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Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*)

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Abstract Wild European rabbits of both sexes have separate linear rank orders, which are established and maintained by intensive fights. This paper presents data from a 14-year study (1987–2000) on the population physiology and behavioural ecology of wild rabbits living in a 22,000 m² enclosure and focuses on the relationship between social rank and reproduction in females. Group composition, social ranks, fecundity and reproductive success were known for all females ($n=197$) from the outset of their first reproductive season at an age of about 300 days until their death. The annual reproductive success of females was influenced to a large extent by their social rank. This depended on two effects of about equal strength: a higher fecundity of high-ranking females and a lower mortality of their offspring between birth and adulthood. The lifetime reproductive success of the females varied greatly. Only about 50% of all females had any reproductive success (range: on to nine adult offspring). The social rank achieved by the females during their first reproductive season substantially influenced their lifetime reproductive success: The mean reproductive lifespan and lifetime fitness of high-ranking females (ranks 1 and 2) was about 60% greater than that of lower-ranking females, although many of the latter also gained dominant positions in subsequent years.

Keywords Social rank · Fecundity · Lifespan · Lifetime reproductive success · Females · Wild European rabbit · *Oryctolagus cuniculus*.

Introduction

The concept of dominance is central to the study of animal social organisation (van Kreveld 1970; Syme 1974). Dominance hierarchies are usually more prominent in males than in females and are thought to regulate access to limited resources (Altmann 1962; Suarez and Ackerman 1971; Floody 1983). In males, priority of access to mating partners should result in a higher reproductive success in dominant individuals, as already suggested in the 1930s by Zuckerman (1932) and Maslow (1936). Because dominant individuals can supplant subordinates from limited food resources and nesting sites, dominant females should be able to rear their offspring more successfully. In addition, in most mammalian species, social subordination leads to stress responses which can greatly impair the reproductive functions of females (reviews in e.g. Kaplan 1986; von Holst 1998).

In the first comprehensive review on dominance and reproductive success, Dewsbury (1982) concluded that the evidence for a positive relationship between dominance and reproductive success is most compelling in carnivores and ungulates. In a more recent review of nearly 700 studies using all available indicators of reproductive success, Ellis (1995) supports this assessment and suggests that rodents can also be added to these groups. However, depending on the indicators used to assess reproductive success, 20–40% of the studies contradicted the hypothesis of a positive relationship between dominance and reproductive success, especially among primates (see also Silk 1993). In these species, factors such as seniority and intricate coalitions probably interact with dominance to a much higher degree than in most other mammalian species. In addition, the absence of differences in reproductive success between individuals in a single reproductive season can obscure a higher reproductive lifetime success, given that the reproductive lifespan of dominant individuals significantly exceeds that of subordinates, since they may either live longer and/or start to reproduce earlier (Wasser and Barash 1983; Sibly 1986; Cowlshaw and Dunbar 1991; Berard 1999; van

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Noordwijk and van Schaik 1999). However, studies bearing on the question of a relationship between dominance and life expectancy in mammals are largely missing.

The present paper provides an overview of some results of a long-term study (1987–2000) on the population physiology and behavioural ecology of wild European rabbits and focuses on the relationship between social rank and fecundity, reproductive success and lifetime fitness of female wild rabbits living in a large enclosure under relatively natural conditions.

Methods

All animals (*Oryctolagus cuniculus* L.) were descended from five adult pregnant females and three adult males from different groups trapped in 1983 near Schwandorf (Bavaria, Germany). All females gave birth to litters within 10 days after capture. Nineteen offspring survived to adulthood and were used together with their mothers and the three males for further breeding. In the beginning, the animals were kept in small enclosures for breeding and methodological studies. Since 1985, the population has lived more or less undisturbed in a 22,000-m² enclosure. The animals can be observed from two separate outlook towers 4 m in height. The study area is encompassed by a 20×20 m grid system, delineated by numbered poles. The location of any rabbit can be recorded accurately to a 5×5 m grid reference. Behavioural data of all adult individuals have been gathered since 1987.

The enclosure is surrounded by two fences preventing escape of the rabbits. However, predators such as stone martens, polecats, domestic cats, stoats, buzzards, goshawks, tawny owls as well as crows and magpies can enter the enclosure (which was intended to allow more or less natural predation). Like rabbits in the wild, the animals of our population are hosts to several species of endoparasites (*Eimeria*, *Trichostrongylidae*, *Oxyuridae*), but we have so far had no cases of myxomatosis or rabbit haemorrhagic disease.

