Fine-scale genetic structuring in a natural population of European wild rabbits (Oryctolagus cuniculus)

Population & Conservation Biology Sector, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

Abstract

The genetic structure of a free-living tagged population of European wild rabbits (Oryctolagus cuniculus) was investigated for two consecutive years (1990 and 1991) using 10 polymorphic microsatellite loci. A specific social behaviour, the formation of stable breeding groups, influenced the genetic structure of the population. These breeding groups were shown to constitute genetically differentiated units with low levels of gene flow between them. The average relatedness among members of a social group was higher than within the population as a whole. As a result of female philopatry coupled with male-biased natal dispersal, the relatedness of females was higher than that of males, both within social groups and in the whole population. Furthermore, the average relatedness of females within groups was twice the relatedness of females between groups. This study reveals marked fine-scale, intrapopulation genetic structure, which is attributable to the social behaviour of the European wild rabbit.

Keywords: European rabbit, female philopatry, microsatellites, natal dispersal, Oryctolagus cuniculus, social structure

Received 6 May 1998; revision received 20 August 1998; accepted 9 October 1998

Introduction

The European wild rabbit (Oryctolagus cuniculus) lives in small, stable breeding groups consisting of one to three adult males and one to seven adult females (Myers & Mykytowycz 1958). Within these groups, stable linear dominance hierarchies are observed in both males and females, with males competing for access to females and females competing for breeding sites. Dominant individuals generally enjoy greater reproductive success (Bell 1983; Webb 1988). Rabbits exhibit gender-biased natal dispersal with males leaving their social group prior to their first breeding season and females remaining within the group (Dunsmore 1974; Webb 1988; Webb et al. 1995).

The social system of the European wild rabbit probably evolved in response to a number of adaptive pressures, including predation and competition for patchily distributed resources such as food and nesting sites (Bell 1983). Group living can result in a reduction in predation risk (Russ et al. 1998), better predator detection and allow more time for foraging (Sadedin & Elgar 1998). Furthermore, being part of a group may be a necessary prerequisite for the construction of burrows (Faulks et al. 1997). Species that live in groups because of a requirement for a limited resource, which is patchily distributed, may evolve social behaviour as this reduces detrimental effects of living together (Alexander 1974). Such detrimental effects could include aggressive interactions between individuals. Under these circumstances, such agonistic interactions can be reduced by co-operative behaviours. By remaining within the natal group, female individual rabbits are expected to be highly related to one another. With all the females within a group being kin, this is likely to lead to a greater co-operation between group members and hence may reduce aggressive conflicts between individuals.

Although philopatry may increase co-operation within group members, it also increases the chance of inbreeding. This does not necessarily reduce the total genetic variation, it reapporions it among the various hierarchical levels (Sugg et al. 1996). Hence, female philopatry is expected to lead to lower relatedness between female lineages from different social groups relative to random individuals within the population (Chesser 1991).

As the spatial (or hierarchical) scale is increased from within breeding group to population level, the rate of
inbreeding, relative to that expected under an overall random mating ($F_{is}$), changes from negative, through zero to positive (Dobson et al. 1997). Hence, at the level of the breeding group (the smallest level within which individuals interbreed) excess heterozygosity may be found, even with random mate choice (Cockerham 1969; Chesser 1991). When these groups are pooled, heterozygote deficit is observed owing to the Wahlund effect (Wahlund 1928).

Gender-biased natal dispersal can result in differing degrees of genetic relatedness among the male and female rabbits in a population. Relatedness among the philopatric gender within an area is expected to be higher than among the dispersing gender, provided that members of the latter show no tendency to move with relatives. The combined effect of gender-biased dispersal and the limited exchange of adults between breeding groups owing to social structure should affect the genetic structure of populations (McCracken & Bradbury 1977).

However, previous studies in Australia using allozyme loci have argued that social structuring in European wild rabbit populations does not have major genetic consequences, concluding that even stable, socially organized populations can approximate a panmictic population (Daly 1981). B. J. Richardson (personal communication) also reported that adult members of local populations of the European wild rabbit in Australia constitute a genetically homogeneous group, despite the high degree of observed social structuring. Recent work in Australia using mitochondrial DNA (mtDNA) markers has shown that the degree of localized genetic structuring can depend on habitat stability (Fuller et al. 1997).

