ORIGINAL INVESTIGATION

Home range of the European rabbit (*Oryctolagus cuniculus*) in three contrasting French populations

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Abstract

Despite their pest status in numerous areas throughout the World, the populations of European rabbits (*Oryctolagus cuniculus*) have strongly decreased in South Western Europe since the mid-20th century. Such a decrease constitutes a major threat on top predators and calls for a better understanding of its mechanisms to provide suitable management responses. Infectious diseases have been invoked as the main responsible factors, but they cannot by themselves explain the magnitude of this decrease. Habitat fragmentation may indeed act as a synergetic factor, and habitat use studies are needed to better understand the impact of fragmentation on rabbit population dynamics. We investigated the variability of home range size with respects to age, sex and season in three wild populations of rabbits using telemetry. Home ranges were smaller in the highest density populations (7333 and 6878 vs. 20,492 m^2) suggesting differences in habitat quality between the populations. In addition, home range sizes were larger during the reproductive season for both sexes, and adults tended to have smaller home ranges than juveniles. Clearly, the home range sizes reported here were smaller than those previously reported in rabbits.
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Introduction

The European rabbit (*Oryctolagus cuniculus*) is a paradoxical species because it has different and opposite status throughout the world. As a highly invasive species in numerous countries and oceanic islands, the most famous being Australia, the rabbit is a major threat for biodiversity at a global scale and claims for very efficient eradication measures (Courchamp et al. 2003). In its original distribution area, in South-Western Europe, the rabbit populations require a particular attention for efficient wildlife management as a major prey for endangered predators (e.g., for the Iberian lynx *Lynx pardinus* or the Bonelli's eagle *Hieraaetus fasciatu*) and as a major game species. In France, rabbit numbers have drastically decreased since the introduction of myxomatosis in 1952. Available data on hunting bags show that 13.2 millions of rabbits were harvested in 1974/1975 against 6.4 millions in 1983/1984 (Arthur and Guenezan 1986) and 3.2 millions in 1998/1999 (Marchandeau 2000). Myxomatosis and rabbit haemorarhagic diseases (RHD) are generally considered to be the main factors explaining such a decrease. However, myxomatosis and RHD alone do not satisfactorily explain the magnitude of this population decrease. Indeed, myxomatosis

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already present in 1974 when the hunting bag was still important and therefore cannot explain the current status of the rabbit. The RHD emerged in China in 1984 and the first occurrence of the disease in France was in 1998 (Morisse et al. 1991). Therefore, RHD cannot explain the decrease of the rabbit population size, since this decrease was already important between 1974 and 1983, before the emergence of the disease. At the same time, the agricultural landscape changed greatly and one can argue that habitat loss and fragmentation combined with the impact of viral diseases should be taken into account to really assess the determinism of the rabbit population decrease in France. To carry out this assessment, spatial dynamics, demographic and genetic studies with regard to landscape features remain the only reliable sources of information for identifying life history stages for which management or control will be most effective.

Home range is a basic but fundamental descriptor of habitat selection and use by animals. For prey species like rabbits, home range size and shape are determined by the availability and spatial distribution of an adequate source of food for maintenance and reproduction, shelters and covers from climatic variability and predators, and a place to breed (Gibb 1993). In wild rabbits, different studies have shown a great variability in home range size across populations living in contrasting environments (Gibb 1993; Hulbert et al. 1996; Daniels et al. 2003; Lombardi et al. 2003; Stott 2003; White et al. 2003) and it has been argued that home range size is directly related to habitat quality and distribution (Daniels et al. 2003).

Here, we estimate home range sizes of rabbits in three wild populations and assess the main factors of their determinism. The three study areas represent contrasted biogeographic conditions. The populations were expected to differ in terms of the spatial distribution of the habitat and its fragmentation levels due to different levels of management and agricultural exploitation. Such contrasts might have strong effects on the mean home range size of the populations, in combination or not with the traditional factors generally invoked as the determinants of home range size: sex (Gibb 1993; White et al. 2003), age and season (Hulbert 1996; Stott 2003).

Material and methods

Studied species and populations

The wild rabbit is a burrowing species living in polygynous groups of 2–10 adults members (Mykytowycz 1958; Bell 1983). Rabbits exhibit both social and territorial behaviour, defending relatively small territories (Gibb et al. 1978). Linear social hierarchy occurs in both males and females, females competing

for breeding sites whereas males compete more for mates. Natal dispersal is male biased (Kunkele and Von Holst 1996).

