

Formation and maintenance of discrete wild rabbit (*Oryctolagus cuniculus*) population systems in arid Australia: Habitat heterogeneity and management implications

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Abstract The wild rabbit (*Oryctolagus cuniculus* L.) is a significant pest in arid and semi-arid Australia, where erratic rainfall and irregular pasture growth cause population sizes to oscillate, increasing virtually without limit and then crashing during drought conditions. Vacant habitat patches can be rapidly recolonized from nearby patches in high rainfall years. Using two adjoining rabbit population systems in arid and semi-arid south-west Queensland, this study evaluates patterns of population differentiation and proposes a mechanism that may lead to the formation of multiple rabbit population systems in the same locality. Using the combined haplotype frequency data from both a local and regional study, estimates of genetic exchange among local populations are considered in conjunction with ecological data to evaluate the significance of habitat attributes (and their spatial distribution) on the local distribution of rabbit populations, both within and between two adjacent population systems. A tentative model is proposed to explain the observed differences in population structure between the two adjoining systems. Under this model, population structure at specific locations is determined primarily by the availability of areas suitable for prolonged colonization and the quality of the intervening habitat that dictates the degree of isolation between locations and therefore the probability of recolonization following local extinctions. It is also suggested that the current rabbit distribution may be a function of the flexibility of behavioural responses in rabbits to the level of spatial heterogeneity of favourable habitats within the two regions.

Key words: genetic differentiation, habitat heterogeneity, local extinction, population management, rabbit, recolonization.

INTRODUCTION

Many population systems take the form of a meta-population of local populations, where the long-term viability of the population system is determined not only by the internal dynamics of each local population, but also the extent of dispersal between them (Hanski 1991). If dispersal success is related to factors such as distance or quality of habitat among local populations, then it follows that the spatial organization of local populations has important implications for the long-term viability of the system (Hanski 1994). These spatial considerations are likely to be most important in systems where fluctuating resource levels lead to large and erratic population fluctuations and local extinctions can therefore be expected to be both frequent and widespread, for example, rabbit population systems in arid and semi-arid Australia (Fuller *et al.* 1996, 1997).

The wild rabbit (*Oryctolagus cuniculus* L.) is a significant pest in Australia. The successful colonization and

exploitation of a wide range of habitats by rabbits in Australia has resulted in considerable economic loss (Wilson *et al.* 1992) and environmental degradation (Byrne 1992).

The local distribution of rabbit populations within a region is likely to be determined by surface cover, water availability, soil fertility and, most importantly, soil type (Parer 1987). High temperatures severely inhibit rabbit reproduction (Cooke 1977) and in arid and semi-arid environments a burrow is required for successful breeding (Myers 1958). Several studies have concluded that rabbits have a preference for sandy soils to enable warren construction (Parker *et al.* 1976; Parer & Libke 1985; Parer 1987). Parer (1987) also reported that the spatial and temporal heterogeneity of green vegetation influences local rabbit distribution, especially in arid and semi-arid areas, but did not quantify the relationship.

Semi-arid and arid ecosystems are characterized by considerable environmental stochasticity, which can elevate the extinction probability of local rabbit populations. Erratic rainfall and irregular pasture growth cause population sizes to oscillate, increasing virtually without limit (Cooke 1981) and then crashing during

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drought conditions (Cooke 1981, 1982). Myers and Parker (1965, 1975a, 1975b) have documented the regular occurrence of local rabbit population extinctions over large areas in arid New South Wales as a result of severe drought. Despite local extinctions, rabbits can rapidly recolonize vacant habitat patches in high rainfall years if there are high rabbit densities in nearby patches (Parer & Parker 1987) or if there are 'refuge areas' (deep warrens adjacent to major drainage channels) within the drought affected area that provide colonists (Myers & Parker 1975a, 1975b). Therefore, it is possible that, in the long term, the persistence, distribution and structure of local populations of rabbits at the regional level may be determined by the availability of acceptable habitat patches, the degree of isolation among them and the probability of their recolonization following local extinction.