The effects of social behaviour on the genetic structure of populations have been examined in other mammalian species using molecular tools. In particular, important aspects of close relatedness and dispersal of individuals within social groups has been explored in African wild dogs (Girman et al. 1997), dwarf mongooses (Keane et al. 1996) and sperm whales (Richard et al. 1996). In addition, in grey wolf packs dispersal was found to be gender biased, an observation not predicted from behavioural data (Lehman et al. 1992). Microsatellite analysis has also facilitated studies of mating systems and paternity in species such as the humpback whale (Clapham & Palsbøl 1997) and the toque macaque (Keane et al. 1997).

This study focuses on a free-living population of the European wild rabbit living on the campus of the University of East Anglia (UEA) in Norwich, UK. The colony has been studied over a number of years; programmes of regular trapping and behavioural observation ensure that all individuals are of known gender, age, social and sexual status and that affiliation to social group and hierarchical relationships within social groups are known (Webb 1988; Webb et al. 1995; D. J. Bell, unpublished).

Variation at microsatellite loci was used to investigate the genetic structure of the population. Previously, Webb et al. (1995) used a combination of behavioural observation, multilocus minisatellites and allozyme analysis to show significant male-biased natal dispersal and high genetic relatedness among female members of the same study population. This new study has enabled a finer-scale exploration of genetic structure within the population in order to address the issue of whether social behaviour has an impact on population genetic structure.

Materials and methods

The study area consisted of a 1.5-ha site naturally colonized by rabbits around 25 years previously. The area had once been part of a golf course and rabbits subsequently colonized the disused sand bunkers. Nonoverlapping territories around these bunkers were closely defended by individuals within specific social groups, and these Warren territories were clearly defined. The location of the main Warren systems (A–E) in 1990 and 1991 are shown in Fig. 1. Rabbits were trapped, tagged and blood samples taken from the marginal ear vein from all adult individuals in the study population (Webb et al. 1995).

Every adult member of the UEA population was genotyped for 10 microsatellite loci: sol03, sol08, sol28, sol30, sol33, sol44, sat5, sat7, sat8 and sat12 (Rico et al. 1994; Mougel et al. 1997; Surridge et al. 1997). Data for two consecutive years, 1990 and 1991 ($n = 43$ and 80 individuals, seven and nine social groups, respectively), were obtained. Polymerase chain reaction (PCR) amplification was carried out in 96-well microtitre plates, and scoring of alleles was performed on an ALF automated sequencer (Pharmacia), as previously described (Surridge et al. 1997).

Genotypic proportions were tested for deviations from Hardy–Weinberg equilibrium using the probability test implemented in GENEPop (Raymond & Rousset 1995). In this analysis, the probability of obtaining the observed genotypic distribution under the null hypotheses of random mating is computed and the $P$-value of the test corresponds to the sum of the probabilities of all the possible genotypic distributions of equal or lower probabilities. Further analysis of population subdivision and relatedness of individuals was performed by treating social groups and gender classes as separate groupings, in order to test the effects of social structure and gender, respectively, on the genetic structure of the UEA population.

Estimators of population subdivision were obtained assuming the infinite alleles mutation model (Kimura & Crow 1964). In this study, the evolutionary timescale was too short for mutation to have had a major impact on the variants estimated, and hence this mutation model can be considered the most appropriate in this case. Weir & Cockerham’s unbiased estimates of Wright’s $F$ statistics, $\theta$
(\(F_{ST}\)) and \(f (F_{IS})\) (Wright 1951; Weir & Cockerham 1984), were calculated using FSTAT (Goudet 1995) and their statistical significance was tested using randomized permutations. Estimates of relatedness between individuals within the population as a whole, and of males and females both within the population as a whole and within social groups, were obtained using Queller & Goodnight's (1989) \(r\), approximated as:

\[
\frac{2F_{ST}}{1 + F_{IT}}
\]

where \(r\) measures the average relatedness of individuals within a subgroup relative to the whole group. Relatedness within a gender group was estimated either relative to all members of the social group or relative to the whole population. For the analyses treating social groups individually, only the five largest groups from 1991, which contained three or more males plus three or more females, were included. The program KINSHIP 1.1.2 (Goodnight et al. 1997) was used to estimate pairwise relatedness between members of the population and within the different social and gender groupings. The program RT 2.0 (Manly 1991) was used to test the statistical significance of the differences between the mean relatedness of male and female rabbits, both within social groups and overall, during 1990 and 1991. Observed mean differences were compared with the differences between the means of 5000 random samples; the probabilities of obtaining, by chance, relatedness differences between the two sexes, which are greater or equal to the observed difference, are shown.