Three contrasting populations have been studied. In all sites, the climate is oceanic with a continental influence. Aubas (1°11′W, 45°4′N, Department of Dordogne) is situated in South Western France. The landscape is a cultivated open land constituted mainly of maize and walnut fields. Mean annual rainfall is 930 mm and mean annual temperature is 11.5 °C. Cerizay (0°40′W, 46°49′N, Department of Deux-Sèvres) is located in Western France. It is a landscape characterised by mixed farming and hedgerows. Mean annual rainfall is 780 mm and mean annual temperature is 11.1 °C. The 110-ha study area is managed for rabbit hunting. A free-living population has been established in artificial warrens. Density is around 5 rabbits/ha in each of these two populations. Saint Benoist (1°53′E, 48°42′N, Department of Yvelines) is located in Central France. The landscape is a cultivated open land with coppices. Farming practices, crops and field margin strips are managed for game. Mean annual rainfall is 630 mm and mean annual temperature is 10.1 °C. The density is lower (1–2 rabbits/ha) in Saint Benoist than in the two previous populations.

In each population, rabbits were caught with wire cage traps. They were equipped with *TW-5 Biotrack* transmitters with a loop antenna with a range of about 1.5 km and weighting 30 g (Biotrack Ltd, Wareham, UK). Their age was determined using the epiphyseal fusion of the cubitus (Morris 1972; Rogers 1982) which enables the classification of the rabbits into subadults (<6 months) and adults. A total of 56 rabbits (24 in Aubas, 20 in Cerizay, 12 in Saint Benoist) were equipped with a radio collar and localized at least 20 times (the strict minimum number of locations advocated in home range analysis, Worton 1987). Monitoring duration and number of locations per individual were extremely variable, ranging from 50 days to 549 days (mean = 269 days), and from 22 to 385 locations (mean = 101 locations) with fewer locations on average in Saint Benoist than in the two other populations (mean = 60, 88, 132 in Saint Benoist, Cerizay and Aubas, respectively, Kruskal–Wallis test $P = 0.08$, df = 2). The end of the monitoring was mainly due to end of life of the transmitters and also to the death of the animals, including by hunting.

We used a *Televilt RX-98E* receiver and a *Televilt Y-4FL* foldable antenna with transmitters' frequencies within the 148–149 MHz range to locate rabbits on the field. Rabbits are mainly active at twilight and during the night whereas they are in their warrens or in above ground resting places during the day. We first determined the radiolocation error by triangulation (Heezen and Tester 1967), which may be used during the night. At a 100 m distance, below which one can consider that the observer disturbs the animals and makes them move, the error on the home range size is about 300 m^2. We considered this error too large with respect to the home range size of rabbits (see Results) and therefore decided to focus on daily home ranges. We thus used the "homing-in" method (White and Garrott 1990), which enabled us to locate rabbits at less than 2 m without disturbing the animals.

Choice of a method for home range estimation

We chose to estimate rabbit home range size with the maximum convex polygon (MCP, Mohr 1947) method rather

than the kernel method (Worton 1989) or the k-nearest-neighbours convex hull method (k-NNCH, Getz and Wilmers 2004) for biological reasons. The European rabbit is a nocturnal species and since the great majority of locations were collected during the day, numerous locations were highly aggregated. Both the kernel and the k-NNCH methods are sensitive to aggregated data (with potential lack of convergence in the smoothing parameters, Hemson et al. 2005, Calenge personal communication). In addition, because the aim of our study was more to estimate the maximum area of activity than to describe the fine-scale habitat use, the MCP method seemed more appropriate. We estimated the home range of rabbits with two levels of outliers exclusion (Kenward 1987): MCP 95% to estimate the activity area of the rabbits, and MCP 50% to estimate the restricted "core area" of each individual.

Estimating the appropriate number of locations

Because of the well-known increase in home range size with increasing number of locations until home range plateaus, we used the 56 rabbits to estimate the appropriate number of locations k_{opt} needed to correctly estimate home range size. We followed the incremental area analysis (Odum and Kuenzler 1955; Kenward 2001) by drawing for each rabbit the relationship between the estimated home range size and the number of locations k used in the estimation. For each of the 56 rabbits, we followed a bootstrapping approach and performed 100 random samples of k locations (k varying from 20 to the total number of locations, with an incrementation of five). For example, if a rabbit had 37 locations, we estimated 100 MCP 95% home range sizes for $k = 20$, 25, 30 and 35 random locations. For each value of k, we calculated the mean of the home range size estimated by the 95% MCP method over the 100 samples. For each rabbit, the appropriate number of locations k_{opt} to estimate home range size was then selected as the value of k for which the home range size estimated is at least equal to 95% of the home range size estimated with the entire set of locations (MCP 95%). We then calculated the median value of k_{opt} over all the individuals, and then tested for a between-population difference in k_{opt} using a Kruskal–Wallis test (Sokal and Rohlf 1981). Only rabbits with a number of locations higher than the median value of k_{opt} were included for the subsequent spatial analyses ($n = 41$, 16 in Aubas, 16 in Cerizay and 11 in Saint Benoist, see Results).