There are groups of trees as well as a pond within the enclosure, the latter being visited frequently by the rabbits during droughts. The vegetation (pasture grass mixture and forbs) provides sufficient food for the animals except during hard winters with deep snow, when the naturally occurring food is supplemented with hay (usually for 3–4 weeks in January). For better observation of the young animals, the ground vegetation is cut twice a year (usually in May and August).

In addition to several rabbit-dug burrows there are 14 artificial concrete burrow systems with six to ten chambers each located in the enclosure, which the rabbits use as main warrens of territories and also for breeding. All chambers and about 50 female-dug breeding stops (length 0.5–2.0 m) are prepared with an opening in such a way that checking of the young from their first day of life is possible without destroying the entrance sealed by the females. More than 100 traps made of wood are evenly distributed over the whole area, and are baited with salted peanuts three times a week. Most of the time the traps are locked, and are used by the animals as sunshade and hiding-places.

Every morning the entire enclosure is patrolled and checked for dead animals. All burrow systems and breeding stops are checked, and the body masses of nestlings and their survival is recorded; on the 12th day of life, the sex of the offspring is determined and all individuals are marked by ear tags.

Once a month, all traps are unlocked for 2–3 days to capture the adult animals (capture success depending on season and animal number: 65–95%). All animals are weighed and scrutinized for wounds, indicators of disease (e.g. for a sticky anal region caused by diarrhoea), and for their state of reproduction (blood circulation (colour) of the vagina, pregnancy, development of mammary glands). In addition, a blood sample is taken from each animal for endocrinological, immunological, and genetic investigations (not discussed here).

During the reproductive season, the abdominal fur of each adult female is dyed with a different colour (silk color; Marabu). Because females pluck out their fur for nest building, the maternity of each litter is indicated by the colour of the fur found in the nest. Maternity is additionally confirmed by behavioural observations of the females, such as entering the nest for nursing, marking and defence of the nest site.

To determine group composition, territory size and social rank, the behaviour of the adults is observed during their peak activity (the last 4–5 h before dawn: Wallage-Drees 1989) with binoculars from the two observation towers at the periphery of the enclosure; behavioural patterns are classified according to Southern (1948), Lockley (1961), Myers and Poole (1961), Mykytowycz and Hesterman (1975) and Cowan (1987). Every adult female is usually observed for a total of 3 to more than 8 h per month spread over several observation units (focal animal sampling: Altmann 1974).

Definitions

- Nestlings: young before age 20 days, when they leave their natal burrows; the weaning period ends around day 30 (own observations; Hudson et al. 1996 for domestic rabbits), when the females usually give birth to their next litters.
- Juveniles: offspring aged between 20 days and adulthood (see below).
- Adults: all animals surviving until 1 March of the year following their birth. Their mean age at that time is 304±2 days ($n=223$ females), and they are sexually mature. Although wild rabbits can reach sexual maturity with 3–5 months (Australia and New Zealand: Parer 1977; Gibb et al. 1985; Gilbert et al. 1987; Myers et al. 1994; Europe: Andersson et al. 1981; Soriguer 1981; Rogers et al. 1994), they do not reproduce until the following spring under our climatic conditions.
- Reproductive season: time span between conception of the first and birth of the last litter of a year. The period of gestation in rabbits is 30 days; since female rabbits exhibit postpartum oestrus they can give birth to litters at intervals of 30 days. To analyse the effects of the season on the reproductive performance of females, the reproductive season of each year was divided into reproductive cycles of 30 days beginning with the first birth of each year.
- Reproductive lifespan: time period between onset of adulthood and death.
- Fecundity: number of young born to a female.
- Reproductive success: number of offspring that survive to adulthood.
- Group: individuals that live in the same area (territory) and interact with each other regularly with agonistic and/or sociopositive behaviour (Mykytowycz 1959, 1960; Myers and Poole 1961; Cowan 1987).
- Territory: area inhabited by members of a group that is established and defended by males (sometimes also by females) against adult individuals of neighbouring groups or other rabbits.
- Social rank: social relationships between the individuals of a group are assessed by the directionality of the aggressive interactions. In wild rabbits, both sexes usually develop independent and strictly linear rank orders with higher levels of aggression between males than between females (review: Bell 1983). Fighting between females is most pronounced at the outset of the reproductive season. Once dominance relations are established, aggressive interactions are usually of a low intensity. Social ranks at the lower end of the hierarchy are often not evident, because the animals do not show any offensive behaviour. Therefore, the lowest rank indicated in this paper is rank 5. The social rank of each adult female was determined for every month. If a rank shift occurred, the rank during the onset (March to May) of the reproductive season was used for analysis.

