus of many studies during the last years (e.g., Lima and Jaksic 1998; Milner et al. 1999; Stenseth 1999; Yoccoz and Stenseth 2000; Aars and Ims 2002; Lande et al. 2003). However, data on specific effects of the weather on different vital rates are rare, because, in small mammals in particular, individually based studies are difficult to conduct, and long-term datasets are needed for obtaining reliable results.

The European rabbit *Oryctolagus cuniculus* is an interesting and very suitable model organism for such a study. Formerly restricted to a relict distribution on the Iberian Peninsula about 3,000 years ago, this species has been spread by man over nearly all continents and to different climatic zones (Flux 1994). This species is characterized by a high reproductive capacity (e.g., Myers and Poole 1962; Gonçalves et al. 2002; von Holst et al. 2002) but also by high mortality rates, in particular in juveniles (e.g., Richardson and Wood 1982). This can result in strong short-term fluctuations in population numbers (e.g., Erlinge et al. 1984; Myers and Poole 1963). Furthermore, several studies on European rabbit populations point out, that climatic and weather conditions have a strong impact on the abundance and on population densities of this small mammal (e.g., Erlinge et al. 1984; Trout et al. 2000; Schröpfer et al. 2000; Calvete et al. 2004).

Since 1988 we have kept and studied a population of European rabbits in a field enclosure of 2 ha in Upper Franconia, Germany. In this chapter, we review our findings about the effects of weather on different reproductive components, on the body mass of juveniles at the end of the vegetation period, and the over-winter survival of adults and first-year individuals' reproduction, survival, and body mass. Many aspects presented here have been described in our previous papers, however not all results have been published.

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Our Study Population in Bayreuth, Germany

Our study population consisted of animals that were descendants of individuals that had been caught at different sites in south Germany. Vegetation in the 2-ha enclosure consisted of homogeneous grassland with interspersed groups of trees and bushes. The vegetation growing in the enclosure was the only food source for the rabbits during the vegetation period. Nevertheless, we provided restricted amounts of hay in ten feeding racks during periods of harsh winter conditions (mostly occurring in late January), when high snow cover or snow crusts prevented the rabbits' access to ground vegetation. The animals in our study population were hosts to several species of endoparasites (Eimeria, Trichostrongylidae, Oxyuridae) as are all rabbits living in the wild, but we had no cases of myxomatosis or rabbit hemorrhagic disease during the study period from 1991 to 2002. The access of most of the common predators (e.g., *Martes foina, Mustela erminea*, *Mustela nivalis*, *Accipiter gentilis*, *Buteo buteo*) was not restricted by the fence. In our study population, the animals never reproduced within their year of birth. However, first-year animals, at least the ones which were born early in the season, have reached physiological maturity by autumn, and are therefore hereafter referred to as 'subadults'.

Methods and Data Collection

Apart from a daily walk to check the enclosure in the morning and a monthly trapping session, there was no other human interference. The entire study site could be observed from two separate outlook towers and all the animals could be identified by their individual ear-tags (colored aluminum tags fixed with Dalton Rototag, 35 × 10 × 2 mm). In addition to the burrows dug by the rabbits, the area contained 16 artificial concrete warrens with interconnecting chambers and removable covers, which were evenly distributed throughout the study area. These were used by the rabbits as the main warrens of their group territories and also for breeding.

Once a month, the animals were caught by the aid of peanut-baited wooden traps set overnight (in summer) or in the morning for several hours (in winter) and the captured animals were stored separately in sacks and later weighed.

We checked for newborn litters every morning during the breeding season. In order to do this, we prepared burrow systems and breeding stops dug by the animals with artificial holes, which we covered with concrete flagstones. At postnatal day 12, we weighed all pups of each litter and marked them individually using colored ear tags (Dalton Rototag, 20 × 5 × 1 mm). We regularly dyed the ventral fur of all adult females of each group with different colors (Marabu silk color). Female rabbits pluck out the hair from their ventral fur in order to build their nests, which enabled us to determine the maternity of each litter by the color of hair found in the nest. We additionally validated this by the behavior and space use of the females in relation to the location of the breeding site. Data on space use, social behavior, group membership, and digging of breeding sites of each adult female were collected by regular direct observations throughout every breeding season. This was done during the last 3–4 h before dawn when the rabbits showed their main social activity (Wallage-Drees 1989). We determined over-winter survival of all subadults that were known to be present in autumn by counting the surviving animals in early March. Thus, each individual studied could be assigned to the category 'survivor' or 'non-survivor'. All weather data were provided by a meteorological station which was situated 400 m away from the enclosure.

