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Social structures, genetic structures and dispersal strategies in Australian rabbit (*Oryctolagus cuniculus*) populations

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Abstract In this study, the pattern of movement of young male and female rabbits and the genetic structures present in adult male and female populations in four habitats was examined. The level of philopatry in young animals was found to vary between 18–90% for males and 32–95% for females in different populations. It was skewed, with more males dispersing than females in some but not all populations. Analysis of allozyme data using spatial autocorrelation showed that adult females from the same social group, unlike males, were significantly related in four of the five populations studied. Changes in genetic structure and rate of dispersal were measured before and during the recovery of a population that was artificially reduced in size. There were changes in the rate and distance of dispersal with density and sex. Subadults of both sexes moved further in the first year post crash (low density) than in the following years. While the level of dispersal for females was lower than that of the males for the first 3 years, thereafter (high density) both sexes showed similar, low levels of dispersal (20%). The density at which young animals switch behaviour between dispersal and philopatry differed for males and females. The level of genetic structuring in adult females was high in the precrash population, reduced in the first year post crash and undetectable in the second year. Dispersal behaviour of rabbits both affects the genetic structure of the population and changes with conditions. Over a wide range of levels of philopatry, genetic structuring is present in the adult female, but not the male population. Consequently, though genetic structuring is present, it does not lead to inbreeding. More long-distance movements are found in low-density populations, even though vacant warrens are available near birth warrens. The distances moved decreased as density increased. Calculation of the effective population size (N_e) shows that changes in dispersal distance offset changes in density, so that N_e remains constant.

Keywords *Oryctolagus cuniculus* · Philopatry · Dispersal strategies · Genetic structures

Introduction

Alternate models of the structure of mammal populations are used by different researchers. Geneticists, developing further the work of Wright (1931, 1978), have seen populations, in the genetic sense, as either consisting of a series of discrete subpopulations in which breeding is effectively at random, or as continuous populations in which isolation by distance allows divergence in allele frequencies to occur by drift or selection (e.g. Richardson et al. 1986; Avise 1994). Parallel to this work, behavioural biologists have developed models of population structure built on the basis of analysing population attributes such as dispersal, breeding patterns and social structures, in the context of inclusive fitness (Alexander 1974; Wilson 1975). The differences in approach can be seen in the priority given to the avoidance of inbreeding as the basis for observed behaviour patterns by geneticists (Frankham 1995; Chesser and Baker 1996) and the need to leave offspring in the next generation as the driving force in behavioural strategies by behavioural biologists (Sugg et al. 1996).

Studies that combine detailed behavioural and genetic approaches are rare (Dobson 1998). Several bird species have been studied (see Wolff and Plissner 1998; Painter 2000), as have a range of different mammal species (see van Staaden 1995; Dobson 1998; Storz 1999). Amongst the mammals, several colonial species with ecologies somewhat similar to the rabbit have been studied, for ex-

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ample blacktailed prairie dogs (Dobson et al. 1997), Richardson's ground squirrels (van Staaden et al. 1996) and kangaroo rats (Waser and Elliot 1991). In prairie dogs and ground squirrels, but not kangaroo rats, geographic and genetic distances between individuals show a strong positive correlation. Thus, from the perspective of genetics, there is a need to identify mechanisms in the behavioural repertoire of species that could reduce the level of inbreeding. In all of the above cases, extreme female philopatry and male emigration from natal territories are observed. The net result is a population showing female-only genetic structuring, thereby avoiding inbreeding.

Behavioural biologists, on the other hand, have predicted that in colonial species that require suitable burrow systems to breed, young animals must make the choice between (a) leaving their colony of birth in the hope of finding a suitable place elsewhere but with a high pay-off in terms of breeding opportunities if they survive, or (b) staying in their colony of birth, with a higher probability of survival, while having their breeding opportunities suppressed by the dominant animal of the same sex (e.g. Keller and Reeve 1994; Emlen 1995; Perrin and Mazalov 2000), and either breeding at a low level or waiting until they can become dominant themselves. There are a number of issues that should enter into this decision including the probability of finding a place elsewhere, and the probability, if one stays home, of living long enough to breed (if male) or finding the necessary resources for gestation and rearing (if female). These issues in turn depend on factors like population density. Most colonial mammals do not show such extreme patterns of dispersal behaviour as the rodent species described above and there is a need to examine the behavioural mechanisms used and their genetic consequences in species showing less extreme dichotomies in behaviour.