A genetic approach has been used in several studies to investigate rabbit population structure, in particular, the degree of isolation (or conversely the level of interaction) among local rabbit populations. In the temperate ecosystems of eastern Australia, effective management may be at the level of the deme (i.e. groups of interacting warrens within a localized area (Daly 1979)). Populations in this type of system generally consist of 50–400 individuals (Richardson 1981). Similarly, in semi-arid north-eastern Australian

systems, Fuller *et al.* (1997) have suggested that genetic exchange is limited among local population units and therefore localized control may be adequate. Fuller *et al.* (1997) also demonstrated that in the adjoining, more arid, western ecosystems of north-eastern Australia, rabbit populations were effectively panmictic over a vast region (at least 750 000 km²), and should therefore be treated as a single management unit.

These studies suggest that within eastern Australia, the size of effective management units for rabbits depends on the type of ecosystem in which the populations are located. In particular, investigations in north-eastern Australia have highlighted the existence of two discrete population systems in the same locality: the western arid region, which exhibits extensive population exchange, and the eastern semi-arid region, where exchange is limited (Fuller *et al.* 1997). In the study of Fuller *et al.*, it was also observed that the two systems appeared to abut around the Mitchell–Maranoa region in Queensland. The continued existence of discrete population systems ('management units' in the case of rabbits) in the same locality is normally considered to be dependent on natural or artificial geographical barriers that lead to the largely independent evolution of isolated gene pools. Alternatively, it is possible that the maintenance of discrete systems in a highly fluctuating environment may