Results and Discussion

Reproduction

The results of our study suggest that the timing of the breeding season of the European rabbit in the temperate zones is modified by at least two different weather variables. Firstly, the onset of breeding was related to the temperature conditions of the previous winter season (Fig. 1; cf. Rödel et al. 2005). Secondly, we found that the decrease in the seasonal reproductive activity in summer was correlated with the amount of precipitation in summer (Fig. 2b). The latter finding has not been published by us elsewhere.

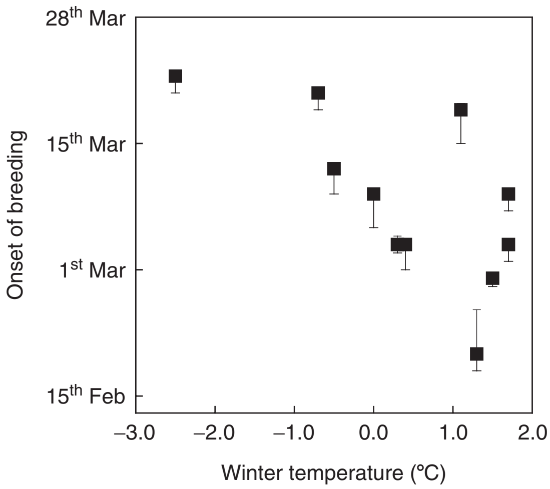

Fig. 1 Correlation between the average winter temperature and the annual onset of the breeding season ($r_s = -0.661$, $n_{years} = 11$, $P = 0.027$), measured as the median parturition date (plotted with 25, 75% percentiles) of the first 25% of the female population less 30 days of gestation (modified from Rödel et al. 2005)

The fact that European rabbits in the temperate zones shift the onset of the breeding season in response to harsh winter conditions has been already described for rabbit populations in southern Sweden (Anderson et al. 1979) and England (Bell and Webb 1991). In addition, the results of our long-term study underline the strong impact of this weather factor: the maximum range in the onset of breeding between the years studied was 33 days, which approximates to the length of the gestation period of this species (30–32 days: Hudson et al. 1995). Similar effects of winter weather have also been reported for other seasonal breeding lagomorph species (e.g., *Sylvilagus floridanus* (Eastern cottontail): Hamilton 1940; Wright and Conaway 1961; *Lepus townsendii* (White-tailed jackrabbit): Kline 1963; *Lepus europaeus* (European hare): Flux 1967), whereas this effect may be primarily based on the lower pre-breeding body condition of the females due to a reduced food availability or quality during harsh winters. However, in contrast to the findings of Bell and Webb (1991), our study did not support a reduction in fecundity or reproductive performance in response to harsh winter weather conditions (Table 1). Our data rather suggest that the females compensated their lower body condition after harsh winters, which might potentially affect their reproductive performance by the observed delay in the onset of breeding (see Rödel et al. 2005). In contrast, we found a negative correlation between the winter temperature and the average fecundity during the subsequent breeding season (see Table 1). We speculate that this unexpected relationship was caused by density-dependent reproductive suppression due to the higher population number, in particular the number of recruits, after mild winters (cf. Myers and Poole 1962; Rödel et al. 2004a, 2004b).

The females of our population showed a strict seasonality in reproduction. During our 11-year study period, no littering was observed from November to February. Every year, the females reproduced at least until autumn (unpublished data). The reproductive activity, which we measured as the

Table 1 Spearman correlation between winter temperature and different measures of reproductive performance/fecundity during the subsequent breeding season, averaged over the annual female population ($n_{years} = 11$). Litter size, litter mass, and litter mass gain during the first 12 days of lactation were tested for litters of the first reproductive cycle/season. Data were average over 16–31 females per season. Only females older than 1 year were included in the analysis, since 1-year-old females were known to have a consistently lower reproductive performance (modified from Rödel et al. 2005)

Response variable	r_s	P
Offspring per season	–0.770	0.006
Litters per season	–0.633	0.036
Litter size	–0.410	0.210
Litter mass	–0.446	0.169
Litter mass gain (day 1–12)	–0.396	0.228

average proportion of reproducing females/months, peaked in May and then sharply declined to July/August (Fig. 2a). Studies in warm and arid regions point out that the availability of green pasture in response to rainfall restricts the reproductive activity of the rabbit during or at the end of the breeding season (Mykytowycz 1958; Soriguer and Rogers 1981; King et al. 1983; Wheeler and King 1985). Even if green pasture was area-wide available until October in all of the years and also the access to water was never restricted in our study population, we also found strong support for this effect: The decrease in the reproductive activity from June to July was significantly correlated with the amount of rain at this period of time (Fig. 2b).