Since the rabbit is a nocturnal species, one can expect a larger home range size when including nocturnal locations in the dataset. We assessed the nycthemeral stability of home ranges by comparing home range sizes estimated on the overall dataset (both diurnal and nocturnal locations) and on a reduced dataset including only diurnal locations. Both home range sizes should be equal if the rabbits visit the same areas during the night and the day. We used only the rabbits having at least 20 nocturnal locations ($n = 10$, 8 in Aubas and 2 in Cerizay). The very low sample size precludes the use of linear models and thus, a paired Wilcoxon test was used to assess the significance of the difference. A significant increase in home range size with the addition of nocturnal locations would make it necessary to remove these nocturnal locations from the dataset as all the rabbits were not monitored by night.

Temporal stability of home ranges

White and Garrott (1990) emphasized that one needs to integrate time in any home range analysis to assess the stability of the home ranges over the study period. To do that, we partitioned the 41 individual datasets into two equal time intervals.

A difference of home range size between the two intervals for some individuals might suggest either a movement of the individuals or an extension/retraction process of the home range. Such processes would lead to an over- or under-estimation of the home range size for some rabbits.

Effects of age, sex, area and reproductive season on home range

We then used both the MCP 95% and MCP 50% methods to describe respectively the home range, i.e. the maximum area of activity, and the core area of the 41 rabbits, to assess the effects of age, sex, studied area and reproductive season on home range and core area size. Home range sizes were log10 transformed before all the following analyses for a better fit with the hypothesis of normality of the linear residuals (Sokal and Rohlf 1981). Age classes were defined as follows: (i) subadults: rabbits first trapped as subadults who became adults during their monitoring; (ii) adults: rabbits first trapped as adults. We expected a larger mean home range for subadults because such individuals might be in pre-settlement (or transience) phase before establishing on a territory (Kunkele and Von Holst 1996 for an example). We also predicted larger home ranges in males than in females as previously shown (Cowan 1987; Gibb 1993, but see also White et al. 2003 for contrasting results). Finally, it has been suggested (Hulbert et al. 1996; Daniels et al. 2003; Stott 2003) that reproductive activity might be an important factor determining home range sizes in wild rabbits. In particular, mean female home range size is expected to increase during the reproductive season (i.e. the period when females are mating or pregnant) due to the search for nesting sites by non-dominant females or increasing foraging activity whereas the reverse is expected in males due to increasing territoriality. We thus tested these two hypotheses. The length of the breeding season was estimated for each area by determining the date of birth of the captured juveniles ($n = 81$ in Aubas, $n = 147$ in Cerizay, $n = 44$ in Saint Benoist). We then considered that, for the adults, the reproduction began one month before the first birth and finished one month before the last birth, to take the gestation length into account. To estimate the birth date of a juvenile, we used the relationship between age and weight (Marchandeau et al. 1995). Both the length and the beginning of the breeding season varied among populations. The reproduction lasted from December to August in Aubas, February to September in Cerizay and January to July in Saint Benoist. Individuals were assumed to be reproductively inactive during the rest of the year. For each individual, we separated the locations during the reproductive season and the locations during the rest of the year. We selected only the individuals having at least 20 locations in each of the two seasons, thus restricting our dataset to 28 individuals (14 in Aubas, 10 in Cerizay, 4 in Saint Benoist). We then estimated the home range size corresponding to the activity area (MCP 95%) and to the

restricted core area (MCP 50%) in both seasons. The mean number of locations during the reproductive season was higher than the mean number of locations during the rest of the year (104 and 48, respectively), mainly due to the difference in the length of the two periods. We did not find any correlation between the difference in number of locations and the difference in home range size for the two periods (result not shown).

Statistical analysis

We used general linear models (GLM) to assess the effects of sex, age (two modalities), and population (three modalities) on home range sizes of the 41 rabbits. The response variable was the MCP 95% home range or the MCP 50% core area. We started the model selection from the model pop × sex + pop × age + sex × age, and removed subsequently the interaction terms and the simple effect of the factors from the starting model. We did not test for the three-way interaction term due to sparseness of the data and lack of biological relevance.

We explored the influence of the reproductive season on home range size using a generalized linear mixed model (GLMM) and a Gaussian link function. This analysis used the 28 rabbits with sufficient data for such a test. GLMM were run with the 'nlme' R function that provides maximum likelihood estimates of the parameters. The response variable was the MCP 95% home range or the MCP 50% core area. Rabbit identity was treated as the random factor because a given rabbit provided two values of home range (reproductive and non-reproductive season) in the analysis. We accounted for the effect of population on home range size (see Results) and started the model selection from the model pop + sex × season, since the effect of the season should interact with the effect of sex (see above for the specific tested hypotheses).