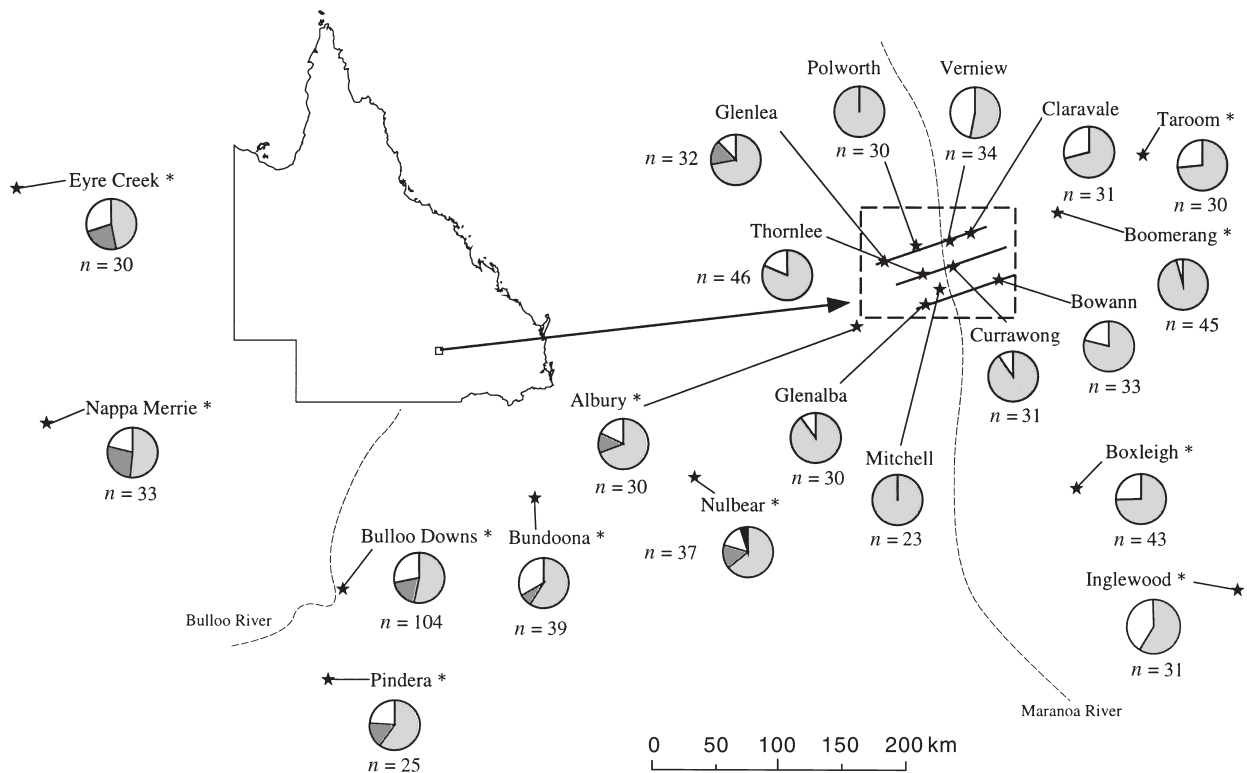


Fig. 1. Location of the intensive study area in the Mitchell-Maranoa region of Queensland including mitochondrial haplotype frequencies from nine local populations sampled in the present study and 11 populations sampled by Fuller *et al.* (1997). (□), Haplotype A; (■), haplotype B; (◻), haplotype C; (■), haplotype D; (*), from Fuller *et al.* (1997); (---), intensive study area, (—), sampling transects.

depend on the spatial distribution of habitat attributes that influence dispersal and limit recolonization. Similarly, the local distribution of rabbit populations within each system may be influenced by these same factors, that is, availability and heterogeneity (size and spatial distribution) of suitable habitat patches. If this is the case, gene flow and population structuring both within and between adjacent systems would be determined primarily by the probability of recolonization following local extinction.

It is the aim of the present study to determine the extent to which the maintenance of discrete population systems in a highly fluctuating environment is dependent on the spatial distribution of habitat attributes that influence dispersal and limit colonization. Using adjoining rabbit population systems in arid and semi-arid south-west Queensland, the present study evaluates patterns of population differentiation and the mechanisms that lead to the formation of multiple rabbit population systems in the same locality. More specifically, we expand the extensive (regional) study of Fuller *et al.* (1997) with an intensive (local) study to examine genetic exchange across the boundary between the two systems that was inferred from genetic data in the regional study. Using combined haplotype frequency data from both the intensive and regional studies, estimates of exchange among local populations are considered in conjunction with ecological data to evaluate the significance of habitat attributes (and their spatial distribution) on the local distribution of rabbit populations both within and between two adjacent population systems.

METHODS

Approximately 50 adult rabbits were collected from each of nine sites located throughout the Mitchell-Maranoa region in Queensland (Fig. 1). Sampling individuals from discrete warren systems within the site ensured that individuals at each site were not drawn from the same family groups. Sites were selected 20–30 kilometres apart, along three axes, north-east to south-west. A small section of liver was dissected from each individual and processed and stored as described by Fuller *et al.* (1997). The mitochondrial haplotype of each individual was determined, using procedures described in Fuller *et al.* (1997). Haplotype frequency data from these nine sites were then used in conjunction with data from 11 other sites (Fig. 1) examined previously by Fuller *et al.* (1997).

Genetic population subdivision was investigated using the analysis of molecular variance (AMOVA) approach of Excoffier *et al.* (1992). Estimates of Φ_{st} were used to calculate levels of gene flow among populations using the island model of Hudson *et al.* (1992).

Topographic changes around the inferred boundary of the two population systems (Fuller *et al.* 1997) were analysed at a scale of 1 : 100 000 (Australian Surveying and Land Information Group maps). Five evenly spaced, 100-km long, east–west transects were overlaid on the intensive study area, and sectional elevation profiles were constructed for each transect from contours at lateral intervals of 0.5 km. Any large or prominent geographical features were also identified.

Daily flow rates for the period 1969–1999 were obtained from the Queensland Department of Primary Industries (QDPI) for the Maranoa River, which is in the vicinity of the inferred systems boundary, and the Bulloo River, situated some 200 km west of the boundary. Flow rates in these rivers above 0.01 cumecs ($\text{m}^3 \text{s}^{-1}$) have the potential to restrict rabbit movement (D. Walker, QDPI, pers. comm.).