Results

All the microsatellite loci screened in the study were polymorphic, having between four and 10 alleles per locus. Observed heterozygosity values ranged from 0.221 to 0.769 in 1990 and 0.149 to 0.760 in 1991. The number of alleles per locus, and the observed and the expected heterozygosities under Hardy–Weinberg equilibrium, are shown in Table 1. The frequencies of the alleles generally showed bimodal distributions with two common alleles and a range of other alleles at low frequencies (Fig. 2).

At the individual loci over the whole population there were some significant deviations from Hardy–Weinberg proportions. In the 1990 data, sol44, sol08 and sat12 showed statistically significant deviations in the form of a deficit in the number of heterozygotes, while in 1991, sol03, sol44, sol08, sol33 and sat12 had significant deviations in the form of an heterozygote deficit (Table 1). The observed heterozygosity in most loci, both in 1990 and 1991, was lower than the expected heterozygosity if individuals are assumed to mate randomly over the whole population. However, tests for the statistical significance

© 1999 Blackwell Science Ltd, Molecular Ecology, 8, 299–307

Fig. 1 Map of the rabbit colony on the grounds of the University of East Anglia. Sand bunkers within which warrens were based are marked as A to E.
of this deviation revealed nonsignificant $P$-values in seven loci for the 1990 data and for five loci in 1991 (Table 1). Within social groups, no significant departures from Hardy–Weinberg proportions were observed, except for sol44 in 1991 where seven of the nine social groups showed significant deviation in the form of an heterozygote deficit (probability test in GENEPOP, data not shown). While deviation in the case of sol44 is probably because of the presence of null alleles, the deficits over the whole population can be ascribed to the Wahlund effect (Wahlund 1928). Across loci, excluding sol44, there were significant departures from Hardy–Weinberg equilibrium in both 1990 and 1991 ($P < 0.005, P < 0.001$, respectively) in the whole population (probability test, GENEPOP), whereas repeating the same test within social groups for both years revealed no significant deviation. The discrepancies between the loci (Table 1) in revealing this expected trend to a statistically significant level could be the result of sampling variance or the fact that much evolutionary stochasticity is associated with the variation at any given locus (Ewens 1983).

Table 1 Number of alleles, and observed and expected heterozygotes for the population in 1990 and 1991. $P$-values indicating deviations from Hardy–Weinberg equilibrium revealed by the probability test implemented in GENEPOP are also given.

