

No effects of dominance rank or sex on spatial behaviour of rabbits

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Abstract: The home range is an important measure of the spatial behaviour of animals. In rabbits (*Oryctolagus cuniculus*), spatial behaviour may be affected by social rank and sex. Subdominant animals are expected to have a larger home range and to forage farther from the burrow than dominant animals. Females are expected to have a smaller home range than males. To test these hypotheses, we determined home range size and distance to the burrow during foraging within a low density, semi-natural rabbit population in the Netherlands, using daytime observations of marked individuals. Individual median distance to the nearest burrow during foraging ranged from 3 to 16 m. Home range varied between 0.01 and 0.43 ha, which is the smallest home range area reported for rabbits in Europe. We found no difference in home range or foraging distance between males or females, or between dominant and subdominant animals. We postulate that this is caused by an interaction of two factors: low animal density and high availability of high quality food. This meant that there was no need to compete for best or safest foraging locations, and males did not need to protect females in their group against other males. This is also our explanation as to why the home ranges in our study are the smallest recorded.

Keywords: minimum convex polygon, MCP, *Oryctolagus cuniculus*, dominance hierarchy, food competition, confined population, home range, The Netherlands.

Introduction

The home range, "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943: 351), has been called the fundamental measure of space use of animals (Hemson et al. 2005). Home range size is useful for a wide range of applications, such as habitat analyses and modeling of population dynamics. It reflects a range of ecological processes, such as the effects of body size (Jetz et al. 2004), habitat quality (Herfindal et al. 2005) and mating behaviour (Sandell 1989).

In rabbits (*Oryctolagus cuniculus*), home ranges are usually situated around the burrow of the animals, which they use as nests for their young and as shelter against predators. It is to be expected that two characteristics of an individual animal can affect its home range size: social rank

and sex. Rabbits have a linear dominance hierarchy for males and females separately (Von Holst et al. 2002). This hierarchy is attributed to competition for females in males, and competition for the best breeding facilities (burrows) in females (Cowan & Bell 1986, Von Holst et al. 2002). As larger distances from the burrow result in more time spent looking for predators (Dekker, unpublished data), one would expect rabbits to compete for the safest foraging locations close to the burrow, with the dominant animals winning this competition. Sex also has an influence on home range size: males maximize survival by defending the females living in a burrow. This results in larger home ranges than those of females (Cowan 1987).

In this paper, we focus on the influence of dominance hierarchy and sex on spatial behaviour. We determine the home ranges of a low density, confined population of rabbits in winter

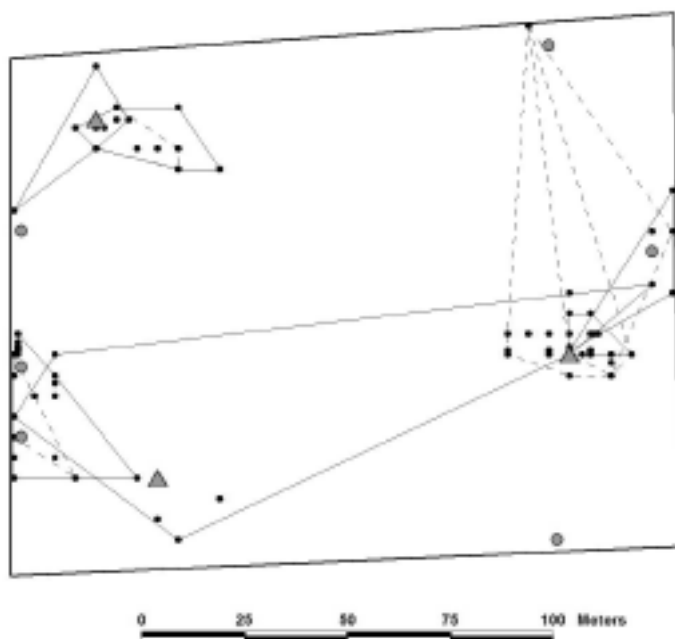


Figure 1. Burrows, rabbit locations and MCP home ranges. The thick line represents the fence around the enclosure. Black circles stand for rabbit locations; grey triangles for artificial burrows; grey circles for natural burrows. Male home ranges are solid lines; female home ranges dotted

and test the hypotheses that males have larger home ranges than females, and that dominant animals have smaller home ranges and forage closer to the burrow than subdominant animals.