GLMM were also used to test for the temporal stability of home range size for the 41 rabbits. In this analysis, the response variable was the MCP 95% home range, the random factor was the identity of rabbit, and the fixed factors were the sex, the population and the time interval (two modalities: beginning and end of each monitoring). We started the model selection from the model pop × sex + pop × int + sex × int, and subsequently removed the interaction terms and the simple effect of the factors from the starting model.

Model selection was based on an Akaike information criterion (AIC; Burnham and Anderson 1998). Following Burnham et al. (1995), we derived an AIC accounting for the effective sample size of our data set, here denoted AICc. We also derived the AICc weights and retained the model with the highest AICc weight for biological interpretations.

All statistical tests were done with R 2.2 software (R Development Core Team 2005) and spatial analyses were performed using the package ADEhabitat (Calenge 2006) developed for R software.

Results

Appropriate number of locations

The median value of k_{opt} for all the individuals was 50. This value did not differ between the three populations (Kruskal–Wallis $X^2 = 1.11$, $P = 0.57$). We therefore included all the rabbits having at least 50 locations in the following spatial analyses ($n = 41$, 4 males and 12 females in Aubas, 11 males and 5 females in Cerizay, 5 males and 4 females in Saint Benoist).

As expected for a nocturnal species, the addition of at least 20 nocturnal locations in the dataset strongly increased the home range size (paired Wilcoxon test $W = 53$, $P = 0.005$, $n = 10$, MCP 95%) with a median increase equal to 7%. As a consequence, we only used the diurnal locations for all the following analyses because most rabbits had only diurnal locations.

Temporal stability

The linear mixed models with the simple effect of the interval (AICc weight = 0.07) and with the additive effects of population and interval (AICc weight = 0.11) on home range sizes received considerably less support from the data than the models with the simple effect of the population (AICc weight = 0.43) and with additive effects of population and sex (AICc weight = 0.18). There was thus no overall difference in home range size between the two intervals. Indeed, more than half of the rabbits (25/41) showed a difference in home range size of less than 5000 m^2 between the two intervals. For the 16 rabbits showing a difference of more than 5000 m^2, we nonetheless mapped (Fig. 1) their locations in chronological order to assess whether or not these individuals had shifted, expanded or retracted their home range during their monitoring. Five out of the 16 rabbits seemed to have moved or shifted during their monitoring (a102, a111, a125 and to a lesser extent, cy114 and cy244, Fig. 1). All of them tended to have a smaller home range size during the second part of their monitoring that might suggest a transience phase before their establishment on a territory. No clear trend was found with regard to the age or sex of these five individuals (three females vs. two males; three subadults vs. two adults). From a methodological point of view, taking into account all the locations for these individuals led to an overestimation of the home range size. We thus used for these five rabbits the "corrected" home range size (i.e. based on locations during the second part of their monitoring) to assess the determinants of home range size in the subsequent analyses.

Effects of age, sex, area and reproductive season on home range

Using the MCP 95% home range as a response variable, two models were equally well supported by the data, underlining a similar effect of the sex in each population but different home range sizes in the population (Table 1, models pop + sex and pop with,
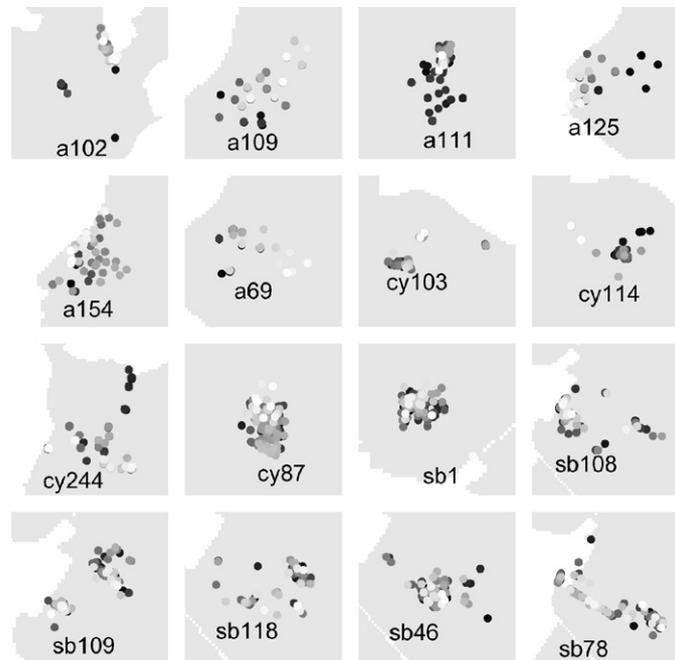
Fig. 1. Chronological mapping (from dark to light) of the locations for each of the 16 rabbits showing an increase in home range size of over 5000 m^2 between the two half of their monitoring (six rabbits in Aubas, four in Cerizay and six in Saint Benoist).