<table>
<thead>
<tr>
<th>Locus</th>
<th>$N_A$</th>
<th>$H_O$</th>
<th>$H_E$</th>
<th>$P$</th>
<th>$N_A$</th>
<th>$H_O$</th>
<th>$H_E$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>sol30</td>
<td>5</td>
<td>0.465</td>
<td>0.407</td>
<td></td>
<td>6</td>
<td>0.425</td>
<td>0.437</td>
<td></td>
</tr>
<tr>
<td>sol03</td>
<td>8</td>
<td>0.535</td>
<td>0.555</td>
<td></td>
<td>9</td>
<td>0.438</td>
<td>0.492</td>
<td>$&lt;0.005$</td>
</tr>
<tr>
<td>sol44</td>
<td>4</td>
<td>0.186</td>
<td>0.351</td>
<td>$&lt;0.001$</td>
<td>5</td>
<td>0.138</td>
<td>0.499</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>sol08</td>
<td>6</td>
<td>0.395</td>
<td>0.445</td>
<td>$&lt;0.005$</td>
<td>5</td>
<td>0.338</td>
<td>0.396</td>
<td>$&lt;0.01$</td>
</tr>
<tr>
<td>sol28</td>
<td>8</td>
<td>0.837</td>
<td>0.689</td>
<td></td>
<td>10</td>
<td>0.713</td>
<td>0.655</td>
<td></td>
</tr>
<tr>
<td>sol33</td>
<td>9</td>
<td>0.605</td>
<td>0.631</td>
<td></td>
<td>8</td>
<td>0.575</td>
<td>0.638</td>
<td>$&lt;0.05$</td>
</tr>
<tr>
<td>sat12</td>
<td>6</td>
<td>0.488</td>
<td>0.662</td>
<td>$&lt;0.05$</td>
<td>7</td>
<td>0.425</td>
<td>0.566</td>
<td>$&lt;0.05$</td>
</tr>
<tr>
<td>sat5</td>
<td>5</td>
<td>0.442</td>
<td>0.499</td>
<td></td>
<td>7</td>
<td>0.475</td>
<td>0.488</td>
<td></td>
</tr>
<tr>
<td>sat7</td>
<td>5</td>
<td>0.651</td>
<td>0.652</td>
<td></td>
<td>7</td>
<td>0.538</td>
<td>0.562</td>
<td></td>
</tr>
<tr>
<td>sat8</td>
<td>4</td>
<td>0.535</td>
<td>0.534</td>
<td></td>
<td>4</td>
<td>0.413</td>
<td>0.440</td>
<td></td>
</tr>
</tbody>
</table>

$H_E$, expected heterozygosity; $H_O$, observed heterozygosity; $N_A$, no. of alleles.

Multilocus measures of genetic substructuring, based on estimates of $\theta$, indicated that there was significant subdivision among social groups within the population in both years (0.099 in 1990 and 0.036 in 1991). The single-locus estimates of this statistic are given in Table 2, with Bonferroni corrections for replication of the test across the data set. Single-locus estimates of $f$ ranged from −0.274 to 0.443 in 1990 and from −0.102 to 0.720 in 1991; however, these values were not significantly different from zero with the exception of locus sol44 in 1991. This is in agreement with the tests for deviations from Hardy–Weinberg equilibrium within social groups presented above. Hence, despite the large deficits in heterozygosity over the population as a whole, there was no evidence for inbreeding within social groups.

The estimates of the average relatedness between a pair of adult rabbits from the 1990 and 1991 populations were 0.0207 and 0.0114, respectively. Positive $r$-values might indicate that individuals were more closely related than would be expected for a randomly mating population. However, these relatedness values did not fall outside the 95% confidence interval of a simulated distribution of 1000 unrelated individuals, generated in KINSHIP (data not presented). The average relatedness within social groups was 0.186 for 1990 and 0.064 for 1991. This essentially confirmed the deficit in heterozygosity observed when the single-locus genotypic distributions were compared with Hardy–Weinberg expectations (Table 1).

When the data were divided into males and females, males overall had negative relatedness values for both years while females had positive values (−0.225 and 0.141 in 1990; −0.166 and 0.185 in 1991 for males and females, respectively). Negative relatedness values indicate that a pair of individuals are less related than would be expected for a pair taken at random from a randomly mating population. This trend was also observed within five individual social groups of 1991, shown in Table 3, with ranges given in parentheses. Randomization tests revealed that these differences were significant for the whole population in both 1990 and 1991, and for two of the five social groups tested (Table 3). The smaller number of either males or females within some of these groups meant that although mean relatedness of males was negative and mean relatedness of females was positive, this difference did not reach formal statistical significance. The fact that the average relatedness of females within groups ($r = 0.327$ in 1991) was nearly twice the average relatedness between any pair of females in the whole population ($r = 0.185$ in 1991) indicated that females not only remain within the population as a whole but also tend to stay within their family group.
Discussion

Long-term studies of the European wild rabbit population at the UEA have revealed various behavioural traits that could have a significant impact on the genetic structure of the population (Webb 1988; Webb et al. 1995). In this section, the main findings of these studies are briefly described with the aim of discussing whether the behavioural attributes contribute to the observed genetic structure of the population, as revealed by microsatellite markers.
First, there was a very low exchange of adults between the breeding groups in the population, also referred to as social groups. Once established within a social group, it is rare for an adult to leave and join another social group. For example, in 1991 only three males were seen to change social groups throughout the year, this largely being the result of intense, within-group, male–male competition (D. J. Bell, unpublished). The relatively large value of \( q \) obtained for two consecutive years supports this. It is also worth mentioning again that all individuals present in the population were included in this study, hence eliminating any experimental sampling error in the estimates of relatedness and population subdivision.