Methods

Study site and population

A population of wild rabbits was established in a 2 ha enclosure in Wageningen, The Netherlands (51.99° N, 5.66° E). The enclosure was fenced off with dense mesh and an electric fence. Three artificial burrows, consisting of a large wooden 2 x 5 m box, with ten interconnected chambers and eight PVC entrance pipes were placed halfway into the earth. The burrows were located 90, 100 and 130 m from each other (figure 1). Self dug burrows were also in use during the study, and some separate pipes were sporadically in use as short-stay refuges. A regular grid of colour-coded pickets interspaced at 20 m was used to facilitate determination of the locations of the animals.

At the time of the present study (January and February 2003), six male and four female adult wild rabbits (table 1) were present in the enclosure, i.e. 5 animals ha⁻¹. The animals were marked using ear tags (Dalton Continental BV, Lichtenvoorde, The Netherlands) with an extra strip of aluminium with an individual colour coding and a number tattooed in the ear. Once a month, animals were trapped with livetraps, and weighed. The animals were vaccinated against myxomatosis and Rabbit Hemorrhagic Disease.

The grassland in the enclosure consisted mainly of Yorkshire fog (*Holcus lanatus*), red fescue (*Festuca rubra*) and common bent (*Agrostis capillaris*). It was grazed by six heifers from April to December of 2002, which resulted in a homogeneous, short vegetation. The grass height was mapped in January by 10 evenly distributed height measurements in 49 plots of 10 x 10 m across the enclosure. The actual height was measured by lowering a circular polystyrene disc with a central slot (a 'drop disc') down a vertical ruler until it rested on the grass (Steward et al. 2001). The distance to the ground was then read from the ruler. Vegetation heights within the

Table 1. Home range and median distance to the nearest burrow during foraging activity between January 17 and February 11, 2003. Home ranges were estimated using MCP methods (see text). Dominant: 1 = dominant, 0 = subdominant animal. *n* = number of locations used for calculation of the MCP home range.

Rabbit	Group	Sex	Dominant	Weight (g)	MCP (ha)	<i>n</i>	Median distance to nearest burrow (m)
Oranje	1	M	1	1580	0.06	565	5
Geen1	1	M	0	-	0.43	151	16
BZZ	1	F	1	1875 ^a	0.02	218	3
WWB	2	M	1	1630 ^a	0.03	243	6
WRB	2	M	0	1710	0.03	94	5
RGG	2	F	1	2020	0.02	271	5
ZRZ	3	M	1	1710	0.01	231	5
GRW	3	M	0	1220 ^a	0.03	103	8
Geen3	3	F	1	1500	0.14	333	5
GBG	3	F	0	1850	0.13	400	7

^a Weight measured one month before the study.

plots were averaged, and then averaged over the plots. The average $\pm$ 1 SE over the plots was 4.9 $\pm$ 0.96 cm.

Dominance hierarchy

The dominance hierarchy was determined by observing which animal supplants which: it is assumed that the dominant animals initiate and win more aggressive interactions than subdominant animals (Martin & Bateson 1993). We observed the animals using a focal sampling method, observing each animal for 30 minutes during 10 days. During these scans we noted the initiator and winner of aggressive interactions. Based on these data, we separately ranked the males and females by the number of supplantments. We tested for difference in weight between dominant and subdominant animals using an ANOVA.

Spatial behaviour

The locations of the animals were estimated using an instantaneous scan sampling design: positions of all animals are determined ('scanned') at a regular time interval. We scanned every 30 seconds, between 15:00 to 17:00. We did this over 13 days, between the 17th of January and the 11th of February 2003. Locations were entered

in a Geographic Information System (ArcView 3.2, Environmental Systems Research Institute Inc., Redlands, USA) for further analyses.