Table 1. Effects of population (pop), sex and age on the size of the MCP 95% home range and MCP 50% core area for 41 rabbits

Model	Parameters	MCP 95% home range		MCP 50% core area	
		AICc	AICc weight	AICc	AICc weight
pop + sex + age + pop × sex + pop × age + sex × age	11	120.63	0	158.42	0
pop + sex + age + pop × sex + pop × age	10	117.36	0	155.16	0
pop + sex + age + pop × age + sex × age	9	115.65	0	153.99	0
pop + sex + age + pop × sex + sex × age	9	114.16	0	151.14	0.01
pop + sex + age + pop × age	8	112.35	0.01	150.75	0.01
pop + sex + age + pop × sex	8	110.90	0.01	148.89	0.04
pop + sex + age + sex × age	7	109.55	0.02	148.73	0.04
Pop+sex+age	6	106.69	0.10	*145.90*	*0.17*
pop + age	5	106.43	0.11	147.71	0.07
sex + age	4	109.81	0.02	149.98	0.02
pop + sex	**5**	**104.43**	**0.30**	**144.03**	**0.43**
pop	**4**	**104.20**	**0.34**	*145.74*	*0.18*
sex	3	108.47	0.04	149.98	0.02
age	3	108.60	0.04	152.56	0.01

The model in bold were retained for biological interpretations given their AICc weights. Linear models were used in this analysis after a log10 transformation of sizes.

respectively, AICc weights equal to 0.34 and 0.30). Age and any interaction terms received considerably less support (Table 1). Home ranges in Saint Benoist were larger (mean = 20,492 m^2) than in the two other populations (mean = 7333 and 6878 m^2 respectively in Aubas and Cerizay, Figs. 2 and 3). As expected, males had larger home ranges than females (mean values: 13,180 vs. 7058 m^2).

Using the MCP 50% core area, the model with the additive effects of the population and the sex remained the best supported one (Table 1, AICc weight = 0.43). Age seemed to have a marginal effect on core area size because the triple additive model pop + sex + age was now equally well supported as the model with only a population effect (Table 1, AICc weights equal to 0.17 and 0.18, respectively). As expected, male core areas
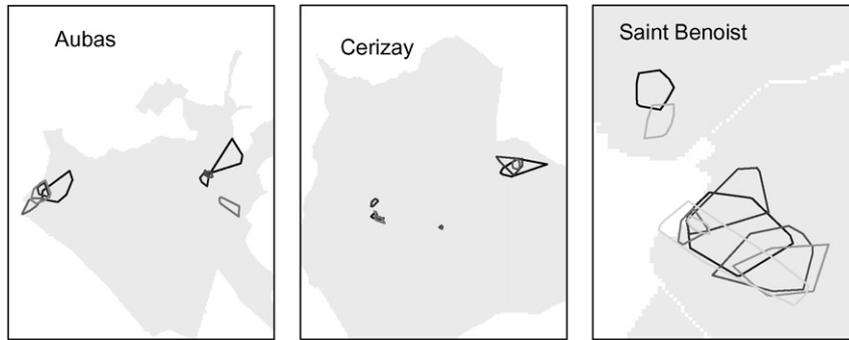
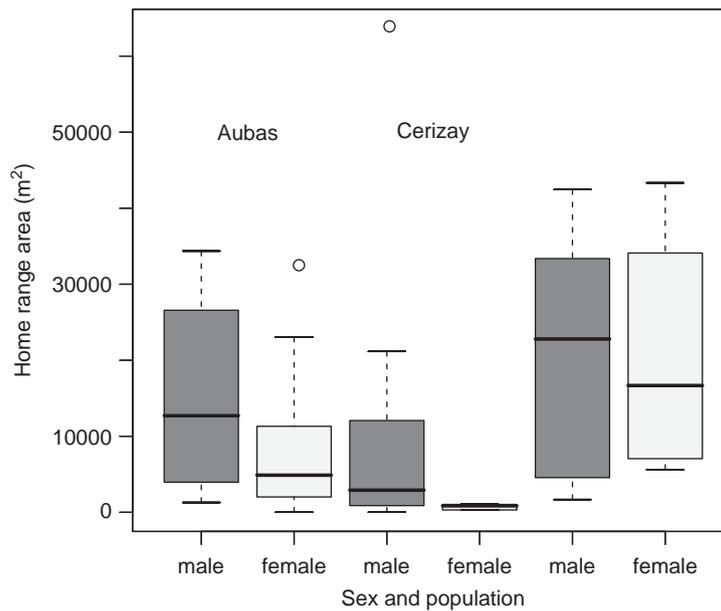**Fig. 2.** Home ranges (MCP 95%) of 41 European wild rabbits in the three French populations.