Second, both males and females defend the group territory, chasing away intruders (Bell 1983). Furthermore, males concentrate energy on pursuing females in their own social group where they are dominant; thus mating is non-random and effectively restricted to within members of the same social group. This social behaviour is expected to have an impact on a number of inter-related population genetic parameters. As in the case of the very restricted migration between groups, it will result in the genetic substructuring of the population among social groups. Also, the average genetic relatedness between a pair of rabbits from the same social group is expected to be higher than that between a random pair from the whole population. Estimates of the latter for the 1990 and 1991 data were 0.0207 and 0.0114, respectively, while the average within-social-group relatedness for the respective years was 0.186 and 0.064, confirming a considerable impact of the observed behaviour.

Third, behavioural observations have shown that of the juveniles born in a social group, the females tend to stay within the group while the males are more likely to disperse prior to their first breeding season (Dunsmore 1974; Webb 1988; Webb et al. 1995). In the UEA population, between 1985 and 1987 all males left their natal groups compared with 29% of females, while between 1988 and 1990, 85% of males dispersed compared with 5% of females (Webb et al. 1995). Thus, female philopatry results in selective recruitment of adults into social groups. The estimates of genetic relatedness within and between gender and social groups clearly indicate that recruitment into social groups is gender biased. The females within groups showed genetic relatedness that was at least twice the average relatedness of the males within groups. This higher relatedness among females can be explained by more female rabbits staying in their family groups compared with males; and because the average rabbit social group tends to have more females than males, this may lead to a greater cooperation between group members (Hamilton 1971). Therefore, male dispersal coupled with female philopatry appears to have led to female members within social groups being more closely related than the males.

The average relatedness between female European wild rabbits within social groups was also found to be

---

### Table 2 Single-locus estimates of \( f \) and \( \theta \) for 1990 and 1991

<table>
<thead>
<tr>
<th>Locus</th>
<th>1990</th>
<th>1991</th>
</tr>
</thead>
<tbody>
<tr>
<td>sol30</td>
<td>-0.246</td>
<td>0.089</td>
</tr>
<tr>
<td>sol03</td>
<td>-0.011</td>
<td>0.054</td>
</tr>
<tr>
<td>sol44</td>
<td>0.443</td>
<td>0.063</td>
</tr>
<tr>
<td>sol08</td>
<td>0.073</td>
<td>0.050</td>
</tr>
<tr>
<td>sol28</td>
<td>-0.274</td>
<td>0.050</td>
</tr>
<tr>
<td>sol33</td>
<td>0.003</td>
<td>0.045</td>
</tr>
<tr>
<td>sat12</td>
<td>0.105</td>
<td>0.200*</td>
</tr>
<tr>
<td>sat5</td>
<td>-0.202</td>
<td>0.292*</td>
</tr>
<tr>
<td>sat7</td>
<td>-0.134</td>
<td>0.135*</td>
</tr>
<tr>
<td>sat8</td>
<td>0.010</td>
<td>-0.014</td>
</tr>
<tr>
<td>All loci</td>
<td>-0.037</td>
<td>0.099*</td>
</tr>
</tbody>
</table>

\*P < 0.05 after Bonferroni correction.