Of the many habitat attributes shown to correlate with the local distribution of rabbit populations in arid and semi-arid regions, water, soil type and vegetation are considered to be major determinants, as they are indicators of suitability for burrowing and availability of food (Myers & Parker 1965; Parker *et al.* 1976; Parer 1987; Rogers *et al.* 1994). The spatial and temporal heterogeneity of vegetation can be assessed using rainfall data and/or plant growth indices (e.g. Fitzpatrick & Nix 1970). However, these indices are inappropriate in the arid regions of Australia, as they do not account for the important influence of water distribution (channel flood, drainage depressions) on vegetation. The best information comes from a direct estimate of the density of green plant cover. An estimate of photosynthetically active, non-wilted plant foliage (green food) throughout the area was obtained using a normalized difference vegetation index (NDVI) derived from 1993 satellite data (CSIRO Division of Oceanography). The temporal variation in green vegetation over an area of 100 km² at each of three sites in both the western (Bulloo Downs, Eyre Creek, Bundoona) and eastern (Mitchell, Taroom, Inglewood) regions (Fig. 1) was obtained by rating the NDVI of each pixel (100 pixels = 1 km) as low, medium or high (< 10, 10–25, 25–55% NDVI, respectively) in spring, summer, autumn and winter and determining the percentage of the area rated in each NDVI category.

A gross estimate of the mean spatial heterogeneity of green vegetation in each region was determined by calculating the number of change points in NDVI rating within the same 100 sequential pixels at each location that were used in the previous analysis. A simple sequential comparison index (SCI) was then calculated as the number of runs of pixels of similar NDVI rating divided by the total number of pixels.

The extent and spatial distribution of soil types in each region were determined in a similar fashion. At the same three locations in each region, soils were categorized based on their suitability for rabbits

(suitable, intermediate, unsuitable) according to the criteria of Parker *et al.* (1976) and Parer and Libke (1985). At each location, a 400-km² area (100 grid cells of 4 km²) was mapped for soil suitability (Atlas of Australian Resources 1980) and the mean proportional area of each category and a mean SCI were determined for each region.

To determine if the boundary between the two systems as determined from genetic data closely coincides with differences in spatial heterogeneity, a fine-scale study of habitat heterogeneity was undertaken in the intensive study area. The region around the inferred boundary was divided into eastern and western regions of approximately the same area (western system, 7808 km²; eastern system, 8034 km²), on the basis of significant differences in haplotype frequencies. Sites included in the eastern region exhibited significant haplotype heterogeneity, while sites included in the western region were homogeneous for haplotype frequency.

A composite map of patches of suitable, intermediate and unsuitable habitat for rabbits around the system boundary was produced from overlays of soil type (1 : 500 000, CSIRO Land Research Series) and vegetation (1 : 25 000 aerial photographs, SUNMAP). Soil suitability was classified with reference to characteristics identified by Parker *et al.* (1976) and Parer and Libke (1985) as in previous analyses. Vegetation having a dense overstorey with few or no gaps in canopy cover was considered unsuitable habitat (Ratcliffe 1959; Myers *et al.* 1994) while all other vegetation types were considered suitable.

RESULTS

Four mtDNA haplotypes (A, B, C and D) were observed in the 752 individuals examined. Haplotype frequencies are presented in Fig. 1 and vary among the 20 sites throughout the region. Across all 20 sites, haplotype distribution was not independent of site ($\chi^2 = 158.9$, d.f. = 38, $P < 0.001$). A k-means clustering analysis (Statistica Version 5.0) of haplotype frequency at all 20 sites identified two distinct clusters ($P < 0.01$) comprising: (1) populations that with all three major haplotypes ('western'); and (2) 'eastern' sites deficient in haplotype B, suggesting significant genetic differentiation between clusters. The eight western sites were homogeneous for haplotype frequency ($\chi^2 = 15.2$, d.f. = 14, $P = 0.366$), while the 12 eastern sites had decreased genetic variation relative to the western sites. Haplotype D was excluded from these analyses, as it was only found in two individuals from a single population at one site.