Body Mass of the Juveniles at the End of the Vegetation Period

In seasonal environments, the survival of juveniles or first-year individuals of many mammal species is strongly affected by the body mass that the animals reach until the end of the vegetation period (Marboutin and Hansen 1998; Loison et al. 1999; Rödel et al. 2004a). For European rabbit populations in arid habitats, the restriction of green pasture by low precipitation is certainly one of the key factors for limited growth rates and therefore low autumn body masses of juveniles, whereas this effect might be enhanced by a high population density (e.g., Dudzinski and Mykytowycz 1960). However, in our temperate zone population, we found a strong negative correlation between rainfall during the early juvenile period and the autumn body mass (Fig. 2; see also Rödel et al. 2004a). Young rabbits that were exposed to a higher proportion of rainy days during the first 2 months after first emergence above ground had a lower body mass in mid November. We suggest two different mechanisms which may have caused the limited growth rates in individuals that experienced rainy weather

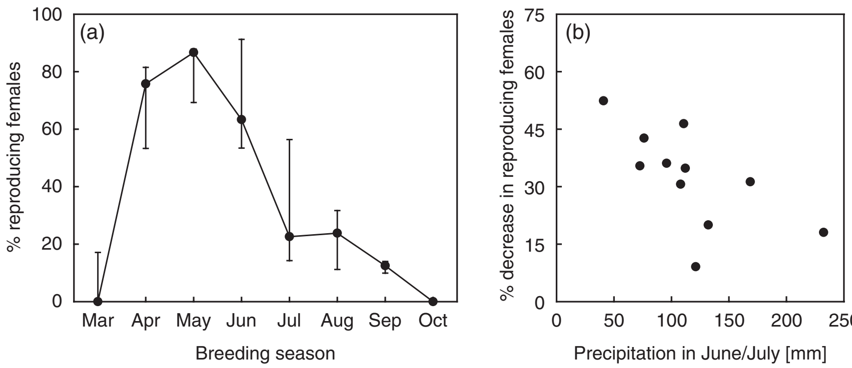

Fig. 2 a Proportion of reproducing females on the total female population per breeding season (median with 25, 75% percentiles), and **b** correlation between the amount of rain in June/July (measured from June 15–July 30) and the annual decrease in the percentage of reproducing females from June to July ($r_s = -0.755$, $n_{years} = 11$, $P = 0.007$)

conditions during their early development: Firstly, the heat loss, and secondly the risk of infections from diseases, which may both increase when the young rabbits are permanently wet, might negatively affect the energy allocation for growth. In particular, the infestation with coccidiosis, which is latently present in almost all European rabbit populations (e.g., Mykytowycz 1962; Stodart 1968; Cowan 1985), may play a major role, since the extracorporeal persistence of the infective sporocysts is prolonged in humid environments.

Winter Survival

Over-winter survival of subadult rabbits was significantly influenced by two weather variables: the precipitation that the animals were exposed to during their early juvenile period after emergence above ground, and the winter temperature (Fig. 3). Cold winters and frequent rain during the early juvenile period lowered the chance of winter survival. Subadults born early in the season had a higher chance of survival, whereas survival was decreased at high population density. Furthermore, the survival in females was slightly higher than in males. In our original paper (Rödel et al. 2004a), we tested various interactions among these candidate factors and also tested the support of simpler models with a lower number of parameters. However, model selection by Akaike's information criterion revealed that the model including the additive