Data analyses and statistics

Data are represented as means±SEs. Differences among several cohorts were tested with general linear models (GLMs) (for details

see text). An intractable statistical problem inherent in most long-term studies of natural populations (cf. Virgin and Sapolsky 1997) is the inclusion of reproductive data of the same females from different years and often with different ranks. We present the reproductive data of all females and years in Fig. 4. However, to prevent mixing of data from the same female taken during different years, the data were analyzed with one-way ANOVA for each reproductive year of the females separately. Furthermore, using ANOVA, we tested for differences in the reproductive data between their first and second reproductive season of females with the same rank, a decrease or an increase in rank. The level of significance was set at $\alpha=0.05$ for all tests (two-tailed). If not mentioned otherwise, all calculations were performed with Statistica, Kernel version 5.5 A, 1999.

From a total of 1,606 litters, 31 had to be excluded from analysis, because their mothers could not be identified.

Results

General results on reproduction

From 1987 to 2000, a yearly average of 23.6 ± 2.9 adult males (range: 9–45) and 36.3 ± 3.2 adult females (range: 16–60) with their offspring lived in 8–14 territorial groups in the enclosure. Within the groups [consisting of 2–3 (range: 1–5) adult males and 3–5 (range: 1–6) adult females], there was a sex-specific linear rank order (Fig. 1). Predation as well as intestinal diseases (caused by several species of *Eimeria* and nematodes) represented the major mortality factors.

The first litters were usually born in early April (range: March 9 to April 25). Considering 30 days of pregnancy, the reproductive season of the rabbits started in early March. The last litters were usually born at the end of September (range: August 26 to October 20), resulting in a mean annual reproductive season of 207 ± 4 days (range: 173–237 days, $n=14$). The duration of the reproductive season and the number of adult rabbits had significant effects on the fecundity and reproductive success of the females (multiple regression for both variables: $R^2_{\text{litters/female}}=0.14$, $P>0.3$; $R^2_{\text{offspring/female}}=0.02$, $P=0.2$; $R^2_{\text{adult offspring/female}}=0.28$, $P>0.5$).

Since female rabbits exhibit postpartum oestrus, they could give birth to up to seven litters at monthly intervals. However, the number of reproducing females decreased from about 80% in the first three reproductive

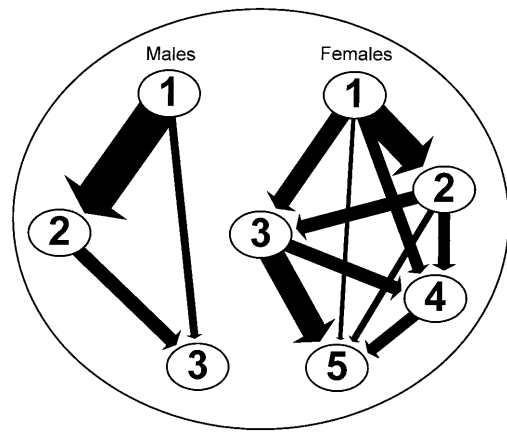


Fig. 1 Social ranks (1–5) of three males and five females of a rabbit group (RG 7) at the start of the reproductive season (March 1991). The ranks were determined by the directionality of the offensive interactions between the individuals during their peak activity before dawn. Arrow thickness indicates the number of interactions (e.g. male 1 vs male 2=10.0 offensive acts/h; female 1 vs female 5=0.2 offensive acts/h). Total observation time >8 h per animal

cycles to less than 10% in the last cycle (Fig. 2a) reducing the mean number of litters per female and year to 3.18 ± 0.05 (range: 0–6, $n=497$) with a mean litter size of 4.83 ± 0.04 offspring (range 1–9, $n=1,575$). Mean litter size varied between years and during the reproductive season with a maximum at reproductive cycles 2 and 3 (Fig. 2b). The mortality of nestlings between birth and day 12 was about 40% and affected litters of all reproductive cycles more or less equally (Fig. 2b, c). The number of offspring per litter surviving to adulthood decreased from the first to the fifth reproductive cycle; offspring born later never survived to adulthood (Fig. 2d; see Table 1 for statistics).