The European rabbit [*Oryctolagus cuniculus* (L.)] is one such colonial species. It has been well studied in Australia where the macro- and microgeographic distribution of genetic variation has been described (Richardson 1980, 1981; Richardson et al. 1980; Daly 1981; van der Loo et al. 1987; Fuller et al. 1996; Zenger 1996) and the effective population size (N_e) has been calculated at 100–200 animals (Richardson 1981; Daly 1981). Ecological and behavioural parameters vary markedly between Australian rabbit populations in different areas; for example, productivity varies between 15–38 kittens/doe per year and survival to 24 weeks of age between 20–55% (Gilbert et al. 1987). As a consequence, the balance of strategies used by young animals in finding a place in the adult world may be different in different areas (Cowan 1987). Previous studies on the biology of the rabbit in Australia therefore provide a context in which to examine both changing behavioural strategies and genetic structures. In this study, the pattern of movement of young male and female rabbits and the genetic structures present in adult male and female populations in four habitats were examined (project 1). In addition, the pattern of changes in movement patterns and genetic structure before, and for several generations after a deliberate reduction in density were followed (project 2). The data presented for project 1 were originally collected for other purposes (see references below).

Methods

Rabbits were trapped in treadle-operated box traps set overnight using either oaten grain or diced carrot as bait. All rabbits were sexed and ear tagged when first captured. Weight, location and condition were noted on each capture occasion. Because rabbits live largely in warrens, trapping was carried out by placing traps on the surface of each warren and rabbits could then be allocated to that warren (social group; but see below). As traps were set near all burrow entrances, young born to subdominant animals using nesting stops would have been detected. Social groups consist of from two to ten or more adult animals. Inspection of the field data for animals captured several times shows that rabbits up to 600 g in weight (kittens) do not move and can be considered to be on their warren of birth. Rabbits greater than 1,250 g in weight have moved and are now adult members of social groups. Blood samples were taken either by bleeding from an ear vein or by heart puncture. The plasma was separated by centrifugation and an equal volume of a mixture containing 40% ethylene glycol and 6% sodium citrate added to the cellular fraction. The samples were stored at –20°C (Richardson and Sharman 1976). Long-term testing shows that such samples can be typed for allozymes for at least 20 years after collection (B.J. Richardson, unpublished data).

Allozyme variation was studied at five loci: adenosine deaminase (ADA; EC 3.5.4.4, three alleles), phosphogluconate dehydrogenase (PGD; EC 1.1.1.44, two alleles), carboxylesterase 1 (EST; EC 3.1.1.1, two alleles), carbonate hydratase II (CA; EC 4.2.1.1, two alleles) and dihydrolipidoamide reductase (DIA; EC 1.6.4.3, two alleles) (Richardson et al. 1980). Electrophoresis was carried out using a cellulose acetate supporting medium (Cellogel; Chemetron). Running buffers were: 15 mM Tris, 5 mM EDTA, adjusted to pH 8.2 with boric acid (PGD); 50 mM Tris, adjusted to pH 7.8 with maleic acid (ADA); 6 mM Tris, 2.6 mM EDTA, adjusted to pH 9.1 using boric acid (CA); 15 mM Tris, 5 mM EDTA adjusted to pH 7.8 with boric acid (EST and DIA). The gels were run and stained as described in Richardson et al. (1986).