Population subdivision was estimated among population sets within the two clusters (1, western: Eyre Creek, Nappa Merrie, Pindera, Bulloo Downs,

Bundoona, Nulbear, Albury, Glenlea; 2, eastern: Thornlee, Glenalba, Polworth, Currawong, Vernview, Mitchell, Claravale, Bowann, Boomerang, Boxleigh, Taroom, Inglewood). The divergence estimate among populations (within the total) was $\Phi_{st} = 0.122$. Divergence between the two clusters (relative to the total) was higher ($\Phi_{ct} = 0.076$) than the divergence among populations within each cluster ($\Phi_{sc} = 0.05$). All variance components were significantly different from those found for a random distribution of individuals (Φ_{st} , $P < 0.001$; Φ_{sc} , $P < 0.001$ and Φ_{ct} , $P = 0.002$). In total, these results suggest a clear dichotomy in structure between the eastern and western sites, with this division centred on the Mitchell–Maranoa region.

The differing pattern of haplotype frequencies between the eastern and western population systems may be the consequence of restricted gene flow due to geographical barriers to dispersal such as rivers and topographic features, or may simply be a function of geographical distance. The region around the boundary of the two population systems was relatively uniform with respect to topography, with a minimum and maximum elevation of 320 and 600 m a.s.l., respectively. The average rate of change of elevation was 3.7 m per 250 m, with the largest rate of change in elevation being just 60 m per 250 m on one transect. With the exception of the Maranoa River, which roughly corresponds to the system boundary, no significant topographic features (mountain ranges, gorges etc.) that may inhibit rabbit movement were identified.

River flows in the Maranoa River were lower than 0.01 cumecs for the majority (60 to 85%) of days in all seasons over the 3-year period (Fig. 2). Maximum flows occurred in summer, when 0.01 cumecs was exceeded for only 40% of days per season. During spring–summer, when high rabbit dispersal is expected (Daly

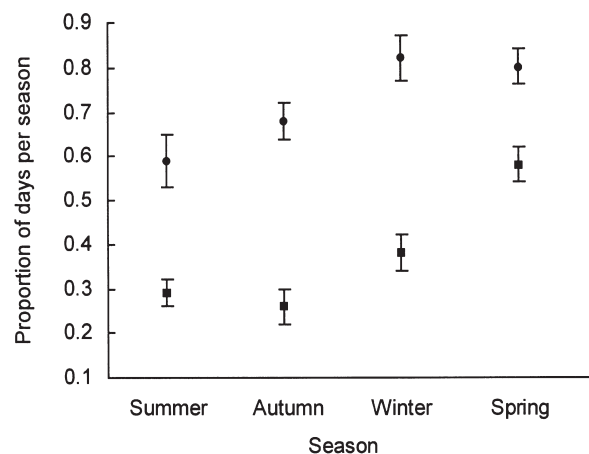


Fig. 2. River flows for the (●) Maranoa and (■) Bulloo Rivers. The mean proportion of days (\pm SE) within each season where river flow does not act as a barrier to gene flow (< 0.01 cumecs ($\text{m}^3 \text{s}^{-1}$)). Source: Queensland Department of Primary Industries.

1981; Parer 1982), flows exceeded 0.01 cumecs for less than 30% of days.

The Bulloo River had flows of greater than 0.01 cumecs for a greater proportion of all seasons than the Maranoa River (Fig. 2), so the Bulloo River has a greater potential as a barrier to rabbit movement than the Maranoa. Because Fuller *et al.* (1996) found no difference in population structure either side of the Bulloo River, it is highly unlikely that the Maranoa River is a significant barrier to rabbit movement.

Distance between pairs of the nine sites in the vicinity of the system boundary varied between 17.1 and 80 km. However, patterns of genetic differentiation were not explained by a geographical distance model (Mantel test; Roger's genetic distance *vs* site/site distance; 1000 iterations; $Z = 289.2$, $r = -0.1718$, $P = 0.227$). Fixation of the A haplotype at the Mitchell site could be the result of extensive and continuous human manipulation of rabbit populations (e.g. Myers 1970; Myers *et al.* 1981, 1994) and could, therefore, confound the results of the distance model, whereas there is no record of manipulation at the Polworth site. Patterns of genetic differentiation were not explained by a geographical distance model with the Mitchell site removed from the analysis (Mantel test; Roger's genetic distance *vs* site/site distance; 1000 iterations; $Z = 190.1$, $r = -0.2385$, $P = 0.189$).