The biomass of entire litters at birth increased linearly with litter size and was more than five times higher in litters of nine juveniles compared to litters of one (334.9 ± 14.9 vs 51.0 ± 2.4 g). Despite the higher investment of females in larger litter size, the mean birth masses of neonates per litter decreased linearly with increasing litter size (Fig. 3; $R^2=0.11$; $n=1,199$; $P<0.001$).

Table 1 Effects of year (random factor) and reproductive cycle nested within year on the reproduction of females, tested with a general linear model (GLM). *Females with litters* is a binary variable and thus not normally distributed. We used a GLM with a binomial error and a logit-link function. To make the statistical test comparative to the others within the table, we applied an analysis

Model term (data per year)	Year of reproduction			Reproductive cycle		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Females with litters (%)	0.26	13,84	>0.5	21.5	84,3331	<0.001
Litter size at birth	0.74	13,76	>0.5	7.76	76,1486	<0.001
Litter size at day 12	4.49	13,76	<0.001	3.28	76,1486	<0.001
Adult offspring per litter	4.36	13,76	<0.001	3.85	76,1486	<0.001

of mean deviance and an associated quasi-*F*-test (for a recent application see Diemer and Schmid 2001). The residual degrees of freedom are much higher in *Females with litters* because females were scored for all reproductive cycles of the year. Note that data of all females and all years are used for the statistics

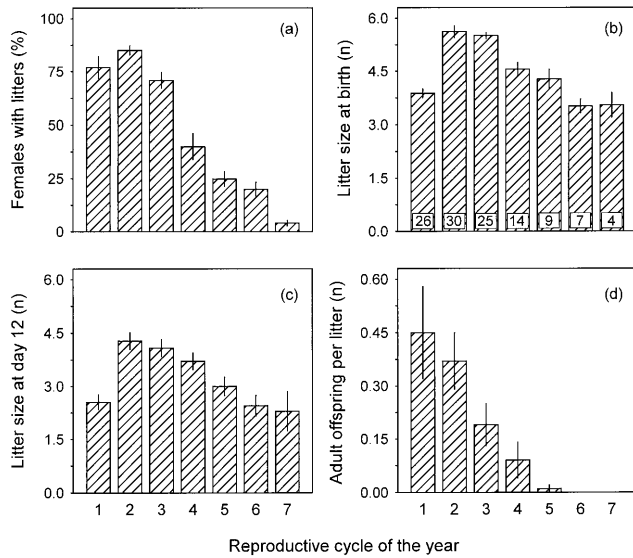


Fig. 2a–d Variation in fecundity and reproductive success of females during the reproductive season (means±SEs of the annual means of 14 years). The reproductive season of each year was divided in reproductive cycles of 30 days starting with the first litter of each season. Data only for females that gave birth to litters within the reproductive season. The mean number of litters per cycle is given at the bottom of **b**

Dependent on the number of adult females, between 58 and 220 litters (112.6 ± 11.2) with 274–1,116 nestlings (543.3 ± 57.3) were born annually (data from 14 years). From the total of 7,608 kittens, only $5.5 \pm 1.3\%$ (range: 0.0–14.9% per year) survived to their first reproductive season. There was no correlation between the number of young born during a given year and the number of offspring that survived until adulthood. The sex ratio of all 882 litters with known sex ratios at day 12 was not significantly different from 1:1 during the 14-year study (2.35 ± 0.05 males to 2.43 ± 0.05 females; sign test: $P=0.3$). Furthermore, the data of those 659 litters with no mortality between birth and day 12, showed a clear 1:1 sex ratio at birth (2.42 ± 0.05 males to 2.43 ± 0.05 females; sign test: $P>0.6$). However, due to a lower mortality rate after weaning, the number of females that survived to adulthood exceeded the number of males by nearly 40% (males: 11.4 ± 2.8 , range: 0–32; females 15.6 ± 3.7 , range 0–51); the difference was, however, not significant (sign test: $P=0.27$; data from 13 years with offspring surviving to adulthood).