Project 1

Populations at four study sites were used. The Urana site consists of a 280-ha fenced area of claypan and sandhills situated 20 km west of the township of Urana in southern central New South Wales (146 10′ E, 35°20′ S). The area has a western mediterranean environment with very hot dry summers. This population has high reproduction and mortality rates and has been used for ecological (Parer 1977, 1982) and genetic (Richardson 1980; Daly 1981) studies. The data considered here were collected during 1973–1974. The Grassy Creek population is at a very wet subalpine site in the Australian Alps in southern A.C.T. (149°20′ E, 35°40′ S). It is in a mountain valley with an area of 70 ha. The ecology of rabbits at the site (Richardson and Osborne 1982; Richardson and Wood 1982) is similar to that found at Snowy Plains (Dunsmore 1974; Richardson 1981) where reproduction and mortality rates are low. The data considered here were collected in 1975/1976. Cape Naturaliste is in far southwestern Western Australia (115°02′ E, 33°34′ S) in a coastal setting with a western mediterranean climate. The site consists of 275 ha of partially cleared heath. Chidlow is also in southwest Western Australia (116°19′ E; 31°57′ S) and the site, of 350 ha, is on open farmland in a western mediterranean environment. Aspects of the ecology and genetics of rabbits at these two sites have been described (Richardson et al. 1980; King and Wheeler 1985a, 1985b; Wheeler and King 1985). Reproduction and mortality rates are intermediate on these sites. The genetic data used in the present study were collected during 1975/1976. Rabbit density at Grassy Creek is high and intermediate at the other sites (unpublished data). As slightly different methods were used, comparative quantitative estimates of density cannot be given. Animal movement between birth and adulthood was calculated from the trapping data collected at each site using those animals caught as kittens and also as adults. The Urana movement data are from Parer (1982). The genetic data set consisted of the allozyme genotypes of sets of male and female adults and for kittens from each site. Only ADA was available for the Western Australia samples, as the data were collected for other purposes (Richardson et al. 1980).

Project 2

This 200-ha temperate study site is in Cattai National Park near Windsor, 60 km west of Sydney, New South Wales (150°40′ E, 33°35′ S) on grassy areas of old farmland. Rainfall is evenly distributed throughout the year. The population normally consists of about 150–200 adult rabbits. To allow study of the effects of a population crash on the genetic structure of the population, it was poisoned by the Rural Lands Board in June 1992 as part of its rabbit control program. The adult population was studied immediately before the crash and for the 5 subsequent years. The allozyme genotypes of animals from before, and for 2 years after the crash were determined and the distance moved by individuals between birth and adulthood in each annual cohort of kittens was determined for the 5 years following the crash.

Data analysis

The genetic structure of each population was measured using spatial autocorrelation, a method which has been used widely in the analysis of spatial structure of genetic variation (Sokal and Oden 1978; Epperson 1993; Epperson et al. 1999). Other methods are available (see Luikart and England 1999; Lynch and Ritland 1999; Smouse and Peakall 1999); however, these are either based on *F*-statistics (Wright 1978) and depend on prior knowledge of the social structure and need sample sets from each social unit sufficiently large to estimate the inbreeding coefficient, or are complex to calculate and are primarily designed for use with data involving many loci. Spatial autocorrelation, measured as Moran's *I*, is a suitable statistic when population structure is unknown or uncertain, because it uses the spatial position of each individual and its genetic constitution as data rather than genotypes combined according to social hierarchy. It has the added attraction that the value is a measure of Wright's coefficient of relationship (Hardy and Vekemans 1999).

Moran's *I* was calculated using the software package SAAP (Wartenberg 1989). It varies in value between –1 and 1 in a manner analogous to a correlation coefficient. Alleles were treated as characters with the states and values, present (as a homozygote '1', or as a heterozygote '0.5') or absent ('0') at each 'location' (i.e. each animal). The closest class (0 m distance) consisted of pairs of animals living on the same warren summed over all warrens, and the second group (1–100 m distance) consisted of all available pairs of rabbits from adjacent warrens (i.e. spatial classes are compared in the analysis, not social groups). The remaining data were divided into approximately equal numbers of pairs in greater distance classes. The significance of the results for each sex/location combination against the null hypothesis of random distribution of *I* between distance classes was tested for each allele/distance class combination using non-parametric rank sum tests on *I*-values over alleles by distance classes. ANOVAs were used to examine the interactions between location and distance (project 1) or year and distance (project 2) for each sex, with the number of observations in each treatment randomly reduced to the same number. Only one allele was used for two-allele systems to ensure independence of data sets. In three-allele systems, the values showed no obvious relationship and the data for all three alleles were used.