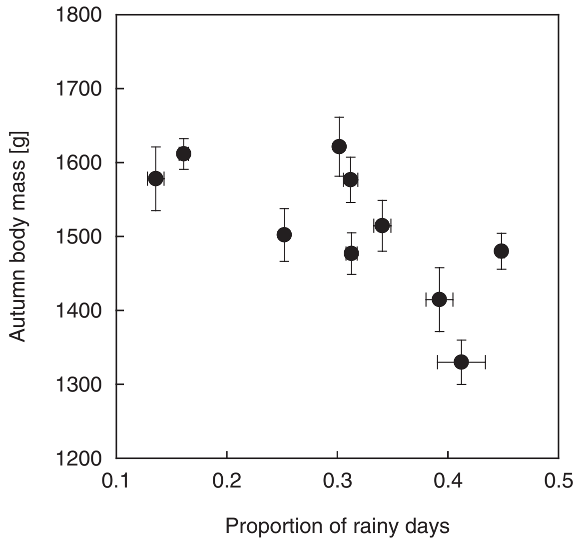

Fig. 3 Correlation between the proportion of rainy days (=days with precipitation >1 mm) to which the individual juveniles were exposed during the first 2 months after emergence above ground at around day 20 after birth (averaged per year, ± SD) and the mean autumn body mass measured in mid November (± SD; $r_s = -0.745$, $n_{years} = 10$, $P = 0.013$). Only data of juveniles born during the first reproductive cycles are included in the analysis (modified from Rödel et al. 2004a)

combination of winter weather, precipitation during early development, population density, date of birth and sex had the best support in explained over-winter survival of subadults.

This limiting effect of winter weather agrees with the findings on other European rabbit populations in temperate zones. Erlinge et al. (1984) noted a population breakdown in southern Sweden after harsh winter conditions, and Wallage-Drees (1986) reported an increased mortality in first-year animals during a winter with heavy snowfall. The higher costs of thermoregulation and the increased thermal stress during harsh winter conditions (e.g., Myers et al. 1977; Katzner 1997) together with the restricted access to high-quality food (Crawley 1983) may be the main reasons for the limiting effects of winter conditions on survival. Therefore, a high body mass, which has been found to be related to a high body fat content in the European rabbit (Wallage-Drees 1986), may substantially increase the chance of winter survival. In turn, the rainy weather conditions after first emergence above ground have been shown to affect the body mass of the subadults in autumn, which explains the observed impact of this factor on the probability on over-winter survival (Rödel et al. 2004a). Furthermore, a higher parasite load of individuals that experienced higher amounts of rain during their juvenile period may also translate into a lower chance of winter survival (Fig. 4).

In contrast to the strong effects of weather conditions on over-winter survival of subadults, preliminary analyses of our data did not support a relationship between winter weather and adult survival, or at least we did not find any significant correlations between the average temperature during the winter season and the survival rates of adults of both sexes (adult males: $r_s = 0.047$, $n_{years} = 15$, $P = 0.869$; adult females: $r_s = 0.100$, $n_{years} = 15$, $P = 0.722$).

Differences between these two age classes were also apparent in our study with regard to winter body mass loss. A study over 1 year revealed that subadults, which survived until the end of the winter season, lost on average 22.3%, whereas adults only lost 9.3% of their autumn body mass (Rödel 2000; Rödel et al. 2005). There are several reasons why young, first-season individuals might react more sensitively to adverse environmental conditions. Adult rabbits have a higher body mass compared to individuals short before reaching maturity: subadults of our study population that were born during the first reproductive cycle, and therefore had an average age of about 7–8 months in mid November, were still about 15% lighter that adults (unpublished data). Furthermore, juveniles or subadults generally obtain a lower social status, which may result in lower access to limited resources important for survival, such as the access to the main warren or high-quality feeding sites. Moreover, young rabbits are frequently chased out of the group territories by resident adults, in particular in autumn and early winter (Myers and Poole 1961; Cowan 1987; von Holst 1998). This behavior might generally cause negative stress effects and increase the energetic costs in this age class.

In conclusion, our studies reveal that different weather factors act together in limiting vital rates of European rabbits in the temperate zones. Firstly,