Table 2 Effects of female social rank during their first 3 reproductive years on their reproduction (ANOVA)

	Year 1 (<i>df</i> =4,195)		Year 2 (<i>df</i> =4,125)		Year 3 (<i>df</i> =3,82)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Litter/female	5.63	<0.001	2.89	<0.03	2.87	<0.05
Offspring/female	5.45	<0.001	2.68	<0.05	3.28	<0.03
Adults/female	2.25	=0.065	0.51	=0.72	0.72	=0.55

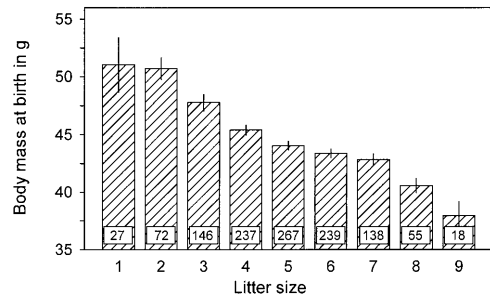


Fig. 3 Birth masses of neonates in relation to litter size. For analysis, the mean weight of the individuals (milk included) of each litter was used. Only those litters were analysed that had been found at the first day of their life. The number of litters is shown at the bottom of the bars

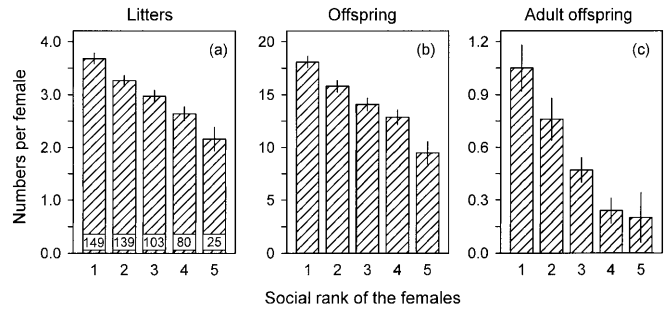


Fig. 4a–c Fecundity and reproductive success of all females in relation to their social ranks. Number of reproductive seasons per rank group is shown at the bottom of the bars in **a**

Social rank, fecundity and reproductive success of females

Fecundity and annual reproductive success of the females depended to a large extent on their social ranks. Dominant females produced more litters and offspring (Fig. 4a, b) than females with lower ranks. In addition, the number of offspring surviving to adulthood was higher in dominant females than in females with lower ranks (Fig. 4c). As a consequence of these two effects of about equal magnitude (higher fecundity and lower mortality rate of their offspring), rank 1 females produced about four times more adult offspring than rank 5 females (Table 2; to prevent mixing data from the same female taken during different years, the data were analysed with ANOVA for each of their first 3 reproductive years separately).

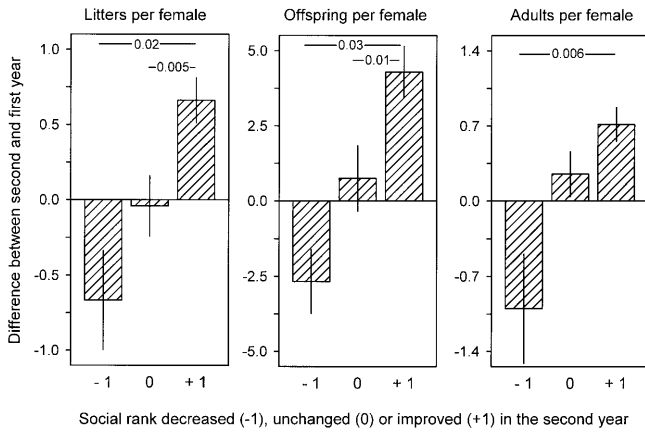


Fig. 5 Fecundity and reproductive success of females with unchanged ($n=48$), improved ($n=76$) or decreased ($n=6$) social ranks, in their first and second reproductive season. Significant differences between groups are indicated (LSD-test)



Fig. 6a,b Relationship between reproductive lifespan vs lifetime fecundity and lifetime reproductive success of 197 females

Further strong support for the relevance of social status came from a comparison of fecundity and reproductive success of females in their first and second reproductive season (Fig. 5): in females that maintained their ranks in both years, reproductive parameters did not change significantly. In contrast, improvement of social status was associated with a significantly increased fecundity and reproductive success, while after a decrease in the social hierarchy, fecundity and reproductive success of the females diminished (ANOVA: litters, $F_{2,128}=5.85$, $P<0.005$; offspring, $F_{2,128}=5.08$, $P<0.01$; adult offspring, $F_{2,128}=4.77$, $P<0.01$).