Comparisons of the distances moved by cohorts of male and female kittens were also made using Wilcoxon rank sum tests on the distances moved between birth and adulthood by the animals. The interactions between either sex and location (project 1) or sex and year (project 2) on log of distance moved were determined using ANOVAs with the number of observations in each treatment randomly reduced to the same size before analysis.

Results

Project 1

The distances moved by male and female kittens from their warrens of birth until captured as adults are summarised in Table 1. Analysis of variance (excluding the Urana data) of log distance in a two-way design with sex as a fixed factor and location as a random factor showed a significant effect of location ($F_{2,234}$=32.47, P<0.0001) and a sex/location interaction ($F_{2,234}$=4.36, P=0.01). The

Table 1 Movement of animals between birth, and adult size. Mean distance is the average distance moved by all animals (including 0 distances); N_i is the number of individuals in the sample. The number given in each category is a percentage (to allow comparison between data sets. The Urana movement data are taken directly from Parer (1982)

	Movement patterns (%)					N_i	Mean distance (m)
	0 m	100 m	200 m	500 m	500+ m		
Cape naturaliste							
Females	32	56	8	2	2	50	57
Males	38	50	10	0	2	50	57
Chidlow							
Females	70	18	6	6	1	90	58
Males	47	25	8	16	4	76	111
Grassy creek							
Females	93	4	2	0	0	45	8
Males	90	5	5	0	0	40	15
	0 m	200 m	400 m	400+ m			
Urana							
Female	87	4	3	7		133	≈80
Male	58	14	8	20		123	≈220

Table 2 Number of juveniles captured away from their home (birth) warrens at Cattai that will ultimately either emigrate or remain on their birth warren (*Explore* caught away from birth warren, *Not caught* not caught away from birth warren). Male and female animals showed the same behaviour pattern and are in equal numbers (contingency table χ^2_1=0.21, P=0.5, n.s.)

	Emigrated	Philopatric
Explore	20	19
Not caught	17	20

significant interaction is due to differences in the level of philopatry between the sexes at Chidlow (χ^2_3=10.5, P<0.05) and Urana (Parer 1982) combined with no significant differences in the patterns of movement of male and female kittens at Grassy Creek and Cape Naturaliste. The patterns at these two sites however differed, with <10% kittens moving from their birth warren at Grassy Creek, while >60% moved at Cape Naturaliste. While equivalent estimates of density could not be obtained because different methodologies were used, the population density at Grassy Creek was very high and in the remaining populations, intermediate.

The reported results could be underestimates of dispersal if there were large numbers of long-distance emigrants, as these would have moved off the study areas. However, spotlight transects and poisoning campaigns on surrounding areas did not detect tagged animals. Furthermore, most sites were partly isolated by inhospitable environments for rabbits.

The different patterns observed at different sites imply different distributions of choices by young animals. The reported exploratory behaviour of young rabbits (Künkele and von Holst 1996) provides a possible process by which rabbits can assess biologically relevant attributes (e.g. density) and opportunities of surrounding areas before committing themselves to leaving, or staying in their birth warren. An examination of the pattern of movement behaviour of juvenile animals (i.e. between 600–900 g; Table 2) shows that 50% of these animals were trapped at least once on non-birth warrens whilst regularly returning to their birth warren. The non-birth warren trap rate was the same for males and females and for rabbits that ultimately ended up, as adults, on their birth warren or that dispersed. These exploratory movements were frequently of several hundred metres. Clearly, young rabbits explored the surrounding habitat before reaching the age where they had to commit themselves to a social group (or, alternatively, were accepted by a social group). The rabbits not trapped off their home warren should not be presumed not to have taken exploratory trips, as the chance of trapping them while exploring was low. All juveniles are likely to make exploratory trips.