---

### Table 3 Mean pairwise relatedness of males and females, overall for 1990 and 1991, within social groups

<table>
<thead>
<tr>
<th>Group</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1990</td>
<td>1991</td>
</tr>
<tr>
<td></td>
<td>−0.225 (−0.514 to 0.574)</td>
<td>0.141 (−0.447 to 0.861)**</td>
</tr>
<tr>
<td></td>
<td>−0.166 (−0.592 to 0.780)</td>
<td>0.185 (−0.530 to 0.944)**</td>
</tr>
<tr>
<td>Warren B</td>
<td>−0.432 (−0.447 to 0.150), n = 8</td>
<td>0.340 (−0.196 to 0.607), n = 4</td>
</tr>
<tr>
<td>Warren C-left</td>
<td>−0.008 (−0.202 to 0.113), n = 3</td>
<td>0.120 (−0.143 to 0.345), n = 4</td>
</tr>
<tr>
<td>Warren D</td>
<td>−0.034 (−0.224 to 0.096), n = 4</td>
<td>0.210 (−0.251 to 0.394), n = 5</td>
</tr>
<tr>
<td>Warren E</td>
<td>−0.153 (−0.267 to 0.241), n = 4</td>
<td>0.177 (−0.137 to 0.231)**, n = 7</td>
</tr>
<tr>
<td>Warren Nelson’s</td>
<td>0.145 (−0.075 to 0.221), n = 4</td>
<td>0.353 (−0.280 to 0.569)*, n = 7</td>
</tr>
</tbody>
</table>

\( n \), numbers of males and females within the social groups.

Ranges are given in parentheses.

Groups refer to independent social groups; the year refers to the same social groups over two consecutive years and hence is not independent.

Results of the randomization tests are indicated as *P < 0.01, **P < 0.005.

© 1999 Blackwell Science Ltd, Molecular Ecology, 8, 299–307
higher than the relatedness between females in different groups, reinforcing the observation of female members staying within their family group and not just within the population as a whole. The fact that females over the whole population showed significantly higher relatedness than males is probably the outcome of gender-biased emigration and immigration (Webb et al. 1995).

Another striking aspect of the genetic data that can also be attributed to the combined effect of the behavioural observations listed above, is the heterozygote deficits observed at some loci. While analysis of a family pedigree of domestic rabbits provided no evidence of null alleles (Rico et al. 1994; A. K. Surridge, unpublished), their presence at some loci may have contributed to the observed homozygote excess. However, further analysis of deviations from Hardy–Weinberg equilibrium within social groups only revealed significant deviations at locus sol44. Hence, the deficits in observed heterozygosity at the population level are probably a result of the pooling of isolated breeding groups, a Wahlund effect. Positive $f$-values were found over the population as a whole, and are expected to increase on an increasing spatial scale (Dobson et al. 1997). Within breeding groups it is predicted that heterozygote excess will be observed (Chesser 1991). Although our data showed negative $f$-values for some loci within social groups, these values were not significantly different from zero (Table 2). The absence of inbreeding at the individual warren level indicates that inbreeding is minimized by the mating system (i.e. male dispersal) and possibly by incest avoidance (Chesser 1991; Sugg et al. 1996).

In contrast to the results of our study discussed above, previous studies in Australia using allozymes revealed no significant genetic differentiation between social groups, leading to the conclusion that the social behaviour of the European wild rabbit does not result in genetic structuring at an intrapopulational level (Daly 1981; B. J. Richardson, personal communication). Allozyme markers generally show lower levels of variability than microsatellites (for studies on the European wild rabbit average heterozygosity = 0.42; Webb 1988) and hence the resolution required to detect differentiation of relatively recent origins or on a small scale may be lacking. Microsatellites, on the other hand, being highly variable with rapid rates of evolution, are useful for revealing population structure at such a localized level, especially when a large number of polymorphic loci are screened. In addition, the differences in genetic structure observed could be explained by differences in ecological and demographic parameters. It has been shown that the genetic structure of eastern cottontail populations is not solely a result of social structure, but is also dependent on ecological and demographic parameters (Scribner & Chesser 1993). In fact, it is the influence of environmental parameters that can determine the social behaviour which, in turn, influences the genetic structure. Gene flow in European wild rabbits can be increased in three ways: population expansion in favourable conditions; successful dispersal into recently occupied areas after a population crash (Daly 1979); and mass emigration when resource shortage develops (Myers et al. 1994). This is illustrated by a comparison of different habitat types in Australia. Rabbit populations in an arid region of Queensland, where population crashes are common, show no genetic differentiation and high levels of gene flow over 1600 km$^2$, but after moving into a semi-arid ecosystem, populations become more genetically structured (Fuller et al. 1997). So we may conclude that in favourable, stable conditions, such as those experienced in the UK, strict, stable, social organization develops, leading to the fine-scale genetic structuring observed in this study. Under less stable conditions, social behaviour may become more relaxed.