Social rank, life expectancy and lifetime fitness

Of the 197 females for which lifespan reproduction data are available so far, only 5 individuals had no offspring at all; the social ranks of the females were 4 and 5, and all of these females died before their second reproductive season. The females gained a mean reproductive age of 712 ± 37 days (range 69–2,086 days) and produced a mean of 7.68 ± 0.52 litters with 34.9 ± 1.9 offspring during

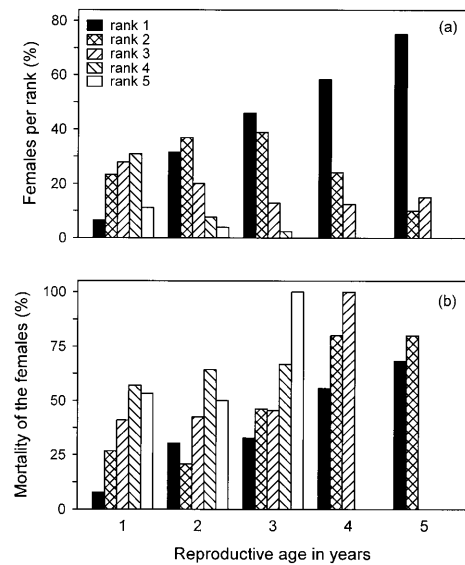


Fig. 7 Percentage of females per rank group and reproductive year (a) and their annual mortality rate (b). Animal numbers per reproductive age: year 1=197, year 2=130, year 3=85, year 4=48, year 5=20, year 6=8

their entire life (range: 0–50 litters and 0–130 offspring). However, only 47.2% of all females had any reproductive success (2.96 ± 0.20 ; range: 1–9 adult offspring). Altogether, there was a significant correlation between the lifespan of females and their fecundity and reproductive success (Fig. 6: litters (not shown): $R^2=0.68$, $P<0.001$; offspring: $R^2=0.78$, $P<0.001$; adult offspring: $R^2=0.25$, $P<0.001$). However, some females with lifespans of even 4 or more years had no lifetime reproductive success at all (Fig. 6b).

Due to a high mortality rate, the number of females decreased linearly from 197 individuals in their first reproductive season to 8 individuals in the 6th season. Only about 8% of the females gained a dominant position during their first reproductive season (Fig. 7a); the other females usually upgraded their ranks in subsequent years. In addition, there was a strong relationship between the social ranks of the females during each reproductive season and their mortality rates [Fig. 7b; GLM: log-likelihood (rank categorized after controlling for reproductive age) $\chi^2=40.4$, $df=4$, $P<0.001$; Crawley 1993].

Most important for the lifetime reproductive success of females was the social rank achieved by the individuals during her first reproductive season: while females with rank 1 and 2 survived a mean of three reproductive seasons, females with rank 3 and lower had only two seasons in which to reproduce (Fig. 8a). Due to their higher fecundity and reproductive success during their first breeding season and their longer reproductive lifespan, the lifetime reproductive success of females with ranks 1 and 2 during their first reproductive season was about 60% higher than that of all the other females, although many of the latter upgraded their ranks in subsequent years (Figs. 8b–d; statistics for Fig. 8 see Table 3).

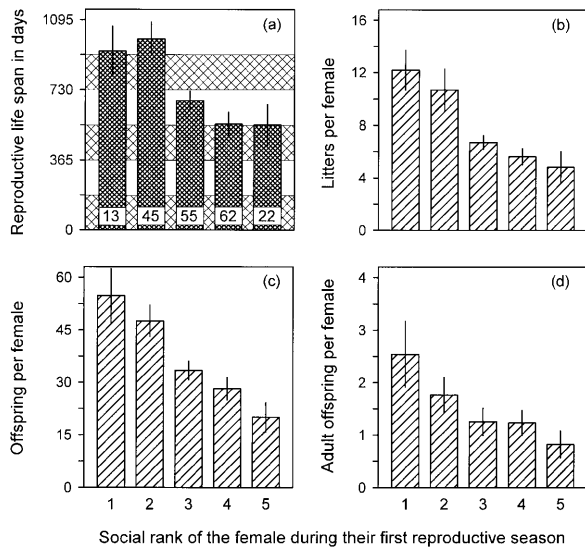


Fig. 8a–d Relationship between the social rank of the females at the outset of her first reproductive season and her reproductive lifespan (a), lifetime fecundity (b, c) and reproductive success (d). The number of females is shown at the bottom of a. The reproductive seasons (March to September) are indicated as *horizontal bars*

Table 3 Effects of year of birth and social rank during the first reproductive season nested within year of birth (random factor) on reproductive age and lifetime reproduction of females with high (ranks 1 and 2) vs lower ranks tested with GLM

Model term (data per lifetime)	Year (<i>df</i> =12,10)		Social rank (<i>df</i> =10,174)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Reproductive age	0.99	>0.5	3.42	<0.001
Litters	0.39	>0.5	4.52	<0.001
Offspring	0.91	>0.5	3.46	<0.001
Adult offspring	1.49	0.27	2.18	=0.02