Analysis of variance of Moran's *I* for females in a two-way design (location and distance class) showed a significant effect of distance ($F_{3,40}$=5.2, P=0.004). Significant spatial structuring of genetic variation was found in all adult female populations except at Grassy Creek (Table 3). In each case, there were similarly large positive values for *I* in the 0-m distance class (i.e. in animals living on the same warren). With the exception of Chidlow, where structuring was also apparently present in the 100-m class, no structuring was found at greater distances. No significant spatial structuring was found for the males at any site. Analysis of variance of the kitten data showed significant effects of location ($F_{3,40}$=10.75, P<0.0001), distance class ($F_{3,40}$=9.64, P=0.0001) and the location/distance interaction ($F_{10,40}$=3.88, P=0.0009). At all sites except Urana, the young kitten population was highly structured, as would be expected since these animals are on their birth warrens and litter mates were included in the samples.

Table 3 Summary of results of spatial autocorrelation analysis (N_a number of alleles used; P_W probability of the non-parametric rank sum test over alleles by distance classes, N_i number of individuals typed)

Population	Mean Moran's *I* value					N_a	P_W	N_i
	0 m	100 m	200 m	500 m	500+ m			
Cape naturaliste								
Adult females	0.08	0.06	0.04	–0.04	–0.02	3	0.04*	132
Adult males	–0.03	0.01	0.01	–0.01	0.01	3	0.08 n.s.	148
Kittens	0.11	0.06	–0.24	–0.03	–0.06	3	0.01**	49
Chidlow								
Adult females	0.14	0.12	0.06	0.01	–0.07	3	0.05*	187
Adult males	0.01	–0.01	0.05	–0.01	–0.01	3	0.08 n.s.	145
Kittens	0.26	0.09	0.03	–0.01	–0.08	3	0.04*	186
Urana								
Adult females	0.07	–0.02	–0.06	–0.01	–0.01	7	0.006**	114
Adult males	0.04	–0.01	0.02	–0.03	–0.01	7	0.12 n.s.	116
Kittens	0.02	0.02	–0.02	–0.01	–0.01	7	0.11 n.s.	193
Grassy Creek								
Adult females	0.12	–0.01	–0.02	–0.04	–0.01	7	0.28 n.s.	64
Adult males	–0.10	0.00	–0.03	–0.01	–0.01	7	0.09 n.s.	75
Kittens	0.11	–0.01	–0.01	0.00	–0.01	7	0.02*	177

Project 2

The adult population size, estimated using standard capture-mark-recapture methods, consisted of approximately 150 animals before the crash and 37 animals during the first breeding season. Less than 10 of these animals were crash survivors; the remainder were immigrants. The population recovered to approximately 120 adults at the beginning of the second breeding season and to pre-poisoning levels by the third season. It continued to rise to about 200 adult animals.

The behavioural and genetic results are shown in Tables 4, 5. Data for 1996 and 1997 have been combined because of the small sample sizes. Two-way analysis of variance of log distance moved with sex as a fixed factor and year as a random factor showed a significant effect of year ($F_{1,70}$=11.95, P=0.0009) and a sex/year interaction effect ($F_{4,70}$=2.52; P=0.049). In the first year post poisoning, average distances moved were quite large (Table 4) and this distance decreased gradually in the following years. χ^2 homogeneity tests showed that there were significant changes in the mean distance moved by males compared to females in the first and third years. Thereafter, the pattern was the same for the two sexes.

The spatial autocorrelation analysis of the allozyme data (Table 5) showed that the population of adult females was spatially structured before the crash at a level similar to that seen at Chidlow and Urana and presented in Table 3. Two-way analysis of variance of Moran's I data for distance class by year showed significant effects for females of distance ($F_{2,27}$=7.59, P=0.002), year ($F_{2,27}$=4.18, P=0.026) and the interaction ($F_{4,27}$=3.01, P=0.036) The structuring was lost in the postcrash population (Table 5). In the males, only distance class was significant ($F_{2,27}$=3.74, P=0.04) but inspection shows this was not due to high values of I in the 0 distance class.