In the UEA population, a reduction in the average pairwise relatedness within the population was observed between 1990 and 1991. The population almost doubled in size between these two years owing to low mortality from myxomatosis and high overwinter survival. Additionally, a number of immigrant males moved into the population between the 1990 and 1991 breeding seasons. Of the 19 new adult males recruited into the population in 1991, eight were immigrants. All immigrants entering the population were male. Hence, the average pairwise relatedness between individuals in the population fell. However, average relatedness within social groups increased between the years. This is also concordant with a rise in the average size of the social groups. Hence, the increased relatedness of both males and females within social groups can be explained by the large number of female relatives that recruited into their natal social group and by a reduction in emigration of males born within social groups.

Extensive study of the rabbit population at the UEA revealed that individuals formed small, stable breeding groups, within which dominance hierarchies were observed, and that natal dispersal was biased in favour of males (Webb 1988; Bell & Webb 1991; Webb et al. 1995). Females were also found to be highly philopatric and there was little movement of adults between social groups. The detailed information available for each individual within the population has allowed an extremely fine-scale study of the genetic structure of the population. In the past, this genetic information has furthered our knowledge of behavioural traits by showing that dominant individuals have a higher reproductive success (Webb 1988). In this study, it has allowed detailed investigation of inbreeding within social groups, the apportionment of variation within the population and the relatedness structure of the population. Further application of the relatedness data...
will include investigating the movement of individuals among groups in relation to competition for resources within groups, reproductive success and geographical location of close relatives. Testing various hypotheses, as to why individuals move between groups, may provide more information pertaining to the evolution of group living in this species.

A comparison of the data generated in this study with the allozyme and multilocus DNA fingerprinting data generated in a previous study (Webb et al. 1995), revealed that smaller standard errors were obtained for estimates of relatedness between classes using multilocus fingerprints. While this may provide evidence that multilocus fingerprints give more accurate measures of relatedness than do screening of multiple single loci (presumably owing to the screening of a larger proportion of the genome), the band-sharing coefficients did not reveal differences between male and female classes. The differences between the two sets of data are probably a statistical artefact, given that minisatellite banding patterns were highly variable across gels and hence unweighted averages across gels were also averaged across the grouping of interest (males or females). It is also observed that while the allozyme data showed a consistent excess of heterozygosity within breeding groups, the data presented here showed an excess of heterozygosity (evidenced by negative $F_{IS}$) in only four breeding groups in 1990 and one in 1991. This could reflect the fact that the allozyme loci used in the above study were less influenced by null alleles and ‘allelic dropout’ (amplification failure of one allele in an heterozygote individual) than were the microsatellite loci screened here.

To conclude, the genetic structure of rabbit populations is influenced by the social behaviour of this species. The interplay between immigration, emigration and stability of social groups can greatly affect the genetic structure. Our study reveals the considerable power of a combination of behavioural observation coupled with microsatellite DNA analysis to reveal fine-scale genetic structuring within a population of a social species such as the European wild rabbit.

Acknowledgements

We wish to thank Terry Burke for comments on the manuscript. This work was supported by a grant from the BBSRC to D. J. Bell and G. M. Hewitt.

References


 Dobson FS, Chesser RK, Hoogland JL, Sugg DW, Foltz DW (1997)


Goodnight KF, Queller DC, Poznansky T (1997) KINSHIP 1.1.2. Department of Ecology and Evolutionary Biology, Rice University, Texas.


Surridge AK, Bell DJ, Rico C, Hewitt GM (1997) Polymorphic microsatellite loci in the European wild rabbit (Oryctolagus cuniculus) are also amplified in other lagomorph species. Animal Genetics, 28, 302–305.


This study was undertaken as part of the PhD work of Alison Surridge, investigating population structure of European wild rabbits using microsatellite markers. The research team is interested in genetic diversity and speciation, encompassing behavioural (Diana Bell), theoretical (Kamal Ibrahim) and genetic aspects (Godfrey Hewitt).