Home ranges were estimated using the minimum convex polygon (MCP) method (Mohr 1947): the home range is estimated by the minimum size polygon that encloses *all* the locations of an individual. This method is a robust non-parametric method that allows comparisons with most other studies. The MCPs were calculated using the software 'Home Range Extension' for ArcView (Rodgers & Carr 1998). We also calculated the distance from each location to the nearest artificial or self dug burrow.

As home range size and distance to the burrow were not normally distributed, we tested for differences in home range and distance to burrow between males and females and dominant and subdominant animals using a two-tailed Mann-Whitney U-test. Since we used each dataset for two tests, we applied a Bonferroni-correction to the critical values, rejecting null hypotheses only when *P*-values were below a critical value of $\alpha = 0.025$. We used Spearman's rank correlation coefficient to test for the relation between body weight and home range.

The study was assessed and approved by the Institutional Animal Care and Use Committee of Wageningen University (experiment code 1025).

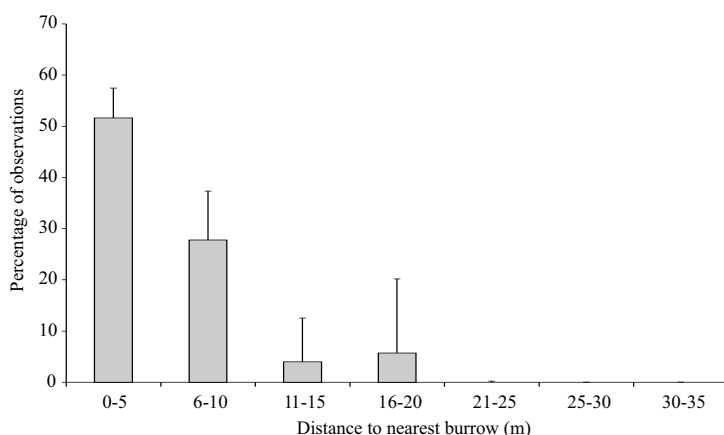


Figure 2. Frequencies (median and 3rd quartile) of observations per distance to the nearest burrow during foraging (n rabbits = 10). The observations were classified in 5-metre classes per individual animal and recalculated to percentages of total observations that fell in that class.

Results

Dominance hierarchy

During this study, rabbits formed two groups of two males and one female, and one group with two males and two females. The males of each group showed a clear linear ranking (table 1). In the group of four animals, the females also showed a dominance ranking. Dominant animals were not heavier than subdominant animals ($F_{1,7} = 0.543$, $P = 0.49$). One male animal, Geen1, moved between several burrows, but was only interacting with animals from one group. There were no aggressive interactions between males or females of different groups.

Spatial behaviour

The animals stayed near the artificial or natural burrows (figure 2): they were foraging within 5 m of a burrow in almost 50% of the observations. All home ranges contained at least one artificial burrow (figure 1). The animal that moved between groups, Geen1, had a relatively large home range.

The individual median distance from the nearest burrow ranged from 3 to 16 m (table 1). There was no difference in median foraging distance between male and female animals ($U = 7$, $Z = -1.14$, $n_{\text{males}} = 6$, $n_{\text{females}} = 4$, $P = 0.35$) or between dominant and subdominant animals ($U = 3$, $Z = -2.08$, $n_{\text{dom}} = 6$, $n_{\text{subd}} = 4$, $P = 0.07$).

MCP home range size ranged from 0.01 to 0.43 ha (table 1). Home ranges of males totally overlapped those of females in two groups (figure 1). Two females from group 3 made excursions far from the burrow, which resulted in a larger home range (table 1, figure 1). The MCP home ranges did not differ between males and females ($U = 12$, $Z = 0$, $n_{\text{males}} = 6$, $n_{\text{females}} = 4$, $P = 1.0$), nor between dominant and subdominant rabbits ($U = 7$, $Z = -1.07$, $n_{\text{dom}} = 6$, $n_{\text{subd}} = 4$, $P = 0.35$). There was no relation between weight of an animal and its home range (Spearman's correlation coefficient, $P = 0.19$).