Table 4 Table of movement patterns in the Cattai population between birth and adult weight (1,250 g) in the kitten population produced during spring and early summer of the year shown. The population was crashed immediately prior to the 1992 breeding season (P is the probability of the Wilcoxon rank sum test between distances moved by males and females, N_I number of individuals; movement patterns are given as % to allow easy comparisons)

	Movement patterns (%)			N_i	Mean±SE distance	P
	0–100 m	101–200 m	200+ m			
1992 (16 adults/km^2)						
Females	70	10	20	20	92±25	0.04*
Males	18	18	64	11	220±41	
1993 (60 adults/km^2)						
Females	86	14	0	21	51±15	0.14 n.s.
Males	44	33	22	9	118±38	
1994 (75 adults/km^2)						
Females	95	5	0	22	30±8	>0.001***
Males	18	45	36	11	111±12	
1995 (90 adults/km^2)						
Female	83	9	9	23	55±18	0.89 n.s.
Males	76	19	5	21	57±17	
1996+1997 (90 adults/km^2)						
Females	71	24	5	21	33±13	0.93 n.s.
Males	75	25	0	8	27±18	

Table 5 Effect of population crash on the genetic structure of the adult population at Cattai (N_a number of alleles used, P_W probability of the non-parametric rank sum test over alleles by distance classes, N_i number of individuals typed)

	Mean Moran I value			N_a	P_W	N_i
	100 m	200 m	>200 m			
Before crash						
Female	0.12	0.14	–0.08	4	0.02*	48
Males	0.02	0.08	–0.05	4	0.27 n.s.	38
Year 1 post crash						
Females	0.18	0.02	–0.09	4	0.06 n.s.	31
Males	0.06	0.06	–0.04	4	0.15 n.s.	41
Year 2 post crash						
Females	–0.04	–0.07	–0.04	4	0.78 n.s	28
Males	0.01	0.31	–0.10	4	0.44 n.s	20

Discussion

Dispersal strategies

This study shows that rabbit populations use different mixes of dispersal strategies in different contexts. Philopatry increases at high densities and the average distances moved differ with conditions. There are significant differences in the strategies used by males and females. While sex-biased dispersal has been previously reported in rabbits (e.g. Parer 1982; Webb et al. 1995; Künkele and von Holst 1996), the reported levels are within a narrower range than those found in this study (males 70–93%, here 10–82%; females 27–64%, here 5–68%). This is probably due to the wider range of conditions found over the study sites used in the present study.

Populations of young rabbits change their dispersal pattern depending on conditions. This was most clearly seen at Cattai in the years following the crash in numbers (Table 4). At low density (1992: 16 adults/km^2) in this population, the rabbits moved at high frequency and over long distances (Table 4). As the density increased, the proportion moving fell as did the distance moved. The females changed their strategy to philopatry at lower densities (60–75 adults/km^2) than did the males (90 adults/km^2). Ultimately, however, at the highest density, both sexes showed the same level of philopatry, matching the situation seen in the high-density population studied at Grassy Creek. When space is available then, young male and female rabbits change social groups. They not only move, but prefer to move relatively long distances. Thus, even though there were empty warrens close to their natal warrens (B.J. Richardson, unpublished data), they moved further away. Consequently, they are not simply following a strategy of settling in the nearest available vacant space in a different social group. As the warrens fill and the rabbit density increases, they tend to move shorter distances and, at high density, few kittens of either sex risk moving or, perhaps, find a place to go. Changes from dispersal at low density to philopatry at high density has been reported in other mammal species (e.g. Wolff 1994).

How are young rabbits making the decision to stay or move? There is evidence that juvenile rabbits of both sexes explore the area surrounding the natal warren at weights of 600–900 g, which is below that at which they migrate. Analysis of the behaviour of young animals that ultimately either were or were not going to change their warren showed that ‘movers’ and ‘stayers’ were equally likely to be caught as juveniles visiting other warrens (Table 2), that is, caught on a strange warren and then later caught again on their birth warren. The yard study of Künkele and von Holst (1996) also showed this pattern of behaviour. This exploratory behaviour likely provides the opportunity for young rabbits to assess the relative risks and advantages of the options of dispersal and philopatry.