The eastern region supported a higher overall abundance of green vegetation than the western region in all seasons (Table 1). The difference in the overall abundance of green vegetation was at a minimum in winter

when cool temperatures and availability of green food would favour rabbit reproduction and kitten survival in both systems (Myers 1970; Cooke 1977). Table 1 also shows that, regardless of the relatively lower overall abundance of food compared with the eastern system, green food is relatively uniformly spatially distributed throughout the western system in all seasons. Conversely, in the eastern system, although the overall abundance of green food is higher in all seasons than in the western system, its distribution is highly patchy in all seasons.

The western region also consists of a high proportion of suitable soils (67%). Moreover, areas of suitable soils are very highly connected (mean SCI = 0.1). Conversely, the eastern region consists of a low proportion of suitable soils (28%) and soil types are highly spatially fragmented (mean SCI = 0.25).

It is apparent that, on a regional scale, the two systems differ greatly in the relative abundance and spatial heterogeneity of both green food and soil types suitable for rabbits.

A comparison of the spatial distribution of habitat types around the system boundary identified by the genetic data (Table 2) suggests that the western region has a greater overall abundance of suitable habitats, larger mean patch size of suitable habitats and extremely low spatial heterogeneity of suitable patches, such that the area of suitable habitat can be considered as predominantly one large patch. Conversely, the eastern region has a significantly lower abundance of suitable habitats and is more heterogeneous, with

Table 1. Extent (mean percentage area categorized according to the normalized difference vegetation index rating (NDVI) and spatial heterogeneity (mean sequential comparison index) of green vegetation in each season, 1993

Season	Western region*					Eastern region†					Difference in mean NDVI between regions
	Low NDVI < 10%	Medium NDVI 10–25%	High NDVI 25–55%	Mean‡ NDVI for region	Mean SCI	Low NDVI < 10%	Medium NDVI 10–25%	High NDVI 25–55%	Mean‡ NDVI for region	Mean SCI	
Spring	32	68	0	13.5	0.35	0	62	38	26.1	0.55	12.6
Summer	23	76	1	14.9	0.36	5	72	23	22.1	0.62	7.2
Autumn	26	73	1	14.5	0.34	3	77	20	21.6	0.59	7.1
Winter	18	82	0	15.3	0.37	7	75	18	20.7	0.56	5.4

*Western region sites: Bulloo Downs, Eyre Creek, Bundoona; †eastern region sites: Mitchell, Taroom, Inglewood; ‡using class interval midpoints of 5, 17.5, 40%.

Table 2. Abundance and heterogeneity of habitats suitable for rabbits within the eastern and western regions

	Western region			Eastern Region		
	Unsuitable	Suitable	Intermediate	Unsuitable	Suitable	Intermediate
Total area (%)	66	24	10	37	32	31
Number of patches	9	41	23	18	35	43
Mean patch area (% of total area)	11	2	4	5	3	2
Maximum patch area (% of total area)	97	24	24	78	25	25

both more patches per unit area and smaller mean patch size of suitable habitat.

These analyses suggest that the overall abundance and spatial distribution of habitats suitable for rabbits identified at a fine scale around the system boundary proposed by the genetic data are consistent with those identified at the regional level.

In summary, (i) the genetic population structuring data and the habitat heterogeneity data are spatially coincident at both the regional and local levels of scale; (ii) the boundary between the systems inferred by the genetic data coincides with differences in the relative abundance and spatial heterogeneity of habitats suitable for rabbits; and (iii) no geographical barrier was evident in the vicinity of the boundary between the two systems.

DISCUSSION

Given the diverse and complex array of interactions that govern the success of rabbits in different Australian ecosystems, it is not surprising that many studies have concentrated on specific population processes or interactions that may lead to effective control. In particular, many studies have concentrated on site-specific temporal variations in population size and structure to answer questions relating to (i) the fluctuations and pattern of rabbit abundance during resource-deficient and resource-abundant years; or (ii) the effectiveness of recently introduced control agents. While providing essential information on specific organism–resource interactions, this approach has inadvertently perpetuated a view that temporal variations in reproduction and mortality are the major population processes affecting the long-term viability of the population under study.