Discussion

Although the population studied is not a natural population of rabbits we feel that the results are comparable with natural free-living populations: the animals showed similar behaviour compared to wild rabbits in natural conditions in the way they reacted to each other and to predators.

As in other studies of rabbit home ranges, all the observations were done during day time when the animals were most active. We assume that space use is not fundamentally different at other times of the day. This assumption is supported by anecdotal observations and by pellet counts: both at night and in the day time animals stayed close to the burrow. Faecal pellet numbers roughly reflect spatial use of the population,

and were highest close to the refuge, especially when corrected for latrines (Dekker, unpublished data).

Effects of rank and sex on spatial behaviour

Three other European studies compare the home range size of males and females separately. Cowan (1987) and McDonald (1989) found that home ranges of males were larger than those of females. Immink (1982) also found indications for this, but he could not test for differences due to a small sample size. In our population, there was no difference in home range size for the two sexes, although there were indications that males did defend the females against the other males living in the same burrow: home ranges of males entirely overlapped those of females in two of the three groups. In our study site, the animals formed pairs instead of breeding groups, often with an additional male, probably due to the low density. In such cases, there is no need to defend several females. Defending one female against other males will hence not lead to a difference in home range between the sexes.

We detected no difference in home range size or in distance to the burrow between dominant and subdominant animals. Again, we attribute this to the absence of competition due to the abundance of resources, in this case foraging space close to the burrow.

Sex and rank can interact however, especially during the breeding season, at high densities. Dominant male rabbits then have a larger home range than subdominant males, in the order of tenths to hundredths of hectares. This is probably caused by defending several females against mating attempts. Subdominant and dominant females have been found to have a much smaller home range (Myers & Poole 1961). The same dominance effect was probably a factor in a study of three rabbits in a dune area in the Netherlands. Animals with larger body weight, which may reflect dominance rank, had larger home ranges (Immink 1982). So, for dominant males the defense of females outweighs risk of being predated.

The subdominant male animal with the relatively large home range, Geen1 (table 1), is probably a so-called floater: a low ranking, (often) young, male animal without a fixed territory. This animal moved between two artificial burrows, foraging farther from these burrows, and was often chased away by the males from the two groups. Its median distance to the nearest burrow is also larger than that of the other rabbits. Floaters occur in many species, from lizards (Stapley & Keogh 2005) to red foxes (*Vulpes vulpes*) (Dekker et al. 2001). Lockley (1961) describes this phenomenon amongst rabbits. In that study, the floaters were in bad condition, whilst in our study, the weight of the animal was well within the range of the other animals.

Comparison of spatial behaviour in European populations

The home range size we observed in our population is the smallest found in Europe. Macdonald (1989) found home ranges of 0.13 ha for males and 0.11 ha for females in Holy Island, UK, but used a 95% harmonic mean estimator, which makes it difficult to compare these results to our study. Rödel (unpublished data) found MPC home ranges of 0.35 ha for females just before the onset of breeding and of 0.27 ha for females during the breeding period, in a confined population of 38 animals ha⁻¹ in Bayreuth, Germany. Immink (1982) reported home ranges of 0.53 ha for male rabbits and of 0.44 ha for female rabbits in a dune-area in the Netherlands. A comparison with this data is difficult since this author used an unconventional method to estimate home ranges. Cowan (1987) reported an average MCP home range of 0.71 ha for males, and 0.44 ha for females for rabbits on chalk grasslands in the south of the UK. Henderson (1979) found MCP home ranges of 0.3 ha to 0.8 ha for non-breeding females, using trapping locations. Other studies, performed in Scotland, found even larger home ranges (Hulbert et al. 1996, Kolb 1991a, Kolb 1991b).