Parer (1982), in considering the results of a long-term study of the effects of environmental conditions on movement behaviour of rabbits at Urana, proposed that there are two steps in the decision process used by young rabbits: first, to go or stay, this proportion changing with conditions, and second, to find somewhere to go. At Urana in the years of his study, the density did not change greatly though environmental conditions did. The result was that the pattern of distances moved did not change from year to year, and only the proportion of young rabbits moving changed in response to environmental conditions. In drier, more difficult conditions, more kittens moved. This was presumably due to the recognition that they would not survive where they were and it was better to take the risk of moving on the chance that they would find somewhere where they would survive. This was not the case at Cattai, because in different years, not only did different proportions move but the pattern of distances moved also changed with density. Again a two-phase process is possible.

The density at which philopatry increases in frequency is different for the two sexes [e.g. at Cattai in females in 1994 (75/km^2) and in males in 1995 (90/km^2); Table 4]. The criteria for choosing philopatry or dispersal seem likely to differ for the two sexes (e.g. breeding resources in the females and unrelated available females for the males; Perrin and Mazlov 2000). Cowan (1987) interpreted rabbit movement patterns as due to asocial behaviour of rabbits, which is usually offset by the limited availability of suitable warrens. This would explain the increased pattern of movement at Cattai following the crash, in that unoccupied warrens were now available. The problem with this explanation is that there were vacant ‘good’ warrens (i.e. warrens that have housed large populations of rabbits in other years) at Cattai even at the highest density. Similarly, in populations where there is space and the production of warrens is easy, e.g. in sandy soils, rabbits still live mainly in groups of more than two rabbits (B.J. Richardson, personal observation). Furthermore, asociality does not explain the observations of Parer (1982) that young rabbits show different patterns of movement in years of different rainfall though there is no change in density. It would be of interest to examine the effect on social structure of the present much lower rabbit densities (often <5% of the levels reported here) found in inland Australia. (These levels have resulted from the lethal effects of rabbit haemorrhagic disease on population sizes.)

Genetic strategies

Even with much lower levels of sex-skewed philopatry than those reported in other studies of colonial species (Waser and Elliot 1991; van Staaden et al. 1996; Dobson et al. 1997), the genetic structure of the rabbit populations is affected, with significant structuring present in the adult female populations at short distances in four of five populations studied, but not in the male populations. The exceptional population was that with the highest level of philopatry (Grassy Creek) where no detectable spatial genetic structuring in the adults was observed. This population was at very high density and included a very large population of adults that were not members of warren-based social groups (‘floaters’). In addition, the warrens on the site were very large, with up to 100 active entrances and 28 adult animals tagged from a single warren. A single warren likely included several social groups, presumably with different genetic attributes. These factors would reduce the level of apparent structuring in the 0-m distance class.

Genetic structuring is likely to be a dynamic phenomenon maintained in each generation by the behaviour of the young animals of that generation. The loss of structuring within two breeding seasons at Cattai when conditions changed would support this interpretation. Changes in the level of philopatry are not simply correlated with changes in levels of genetic structuring, which are remarkably consistent across the study populations. Even though female philopatry varies from 32–95%, the I values (i.e. coefficients of relationship) for adult females ($\cong 0.12$) are at the level expected for first cousins at all sites. The different genetic structures seen in males and females mean that inbreeding is avoided and different levels of philopatry in males and females are likely to be critical in maintaining this balance. Sex-biased dispersal is in fact the mechanism used to avoid inbreeding at intermediate densities. However, there seem likely to be further unknown behavioural factor(s) stopping genetic structuring from reaching higher levels, especially in populations with high levels of philopatry in both sexes. Possible factors would include radical changes in local population sizes (e.g. associated with droughts) or olfactory cues providing information on relatedness. It should also be remembered that the rabbit is a feral species in Australia and, in the face of the very high levels of predation seen on natural populations of rabbits in the Iberian Peninsula where it evolved (Rogers et al. 1994), population levels such as those seen at Grassy Creek were probably not experienced during its evolution.