Fig. 3. Boxplot of the home range size (MCP 95%) for the two sexes in the three populations of European wild rabbits.

were larger than female ones (mean $= 4611$ and $738\,m^2$, respectively, for males and females). As for the MCP 95% home ranges, the larger core areas were found in Saint Benoist (mean $= 6332\,m^2$), Aubas and Cerizay having similar core areas sizes with mean values, respectively, equal to 1651 and $1519\,m^2$. Finally, subadult rabbits (mean $= 3194\,m^2$) tended to have a larger core area than adults (mean $= 2184\,m^2$).

Modelling the home range size as a function of population, sex and season with linear mixed models for the 28 rabbits with sufficient data led to contrasting results depending on the variable response used in the analysis. As previously shown, the population of origin had a strong effect on both MCP 95% home range and MCP 50% core area size (Table 2). However, the best model differed in the two cases. Using the core area sizes, the model pop + season is two folds more supported than the model pop + season + sex (Table 2,

AICc weights: 0.54 vs. 0.27). The effect of sex on core area size, if it occurs, is additive with the season effect. The core areas are larger during the reproductive season for the two sexes (385 vs. $348\,m^2$ in females; 1622 vs. $1246\,m^2$ for males), males having on average a large core area than females. Using the MCP 95% home range sizes, the best model was pop + sex × season (Table 2, AICc weight $= 0.51$) and was two folds more supported than the models pop + season and pop + sex + season (Table 2, AICc weights $= 0.23$ and 0.26, respectively). The MCP 95% home ranges were larger during the reproductive season both for males (10,295 vs. $6027\,m^2$) and females (7971 vs. $1958\,m^2$). It was not expected in males (Fig. 4).

To understand the dynamics of the increase in both home range and core area sizes, and its interaction with the sex of the rabbit, we analysed separately the data for the reproductive and non-reproductive season. On each

Table 2. Effects of population (pop), sex and season on the size of the MCP 95% home range and MCP 50% core area for 28 rabbits with enough data in both seasons

Model	Parameters	MCP 95% home range		MCP 50% core area	
		AICc	AICc weights	AICc	AICc weights
pop + sex × season	8	**208.72**	**0.51**	276.47	0.07
pop + sex + season	7	210.02	0.26	273.74	0.27
pop + season	6	210.22	0.23	**272.37**	**0.54**
pop + sex	6	220.02	0	277.63	0.04
Pop	5	219.79	0	276.37	0.07

The model in bold were retained for biological interpretations given their AICc weights. Linear mixed models were used in this analysis after a log10 transformation of sizes.
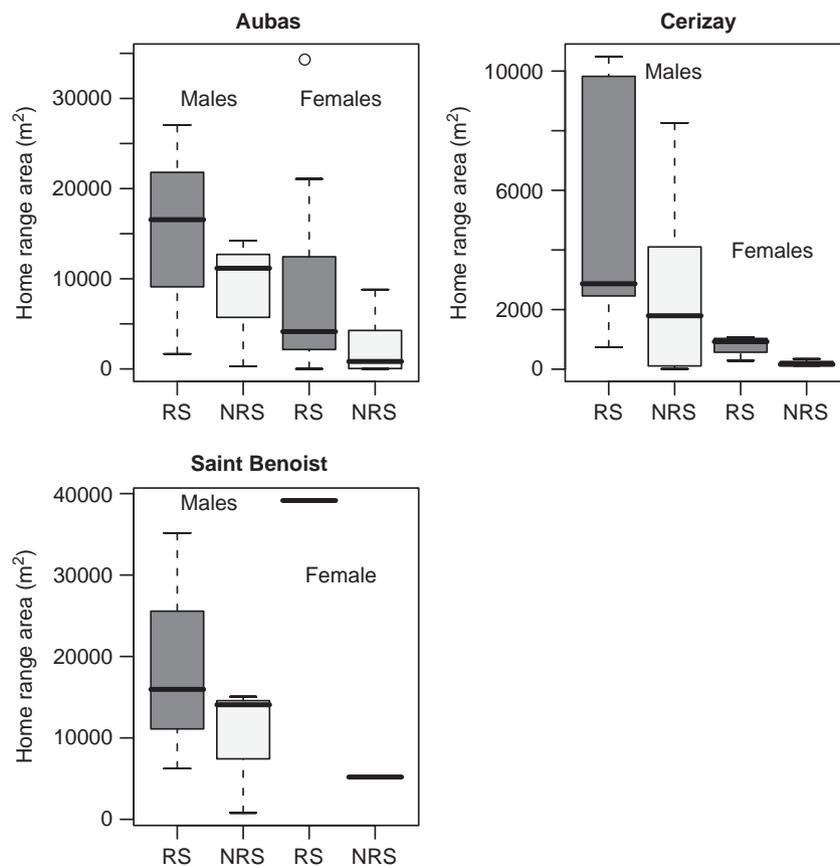
Fig. 4. Boxplot of the home range size (MCP 95%) for the two sexes during the reproductive and non-reproductive season.