The above model assumes that there is a discontinuity that substantially isolates the population under study from the influence of neighbouring populations. This situation, however, is rare in nature. More useful is a model that considers individuals distributed in space such that natural groupings are evident but no group can be considered entirely discrete. In this latter model, the probability of dispersal and colonization among natural groupings must be included as potentially significant processes that contribute to the observed distribution pattern and temporal changes in abundance of rabbits within a region.

Except for the studies of Birch (1970), Parer (1982) and Fuller *et al.* (1997), spatial dynamics as a set of interactions between localized populations and the importance of these interactions in influencing the long-term success of rabbit populations has only received cursory attention in the literature. Several studies have investigated the interaction between specific sites and refuges, and the concept of refuges as areas of temporal population stability in otherwise

temporally unstable systems (e.g. Newsome 1969a,b) is well established. These studies are only relevant, however, in situations where the refuge and the recipient site are within the dispersal range of individuals.

At the regional scale in particular, interaction between local rabbit populations may be a major determinant of long-term population success, where the extinction of localized populations can be considered a normal component of the regional system. These spatial considerations are likely to be most important in systems where fluctuating resource levels lead to large and erratic rabbit population fluctuations and hence local extinctions can be expected to be both frequent and widespread. Given that locations suitable for prolonged colonization may be spatially distributed within a region at a scale greater than the dispersal range of individual rabbits, a stepping-stone model of dispersal may be appropriate. The probability of colonization of suitable but vacant (or severely depleted) locations will therefore depend not so much on distance, but on the quality and spatial heterogeneity of intervening habitats.

Rabbit populations in arid and semi-arid Australia are known to undergo large and erratic annual fluctuations. All suitable habitats are not occupied continually and can be recolonized, depending on overall population density and environmental conditions. It is therefore highly probable that rabbits in these environments exist as local populations that interact within a larger metapopulation. Given that the harsh environment of these regions is characterized by high and widespread (regional) environmental stochasticity, relatively high extinction probabilities for many local populations would be expected. In these types of systems, recolonization following local extinction may be a critical process in maintaining the long-term integrity of the system. Arid western Queensland is one of the driest regions of Australia; however, rabbits persist and local populations are capable of sustaining high densities. This region therefore provides the characteristics necessary to assess the influence of spatial heterogeneity of habitats on the connectivity between local rabbit populations.

The genetic data from the present and previous (Fuller *et al.* 1996, 1997) studies provide an assessment of the historical interchange (gene flow) that has occurred between 20 locations over a large geographical area. These data have identified two distinct rabbit population systems, with the boundary between the two systems located in the vicinity of the Maranoa River. The two systems possess very different connectivity characteristics (historically). The western system is characterized by a lack of genetic structuring among local populations and high levels of gene flow, indicating that local populations are highly interconnected over large geographical areas. Conversely, the restricted gene flow evident in the eastern system is consistent with a

system with much lower connectivity between local populations. An intensive study around the boundary has shown that physical barriers to gene flow do not explain the significant difference in population structuring between the two systems.

If dispersal and colonization (and hence gene flow) are significant processes in maintaining the long-term integrity of these systems, the observed differences in genetic population structuring should be reflected in the spatial and temporal distribution of factors affecting the probability of recolonization within each system.

This is indeed the case, and the two independent data sets (genetic population structuring data and habitat heterogeneity data) are spatially coincident at both regional and local scales. This suggests that the differences in population structure observed between east and west are most likely a function of the flexibility of ecological and behavioural responses of rabbits to very different degrees of spatial heterogeneity of resources within the environment.

A tentative model can be proposed to explain the observed differences in population structure between the eastern and western systems. Under this model, population structure at specific locations will be determined primarily by the availability of areas suitable for prolonged colonization and the quality of the intervening habitat that dictates the degree of isolation between locations and therefore the probability of recolonization following local extinctions. Table 3 provides a summary of the system attributes that we suggest may contribute to the level of population structuring.

In the western system, estimates of gene flow indicate that rabbit populations are highly interconnected over large geographical areas. Although long-distance migration cannot be completely discounted (Douglas 1969; Newsome 1989), it is unlikely that sufficient numbers of long range dispersers would be successful each generation to homogenize haplotype frequencies.