Discussion

General results on reproduction

Due to its worldwide distribution and its economic importance, the social behaviour of rabbits has been studied intensively during the last 50 years in fenced areas as well as under natural conditions (summaries e.g. Mykytowycz 1958, 1959, 1960, 1961; Lockley 1961; Myers 1970; Gibb et al. 1978, 1985; Andrewartha and Birch 1984; Gibb 1993; Thompson and King 1994; Webb et al. 1995; Surridge et al. 1999). Nevertheless, complete data on social rank, fecundity and lifetime reproductive success of females are missing.

Our study was conducted on animals living in an enclosure in up to 14 territorial groups. The enclosure was large enough to allow natal and breeding dispersal, but prevented emigration and immigration over long distances (Daly 1981; Webb et al. 1995; Fuller et al. 1996;

Künkele and von Holst 1996). Since the number of founder rabbits trapped in the wild was small, fixation or loss of different alleles and a reduction in the genetic variation within the population was possible (Whitlock and McCauley 1990). However, the genetic variability of our population (band-sharing index=0.60, analysis of multilocus DNA fingerprints of 6 years) was in the range of three populations of wild rabbits living under natural conditions in Germany (Sylt, Oberlangenstadt, Schwandorf; $P_b=0.48-0.74$; Niedermeier and von Holst 1998).

The breeding season of the rabbits of our population started between the end of February and early March with the appearance of green vegetation. Most females usually reached oestrus within a few days and became pregnant. Because of a postpartum oestrus (Brambell 1948), females can deliver up to 7 litters during the reproductive season, but the mean number of litters was only 3.2 per female and year in our study. The same results have been found in shot samples of rabbits from natural populations in England, Australia and New Zealand (McIlwaine 1962; Boyd and Myhill 1987; Parer and Libke 1991). This reduced fecundity is probably due to uterine losses of whole litters (Brambell 1942, 1944, 1948; Thompson and Worden 1956; McIlwaine 1962; Lloyd 1963; Mykytowycz and Fullagar 1973; Boyd and Myhill 1987; Parer and Libke 1991).

The litter sizes varied between 1 and 9 with a mean of 4.8 offspring. This is in accordance with the results of other studies (Boyd 1985; Wallage-Dress and Michielsen 1989; Trout and Smith 1995, 1998). The reasons for the great variation in litter sizes in our and other studies with wild rabbits are unknown so far. Female age and rank had no significant effects on litter size in our study. In shot samples of rabbits from a natural population in New Zealand, Gibb et al. (1985) found a maximal litter size in 10- to 12-month-old females; since no rabbits of our study that survived to adulthood were born before March, at this age, the reproductive season of our rabbits had not yet started due to the climatic conditions.

Birth mass of the offspring was influenced by litter size, which is in accordance with the results Breuer and Claussen (1977) with domestic rabbits and studies with other species (e.g. Small 1981; Clutton-Brock et al. 1988), while Boyd (1985) found no effect of litter size on body mass of neonates in wild rabbits living in larger field enclosures; this conclusion is, however, based on the analysis of only 29 litters, which may be insufficient to detect effects of litter size on birth masses due to the large variation even between litters of the same size. Despite the great differences in energetic expenditures of the females, the number of young surviving to adulthood were not different between litters of one to nine offspring. A similar result was found by Mappes et al. (1995) in an experiment with bank voles. Litter enlargement did not change the number of young per female surviving to an age of 3 months. However, in a recent study with controlled manipulation of offspring number and body size in bank voles, the same research group

found a higher number of offspring surviving to the next breeding season in litters with increased number, despite the smaller body size of the individuals at weaning. Offspring size manipulation had no effect on offspring growth or survival (Oksanen et al. 2001).

High maternal investment in number of litters and their size did not affect the fecundity of females in subsequent reproductive seasons. In addition, we found no evidence for differential investments in male and female offspring before and after birth, as found in some other mammals (e.g. Clutton-Brock and Iason 1986; Clutton-Brock et al. 1988; Bacon and McClintock 1994; Kojola 1998). The sex ratio at birth and day 12 was 1:1, which is in accordance with the results of other authors (e.g. Brambell 1944; Watson 1957; Myers and Poole 1962; Parer 1977). Differences in mortality rates of the sexes were not present before the first winter period, which was survived by an average of about 40% more females than males. However, probably due to the large variation between years, this difference was not significant.