data set, we specifically tested for the effect of the sex by contrasting the models sex against the null model intercept using linear models (Table 3). The reproductive season seemed to have an opposite effect on the between-sex difference in size depending on the area measured. Indeed, the sex effect on core area sizes mainly occurred during the reproductive season (Table 3, AICc weight for the model sex: 0.69 vs. 0.36 respectively for the reproductive and non-reproductive season), males enlarging their core area more than female during this period

(see above for the mean values). On the contrary, the model sex was better supported during the non-reproductive season (Table 3, AICc weight for the model sex: 0.64 vs. 0.49, respectively, for the non-reproductive and reproductive season), females enlarging more their MCP 95% home range than males during this period (see above for the mean values).

Finally, in all populations, there was extensive home range overlap (MCP 95%, Fig. 2), in agreement with the warren lifestyle of this species. Core areas (MCP 50%)

Table 3. Comparison of AICc weights of the null model intercept and the sex model in relation to reproductive season and the percentage of exclusion of locations: MCP 95% home range vs. MCP 50% core area

Season	Model	MCP 95% home range	MCP 50% core area
Reproductive season	sex	0.49	0.69
	intercept	0.51	0.31
Non-reproductive season	sex	0.64	0.36
	intercept	0.36	0.64

logically overlapped less than home ranges (MCP 95%, results not shown).

Discussion

In the preliminary step we determined the radiolocation error by triangulation, this technique being the most appropriate to record precise locations of the rabbits by night. This error was large with respect to the home range size of the rabbits and led us to focus on day locations. However, we measured the underestimation of the home range of some rabbits by using both telemetry and spotlights to record their precise location. We showed that nocturnal locations in the dataset increased by 7% the mean home range size, leading us to remove them from the dataset, as all individuals were not monitored by night. However, one may ask about the actual significance of these nocturnal locations. Indeed, the animals are active during the night and the disturbance caused by the observers may generate some unnatural movements, leading to a potential bias in the recorded locations.

We then showed the overall temporal stability of home range size across individuals, but we detected a strong heterogeneity among individuals. Indeed, five rabbits clearly moved during their monitoring, suggesting the occurrence of transience before the establishment on a territory, but with no trend regarding the sex or the age of these rabbits. Hence, such a pattern of movement could also be due to local disturbance of the habitat due to human activity (e.g. crop harvesting). A long-term study of dispersal including the monitoring of younger individuals as well as the description of the local spatio-temporal variability of the habitat of these populations is strongly required for a better understanding of the patterns of movement and establishment in rabbits.

When assessing the main factors influencing home range size, we did not find any effect of age on MCP 95% home range whereas this age effect was only marginal on core area sizes. As expected, sub adults tended to have larger core areas than adults. In rabbits, more than 50% of juveniles of both sexes disperse before they are 5 months old (Kunkele and Von Holst 1996). Pre-dispersing or dispersing rabbits are expected both to make exploratory movements and to shift their area of activity (Bray 1998 for an example in European hare *Lepus europaeus*), which might explain the larger core area of sub adults.

As expected, males had larger MCP 95% home ranges and MCP 50% core areas than females. But the magnitude of the between-sex difference in home range size seemed to depend on the reproductive activity and on the level of exclusion in the MCP home range estimation. Indeed, the reproductive season led to a similar increase in core area sizes in males and females whereas females enlarged more their MCP 95% home range than males did during the reproductive season (model pop + sex × season). Increasing home range and core area sizes during the reproductive season in males was not expected (Hulbert et al. 1996; Daniels et al. 2003; Stott 2003). On the contrary, it has been suggested that the increase in female ranging during the reproductive season is related to a peak in vegetal production, coinciding with maximum social interactions between males and females related to breeding (Gibb 1993, see Daniels et al. 2003 for similar results). It appeared that the same factors might explain the unexpected increase in male ranging during the reproductive season. However, there could be an alternative explanation to this pattern. Indeed, it appeared that males enlarge their core area more than females during the reproductive season, whereas the reverse occurred for the MCP 95% home range (Table 3). Hence, the unexpected increase in male home range size might be a behavioural response to the increasing activity of females. Males should enlarge the area they oversee in order to maintain their exclusive access to females, suggesting a female-defence mating system rather than a territory-defence mating system.