It is likely that in this arid sandhill/claypan region, where green food is a limiting resource, that a scattered female dispersion pattern and scramble competition for food and mates have resulted in a relatively relaxed social system characterized by a promiscuous mating system (Cowan & Garson 1985). As erratic rainfall and irregular pasture growth will cause large fluctuations in population size (Cooke 1981), the harsh environment of this system would result in considerable (regional) fluctuations in resource abundance, resulting in local extinctions (Myers & Parker 1965, 1975a, 1975b). This region is characterized by a high proportion of favourable habitats, large patch sizes and low spatial habitat heterogeneity. These attributes, coupled with a relaxed mating system and enhanced reproduction and kitten survival due to the availability of green food in the communal feed grounds (claypans) between favourable patches that are characteristic of this region during the cooler season, would result in a high probability of recolonization of vacant patches and hence high levels of gene flow between geographically distant locations.

The situation in the eastern region is quite different, with low connectivity between local populations. The small proportion of favourable soil types, small patch sizes and high degree of spatial habitat heterogeneity

Table 3. System properties that contribute to differing levels of population structuring within and between rabbit populations in north-eastern Australia

System property	Western region	Eastern region
Resource availability: Burrows	Extensive areas of suitable soil types	Limited areas of suitable soil types
Resource availability: Food	Moderate but coincides with breeding season	Extensive but does not coincide with breeding season
Social system*	Relaxed	Structured
Mating system*	Promiscuous	Resource defence
Degree of isolation between local populations	Low Low levels of spatial heterogeneity Large mean suitable patch size High overall abundance of suitable areas	High High levels of spatial heterogeneity Small mean suitable patch size Low overall abundance of suitable areas
Potential for interchange between local populations	High (regardless of population density)	Low (except for periods of high resource pressure)
Probability of local extinction without recolonization	Low	High
Population structuring	Low	High

*Inferred from resource availability/distribution and the research of Cowan and Garson (1985).

result in small and scattered patches of favourable habitat separated by large areas of highly unfavourable habitat. Under these conditions, where nest sites are limited or clumped in small, isolated pockets of favourable habitat interspersed with large areas of unfavourable habitat (Parer 1987), a more rigid social organization with competition for both burrows and mates is likely (Cowan & Garson 1985). A resource-defence mating system would be reinforced by the lesser availability of green food resources during the reproductive season compared with other times of the year. The result of these social interactions and the scattered spatial configuration of suitable habitats is a system characterized by a discontinuous distribution of rabbits, with populations existing as relatively separate entities with high probabilities of local extinction, but low probability of recolonization of vacant patches and hence restricted gene flow between geographically distant populations.

In summary, this model suggests that the current rabbit distribution may be a function of the flexibility of behavioural responses in rabbits to the level of spatial heterogeneity of favourable habitats within the two regions. It is further suggested that the type of system that develops at a specific locality is determined by those habitat attributes (quality and distribution) that influence the availability and degree of isolation between acceptable habitat patches and therefore the probability of recolonization following extinction.

If this model adequately reflects the factors that determine 'connectivity' among rabbit populations, then it has important implications for management. Effective management of rabbits will depend on the identification of the geographical scale at which exchange between local populations becomes limited. Local control methods that result in individual warren depopulation are unlikely to be effective in the long term in situations where populations are large and the potential for exchange and recolonization are extensive. Equally, where rabbit populations consist of relatively small and isolated subunits with a low probability of exchange, then broad-scale control approaches that require passive transport of control agents by dispersing rabbits (e.g. myxomatosis, rabbit calici disease) are also unlikely to produce effective control.

If the regional distribution of rabbit populations is influenced by connectivity among local populations resulting from the degree of spatial heterogeneity of favourable habitats, and if the population processes and interactions determining connectivity can be modelled, then the outcomes may have broader implications. For instance, the effects of habitat heterogeneity may place results from site-specific studies into a regional perspective and help resolve questions relating to the patchy success of rabbit-borne control vectors (Smyth *et al.* 1997). At first glance, this seems a daunting task but, as the present study shows, genetic data can

provide independent evidence of interactions among geographically distant locations against which a habitat heterogeneity model can be assessed.

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