The high reproductive potential of the rabbits resulted in a tremendous overproduction of young every year (up to more than 1,000 offspring); however, over the past 14 years (1987–2000) only a mean 5.5% of all neonates survived to adulthood, which corresponds to many other studies of wild rabbits living in fenced areas or in the wild (Southern 1940; Tyndale-Biscoe and Williams 1955; Lloyd 1970, 1981; Parer 1977; Arthur 1980; Wood 1980; Richardson and Wood 1982; Wheeler and King 1985a, 1985b; Webb 1993; Gibb and Williams 1994). An especially high mortality rate was evident during the nestling period (nearly 40%), caused by predation or starvation, due to insufficient nursing and/or milk production of the females and insufficient nest quality.

After weaning, predation seems to be the major cause of death. However, the impact of diseases on the mortality rate is probably extremely underestimated. Because moribund or dead individuals are usually partially or completely eaten by predators before they can be found during the daily controls, they are counted under “predation” in our study (see also Tyndale-Biscoe and Williams 1955). The same conclusion was drawn by Dunsmore (1971) on the basis of a study of wild rabbits living in a coastal region of Australia. Having reviewed the evidence for food, vertebrate predation and diseases, he suggested coccidiosis as the most relevant mortality factor in subadult rabbits.

Social rank and reproductive success

The reproductive success of females depended to a large extent on their social ranks. The mechanisms responsible for the higher reproductive success of dominant females were manifold and were based on pre- and post-natal effects, which were probably caused by a better physical condition of the females. Although food can affect the health of females, food was never limited during

the breeding season in our study and competition for food is unknown in rabbits under natural conditions (Mykytowycz 1961; Cowan and Bell 1986). As shown by others, the most important factor affecting a female's condition was her relationship with other females in the group: Offspring born by subordinate (socially stressed) mothers usually show severe stunting (e.g. Myers et al. 1971; Mykytowycz and Fullagar 1973) in rabbits and other species (reviewed in von Holst 1998). While the social rank of females showed no significant influence on litter size, the total number of litters was higher in dominant than in subordinate females, which may be due to a lower intrauterine mortality rate in dominant females (Mykytowycz 1960). In addition, the survival rate of dominant mothers' offspring before and after weaning was much better. Altogether, the higher fecundity of females with high social ranks and the lower mortality of their offspring contributed equally to the rank-dependent differences in the reproductive success of the females.

An animal's lifetime reproductive success increases either by a longer lifespan and/or by an earlier start of breeding (Sibly 1986). In attempts to demonstrate rank-dependent lifetime reproductive success, one must determine the duration of rank occupancy as well as the reproductive success and mortality rate associated with each rank, because individuals of many species usually change ranks throughout their lifespan (Hausfater 1975). This was also the case in our rabbit population, where many changes in rank positions and high mortality rates occurred, especially between the end of the first and the onset of the second reproductive period. However, females that gained a dominant position during their first breeding season maintained their ranks usually until a few months before their death. The social ranks of females at their first reproduction period were clearly associated with their mean life expectancies. Females with rank 1 and 2 had one season more to reproduce (=50%) than females with lower ranks. Consequently, the lifetime reproductive success of females with high ranks (rank 1 and 2) at the onset of their first reproductive season was about 60% higher than in the females of lower rank, although many of the latter became dominant in the following years.

Reproductive lifespan as an important factor in lifetime fitness has also been found in primates (Altmann et al. 1988; Fedigan 1991; Bercovitch and Berard 1993; Kuester et al. 1995). However, life-table analyses, combining social ranks with life expectancies and reproductive success, are missing from other mammalian species living under more or less natural conditions, with one exception: van Noordwijk and van Schaik (1999), in a 12-year field study of *Macaca fascicularis*, demonstrated a clearly reduced reproductive lifespan in low-ranking compared to high-ranking females.

The underlying mechanisms for these rank-dependent differences in life expectancy are not known. However, stress responses, such as increased adrenocortical activities and heart rates as well as lowered immunoglobulin

levels are evident in subordinate wild rabbits of both sexes in our population (Eisermann 1992; von Holst 1998; von Holst et al. 1999), which suggests that stress responses associated with low social ranks are the cause of earlier death. Such stress responses may directly accelerate ageing (Everitt 1976; Selye and Tuchweber 1976; Arking 1991) or increase mortality due to infectious or other stress-related diseases (reviewed in von Holst 1998).

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