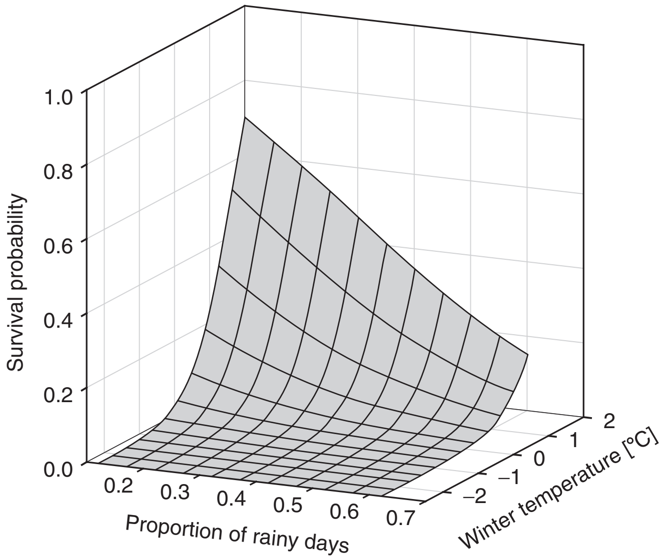

Fig. 4 Model graph for the probability of over-winter survival *S* of subadults in relation to winter temperature *t* and the proportion of rainy days *p* (=days with precipitation >1 mm) to which the individual juveniles were exposed during the first 2 months after emergence above ground. The logistic model is based on the data of winter survival of 657 individuals from 10 years, see statistics in Rödel et al. (2004a). Estimates were based on the logistic regression model $S = 1/(1+e^{(4.84 + 2.07t - 0.056d - 0.016b - 5.20r - 0.259s)})$, where *s* represents sex ($s_{male} = 0.5$, $s_{female} = -0.5$). Only exemplary data of female subadults are shown. The graph for males follows the same run, however on a lower level. The effects of population density *d* and date of birth *b* were set constant at their means

the onset and the regression of reproductive activity were affected by winter temperature and summer rain, respectively. Secondly, over-winter survival of first-year animals was directly affected by winter temperature and by the indirect action of rain in spring and early summer on the animal's pre-winter body mass.

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References

Aars J, Ims, RA (2002) Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology 83:3449–3456

Andersson M, Borg B, Meurling P (1979) Biology of the wild rabbit, *Oryctolagus cuniculus*, in southern Sweden. II. Modification in the onset of breeding, in relation to weather conditions. Swedish Wildl Res (Viltrevy) 11:129–137

Bell DJ, Webb NJ (1991) Effects of climate on reproduction in the European wild rabbit (*Oryctolagus cuniculus*). J Zool 224:639–648

Calvete C, Estrada R, Angulo E, Cabezas-Ruiz S (2004) Habitat factors related to wild rabbit conservation in an agricultural landscape. Landscape Ecol 19:531–542

Cowan DP (1985) Coccidiosis in rabbits In: Mollison D, Bacon P (eds) Population dynamics and epidemiology of territorial animals. I.T.E. Merlewood, Cumbria, pp 25–27

Cowan DP (1987) Aspects of the social organisation of the European rabbit (*Oryctolagus cuniculus*). Ethology 75:197–210

Crawley MJ (1983) Herbivory: the dynamics of animal–plant interactions. Blackwell Science, Oxford

Dudzinski ML, Mykytowycz R (1960) Analysis of growth rates of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). *CSIRO* Wildl Res 5:102–105

Erlinge S, Göransson G, Högstedt G, Jansson G, Liberg O, Loman J, Nilsson IN, von Schantz T, Sylvén M (1984) Can vertebrate predators regulate their prey? Am Nat 123:125–133

Flux JEC (1967) Reproduction and body weights of the hare *Lepus europaeus* Pallas in New Zealand. NZ J Sci 10:357–401

Flux JEC (1994) World distribution. In: Tompson HV, King CM (eds) The European rabbit. The history of a successful colonizer. Oxford University Press, Oxford, pp 9–21

Gonçalves H, Alves PC, Rocha A (2002) Seasonal variation in the reproductive activity of the wild rabbit (*Oryctolagus cuniculus algirus*) in a Mediterranean ecosystem. Wildl Res 29:165–173

Hamilton WJ (1940) Breeding habits of the cottontail rabbit in New York State. J Mammal 21:8–11

Helle E, Kauhala K (1995) Reproduction in the raccoon dog in Finland. J Mammal 76:1036–1046

Hudson R, Müller A, Kennedy GA (1995) Parturition in the rabbit is compromised by daytime nursing: the role of oxytocin. Biol Reprod 53:519–524

Katzner TE, Parker KL, Harlow HH (1997) Metabolism and thermal response in winter-acclimatized pygmy rabbits (*Brachylagus idahoensis*). J Mammal 78:1053–1062

King DR, Wheeler SH, Schmidt GL (1983) Population fluctuations and reproduction of rabbits in a pastoral area on the coast north of Carnarvon, W.A. Austral Wildl Res 10:97–104

Kline PD (1963) Notes on the biology of the jackrabbit in Iowa. Proc Iowa Acad Sci 70:196–204

Lande R, Enden S, Sæther BE (2003) Stochastic population dynamics in ecology and conservation. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford

Lima M, Jaksic FM (1998) Population variability among three small mammal species in the semiarid Neotropics: the role of density-dependent and density-independent factors. Ecography 21:175–180

Loison A, Langvatn R, Solberg EJ (1999) Body mass and winter mortality in red deer calves, distengling sex and climate effects. Ecography 21:175–180