In our study, the animals concentrated their foraging close to the burrow. The only other authors that report the distribution of activity as a

function of distance to the burrow are Armstrong (1987, sightings of animals), Bakker et al. (2005, as number of pellets and counts of movement) and Monclús & De Miguel (2003, as number of pellets). Compared to these studies, our data seem most skewed towards the burrows.

We postulate that the small home range and skewness of foraging distance to the burrow found in our study are the result of an interaction between two factors: population density and food quality. The density in our population was 5 animals ha⁻¹, which was the lowest of all the above mentioned studies that report rabbit density: density was 15 animals ha⁻¹ at Cowan's (1987) study site, 22 animals ha⁻¹ at McDonald's (1989) study site, and 38 animals ha⁻¹ in that of Rödel (H. Rödel, unpublished data). It is possible that with higher densities, lower ranking animals are forced to forage farther from the burrow, increasing the average home range. Another possible consequence of high density is an increasing number of floaters in the population, which results in a larger average home range. In a dense population rabbits do not form pairs but breeding groups of males and several females. In that case a male will have to increase its home range size because it has to defend more than one female.

In sub alpine areas of Australia, home ranges expand when growth rate of the vegetation declines (Myers & Bults 1977). It is therefore surprising that in our study winter home ranges were so small, when compared to the year-round ranges in other studies. This could be caused by the type of vegetation in our enclosure: the enclosure was grazed by cattle all summer. Grazing by larger herbivores can keep vegetation in a short state, with many tillers and nutrient-rich leaves (McNaughton 1984), a structure that rabbits prefer for foraging (Iason et al. 2002).

Conclusion

Although the rabbits in our study showed a dominance ranking, this did not result in differences in home range size or distances to the burrow be-

tween sexes or ranks, as reported in other papers. We attribute this to the low population density and good food quality, allowing animals to freely choose their feeding location. Our study was undertaken in a 'boring' time of the year for the researcher, but a calm time for the animals: there was no competition for space or females. This corroborates with Von Holst et al. (1999), who show that in winter months the number of aggressive interactions, offensive behaviour between individuals and stress hormone levels of rabbits are much lower than during mating and breeding in spring and summer.

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Samenvatting

Geen effect van rang of geslacht op het ruimtelijke gedrag van konijnen

De home range (activiteitsgebied) is een belangrijke maat van het ruimtegebruik van een dier en wordt veel gebruikt in fundamenteel onderzoek en in studies gericht op natuurbeheer. Bij konijnen (*Oryctolagus cuniculus*) hebben geslacht en sociale rang van het dier mogelijk invloed op de omvang van de home range. Van dominante

dieren is te verwachten dat ze kleinere home ranges hebben dan subdominante dieren, en vrouwelijke dieren kleinere home ranges dan mannelijke. Daarnaast zouden subdominante dieren op grotere afstand van de burcht moeten foerageren dan dominante. We hebben deze hypothesen getest door de home range grootte en afstanden tot de dichtstbijzijnde burcht van konijnen te bepalen in een halfnatuurlijke populatie konijnen met een dichtheid van 5 konijnen ha⁻¹. De mediane afstand tot de dichtstbijzijnde burcht varieerde van 3 tot 16 m. Home range grootte (minimum convex polygon), bedroeg 0,01 tot 0,43 ha. Dit is de kleinst bekende home range van konijnen in Europa. Eén mannelijk, subdominant dier had een zeer grote home range, dat overlapte met meerdere groepen en meerdere

burchten omvatte. We vonden geen verschil in home range of afstand tot de burcht tussen mannelijke en vrouwelijke, of dominante en subdominante dieren. We wijten dit aan de lage dichtheid van dieren en de begraasde, korte vegetatie. Doordat er weinig dieren waren en veel geschikte foerageerplaatsen, was er geen reden voor competitie voor de beste of veiligste foerageerplekken. Vanwege de lage dichtheid was er geen reden voor de mannelijke dieren om alle vrouwen uit de groep te beschermen tegen andere mannetjes. Hierdoor waren de home ranges van de mannelijke dieren niet groter dan die van de vrouwelijke dieren.

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