Among our three populations, home range sizes in Saint Benoist were larger than in the two other areas. This difference might be related to differences in habitat quality between the populations. Indeed, any individual home range is assumed to encompass all the necessary requirements for maintenance and reproduction. In rabbits, Gibb (1993) argued that home range size and shape depend on the distribution of shelters and covers, on the availability of food resources and of a place to breed. As a consequence, rabbits have to burrow in one type of habitat (e.g. gorse scrub, Daniels et al. 2003) and feed in another (e.g. improved and rough pasture, Daniels et al. 2003; Gibb 1993; Moreno et al. 1996). An optimal habitat would be one minimizing the distances between its various components. Indeed, Daniels et al. (2003) argued that the difference in home range size

between the low lying agricultural land they studied and the higher and afforested habitat (Hulbert et al. 1996) in Scotland suggests that the former habitat is more suitable for rabbits. At a more local scale, they also showed that habitat composition may affect both home range size and habitat use (Daniels et al. 2003). Despite the fact that we did not have a precise description of the habitat differences between the three populations in terms of floristic composition or availability of shelters and pasture vegetation, we can argue that habitat seems to be more adequate in Cerizay than in Saint Benoist, and to a lesser extent than in Aubas.

Overall, home range size estimates in the three populations of free-living rabbits were smaller (less than 2 ha) than those previously reported for this species (from 1.3 to 9.7 ha depending on sex, habitat and season, Hulbert et al. 1996; Daniels et al. 2003; Stott 2003; White et al. 2003) and than the one predicted by Kelt and Van Vuren (2001) for herbivores of rabbit size (7 ha, range [2.8–17.2]). Such a difference cannot be exclusively due to the use of diurnal locations only, resulting in a 7% underestimation in our study. Indeed, previous studies followed nearly the same protocol, mixing diurnal and nocturnal locations (Hulbert et al. 1996; Daniels et al. 2003 for examples), but the difference between our estimates and those previously reported are considerably greater than the expected 7% coming from our analysis. Again, one can argue that the French habitats studied are better quality habitats than the ones in other studies, that might be inconsistent with the strong decrease of rabbit populations in France (Marchandeau 2000). Undoubtedly, our results call for a better description and understanding of the temporal and spatial variability of the landscape features for each population, regarding both natural (e.g. vegetation, climate) and anthropogenic (e.g. agricultural, hunting) sources of local heterogeneities, that might act on habitat use and home range in this herbivore game species. For example, recent works have shown that there is a strong interaction between the spatial structure of rabbit populations and the impact of viral diseases such as myxomatosis (Fouchet et al. 2006): myxomatosis is epizootic, i.e. with a strong impact in small populations, but enzootic, i.e. with a moderate impact in large populations. This particular trait of the species may likely be partly responsible for the decline of rabbit populations observed in France.

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Zusammenfassung

Streifgebietsgröße von Wildkaninchen (*Oryctolagus cuniculus*) in drei französischen Populationen

Obwohl weltweit vielerorts als Plage verschrien, ist in Südwesteuropa seit Mitte des 20. Jh. ein starker Rückgang des Wildkaninchens (*O. cuniculus*) zu verzeichnen. Dies kann zu einer Bedrohung für Beutegreifer des Kaninchens werden, so daß ein tieferes Verständnis der Rückgangsursachen als Grundlage für Managementreaktionen wünschenswert ist. Infektionskrankheiten sind als Ursache angeführt worden, doch können sie allein das Ausmaß des Rückgangs nicht erklären. Habitatfragmentierung hingegen kann ein relevanter Faktor sein, und Untersuchungen zur Habitatnutzung sind unerläßlich, um die Auswirkungen der Fragmentierung auf die Populationsdynamik bei Kaninchen besser zu verstehen. Wir haben mittels Telemetrie die Variabilität der Streifgebietsgröße in drei freilebenden Kaninchenpopulationen mit Bezug auf Alter, Geschlecht und Jahreszeit untersucht.

Streifgebiete waren kleiner in den Populationen mit hoher Dichte (7333 und 6878 vs. 20492 m^2), was auf Unterschiede in der Habitatqualität schließen läßt. Während der Fortpflanzungsperiode waren die Streifgebiete in beiden Geschlechtern größer. Adulte Tiere hatten tendenziell kleinere Streifgebiete als juvenile Kaninchen. Die von uns ermittelten Streifgebietsgrößen waren kleiner als diejenigen, die in früheren Arbeiten für Kaninchen gefunden wurden.

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