Marboutin E, Hansen K (1998) Survival rates in a nonharvested brown hare population. J Wildl Manage 62:772–779

Milner J, Elston DA, Albon SD (1999) Estimating the contribution of population density and climatic fluctuations to interannual variation in survival of Soay sheep. J Anim Ecol 68:1235–1247

Myers K, Bults HG, Gilbert N (1977) Stress in the rabbit, Part XI in the series “The biology of the wild rabbit in climatically different regions in eastern Australia”. Austral J Ecol 10:103–136

Myers K, Poole WE (1961) A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. II. The effects of season and population increase on behaviour. CSIRO Wildl Res 6:1–41

Myers K, Poole WE (1962) A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. III. Reproduction. Austr J Zool 10:225–267

Myers K, Poole WE (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 (1958) Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). I. Establishment of the colony. CSIRO Wildl Res 3:7–25

Mykytowycz R (1962) Epidemiology of coccidiosis (*Eimeria* spp.) in an experimental population of the Australian wild rabbit, *Oryctolagus cuniculus* (L.). Parasitology 52:375–395

Richardson BJ, Wood DH (1982) Experimental ecological studies on a subalpine rabbit population I. Mortality factors acting on emergent kittens. Austr Wildl Res 9:443–450

Rödel HG (2000) Low temperature effects and social influences on physiological condition of subadult wild rabbits. In: Heldmaier G, Klingenspor M (eds) Life in the cold. Springer, Berlin Heidelberg New York, pp 511–518

Rödel HG (2005) Winter feeding behaviour of European rabbits in a temperate zone habitat. Mamm Biol 70:300–306

Rödel HG, Bora A, Kaetzke P, Khaschei M, Hutzelmeyer H, Zapka M, von Holst D (2005) Timing of breeding and reproductive performance of female European rabbits in response to winter temperature and body mass. Can J Zool 83:935–942

Rödel HG, Bora A, Kaetzke P, Khaschei M, Hutzelmeyer H, von Holst D (2004a) Over-winter survival in subadult European rabbits: weather effects, density-dependence, and the impact of individual characteristics. Oecologia 140:566–576

Rödel HG, Bora A, Kaiser J, Kaetzke P, Khaschei M, von Holst D (2004b) Density-dependent reproduction in the European rabbit: a consequence of individual response and age-dependent reproductive performance. Oikos 104:529–539

Schröpfer R, Bodenstein C, Seebass C (2000) A predator-prey-correlation between the European polecat *Mustela putoris* L., 1758 and the wild rabbit *Oryctolagus cuniculus* (L., 1758). Z Jagdwiss 46:1–13

Soriguer RC, Rogers PM (1981) The European wild rabbit in Mediterranean Spain. In: Myers K, MacInnes CD (eds) Proceedings of the world lagomorph conference, Guelph, Ontario, pp 600–613

Stenseth NC (1999) Population cycles of voles and lemmings: density dependence and phase dependence in a stochastic world. Oikos 87:427–461

Stodart E (1968) Coccidiosis in wild rabbits, *Oryctolagus cuniculus* (L.), at four sites in different climatic regions in Eastern Australia. I. Relationship with age of the rabbit. Austr J Zool 16:69–85

Trout RC, Langton S, Smith GC, Haines-Young RH (2000) Factors affecting the abundance of rabbits (*Oryctolagus cuniculus*) in England and Wales. J Zool 252:227–238

von Holst D (1998) The concept of stress and its relevance for animal behavior. Adv Study Behav 2:71–131

von Holst D, Hutzelmeyer HD, Kaetzke P, Khaschei M, Rödel HG, Schrutka H (2002) Social rank, fecundity and lifetime reproductive success in wild European rabbits. Behav Ecol Sociobiol 51:245–254

Wallage-Drees JM (1986) Seasonal changes in the condition of rabbits, *Oryctolagus cuniculus* (L.), in a coastal dune habitat. Z Säugetierkd 51:26–36

Wallage-Drees JM (1989) A field study of seasonal changes in circadian activity of rabbits. Z Säugetierkd 54:22–30

Wheeler SH, King DR (1985) The European rabbit in south-western Australia II. Reproduction. Austr Wildl Res 12:197–212

Wright HM, Conaway CH (1961) Weather influences on the onset of breeding in Missouri cottontails. J Wildl Manage 25:87–89

Yoccoz NG, Stenseth NC (2000) Understanding the dynamics of bank vole populations, demographic variability, stochasticity and density dependence. Polish J Ecol 48:75–86