Kitten populations usually show high levels of genetic similarity if taken from the same social group. The exception to this pattern was Urana where no structuring was detected in the kitten population. The cause of this difference is unknown. While warrens are large and reproduction at this site is very high, survival rates are low (Parer 1977) and it may be that fewer sibs were sampled than at other sites.

Of interest would be to analyse further years of the recovery process at Cattai using a wider range of genetic variation to see how long the population took to recover its original structure, and to examine mechanisms of inbreeding avoidance at high density where philopatry is found in both sexes. At the genetic level, density-dependent behaviour is interesting as the increased distance moved at lower density increases the size of the genetic neighbourhood (which is a measure of the variance of distance moved by the individuals making up a population between the place where they were born and where they bred). The number of independent individuals in a genetic neighbourhood is the effective population size. The observed changes in movement pattern with density therefore limit the effect of changes in density on the effective population size. If $N_e=4\pi\sigma^2 d$ where σ^2 is the variance of the distance moved between birth and breeding and d is the density (Wright 1978), then N_e at Cattai in the 3 years following the crash have the ratios 1.0:1.1:1.0 over a fourfold change in density.

The results of this and previous studies of genetic structuring of rabbit populations in Australia (Richardson 1980; Richardson et al. 1980; Daly 1981; Fuller et al. 1996, 1997; Zenger 1996) show that rabbit populations are structured at three levels. The finest scale, which was studied here, consists of rabbit social groups containing from two to ten adult animals. Detectable levels of genetic structuring occur in the females at this level in most populations, but not in the males. Not surprisingly, kittens on their warrens of birth also show genetic structuring. Webb et al. (1995) similarly reported the presence of genetic structuring within the females in social groups in an English rabbit population. At the next scale up, Daly (1981) showed that movement rates between social groups at Urana are such as to ensure genetic contiguity of the population, and that allele frequency differences at the finer scale are ephemeral. This is the scale of a genetic neighbourhood as determined by Daly (1981) and by Richardson (1981). The work presented here shows that this contiguity is usually maintained by the males through differential migration at intermediate densities. At a coarser scale, Richardson (1980) showed that there are large, significant changes in allele frequencies between populations separated by 1–10 km. Surridge et al. (1999) describe similar structures in English rabbit populations. At this scale, there are discontinuities in the habitat used by rabbits and these population groups have a geographical size equivalent to one or a few genetic neighbourhood diameters. There are, however, differences in different habitats for this level of structuring. In the arid zone, there was consistency in allozyme, mtDNA and microsatellite allele frequencies over geographical distances as great as 600 km in two studies (Fuller et al. 1996, 1997; Zenger 1996; A.-M. Vachot, unpublished data). There is no relationship between genetic distance and geographic distance at even larger scales (10–3,000 km) within Australia (Richardson 1980). This may be due, however, to the limited number of generations that the rabbit has been in Australia, as there are very large differences in allele frequencies at this scale in Europe (Richardson et al. 1980; Monnerot et al. 1994).

Consideration of the nature of this observed structuring in the light of Wright's shifting-balance theory (Wright 1931; Storz 1999) shows that rabbits can effectively scale their responses to the nature of the challenge. Allele frequencies can shift at a fine scale (social group) by drift and new combinations can then be tested over a few generations. Effective combinations can be exported to the rest of the genetic neighbourhood which consists of 10–50 social groups and, ultimately, if it is larger than a neighbourhood, to the local population, which Richardson (1980) considered a deme for the rabbit and between which significant differences in allele frequencies can be found. Successful gene combinations can then extend their range to other demes through the natural cycles of population crash, invasion and increase.

Genetics and behaviour

This study shows that the behavioural and genetic factors driving the dispersal behaviour of young rabbits are inextricably intermixed (Gandon 1999). The choice to disperse or not, for example, is likely a strategic one based on the likelihood of breeding successfully estimated by each young rabbit during its 'visits' to surrounding warrens, but the distance moved may be driven indirectly by genetic factors, particularly the need to maintain suitable values of N_e in local populations.

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