Microgeographic variation in two relict island populations of the quokka, *Setonix brachyurus* (Macropodidae: Marsupialia), assessed by allozyme electrophoresis

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Abstract

Genetic variation was examined in two relict island populations of the quokka, *Setonix brachyurus*, on Rottnest and Bald Islands. Allozyme electrophoresis was used to examine subdivision among the two islands, at a broad-scale population level within Rottnest Island, and a fine-scale subpopulation level within West End, Rottnest Island. Low levels of variation were detected (two loci). However, significant heterogeneity was observed among the Bald and Rottnest Island populations (F_{ST} = 0.288) and among the Rottnest Island populations (F_{ST} = 0.193). No significant fine-scale subdivision was detected within West End (F_{ST} = 0.023). The population level subdivision may be playing an important role in slowing the rate of loss of variation.

Keywords: microgeography, population structure, allozymes, *Setonix*, marsupial, relict, island populations

Introduction

Two fundamentally different views on the structuring of populations have been developed; the classical subpopulation paradigm from genetics and the social structure paradigm from behavioural ecology (Sugg *et al.* 1996). The subpopulation models assume random mating within subpopulations. However, populations are often composed of more than just randomly mating subpopulations; many organisms form small, local breeding groups with gene flow being restricted by the social structure (Liu & Godt 1983; Sugg *et al.* 1996). Therefore, the genetic structure of a species will be influenced by the dispersal, demography, and mating system characterising that species (Shields 1987). In the absence of selection, the interaction of population size, amount of gene exchange, and breeding patterns will also be reflected in the genetic structure (Patton & Feder 1981). Those populations characterised by high gene flow and random mating will be much less structured than those in which the reverse conditions hold. Where social structure is strong within the subpopulations, random mating will not occur among the breeding groups.

The organisation of populations into independent breeding units may have important effects on the short-term evolution of populations (Wright 1980), as well as on the maintenance of genetic polymorphisms (Chesser *et al*. 1980). Genetic drift due to small effective population size could lead to heterogeneity among the groups. Genetic heterogeneity over short geographic distance has been observed among populations of small mammal species (*e.g.* Selander 1970; Wright 1978; Patton & Feder 1981; Chesser 1983; Kessler & Avise 1985).

Although the relationship between mating systems and sexual dimorphism has more commonly been studied in birds (Lack 1968; Orians 1969; Selander 1972), Jarman (1983) suggested that the degree of sexual dimorphism in mammals can be used as an indicator of mating strategy and hence social structure. Among Australian marsupials, sexual dimorphism is greatest in the larger macropod species (see Jarman 1989). In moderate to highly dimorphic species, the males are organised into dominance hierarchies (Jarman 1983; Croft 1989) and the mating system is either promiscuous (Croft 1989; Jarman 1991) or polygamous (*e.g.* Croft 1981; Sander *et al*. 1997). Smaller species show little sexual dimorphism (Jarman 1989) and tend to be monogamous. Moderate sexual dimorphism, based on five morphological measures, was detected in the quokka, *Setonix brachyurus* (Sinclair 1998) and dominance hierarchies have been reported (Kitchener 1970). Adult males form a linear hierarchy and are dominant to females and juveniles. Infrequent changes were observed in the ranking order of adult males during Kitchener's (1970) study, indicating that the hierarchy was relatively stable. The existence of dominance hierarchies among males and prevalence of polygamy would enhance inbreeding and small effective population size (Wilson *et al.* 1975).

In mammals, males show a greater tendency than females for movement between their birth place and first breeding location (Greenwood 1980). Information on dispersal and philopatry is available for nine macropod species, for which dispersal is predominantly by juvenile males (Johnson 1989). Breeding dispersal in macropods is generally rare (Johnson 1989; but see Christensen 1980; Oliver 1986). Natal dispersal was absent in both the tammar wallaby (*Macropus eugenii*) and *S. brachyurus*. Nicholls (1971) concluded that for *S. brachyurus*, the

group home ranges were constrained by resource distributions and not social structure on Rottnest Island. Three capture-mark-release-recapture studies failed to find any evidence for dispersal in any age class on Rottnest Island (Dunnet 1962; Holsworth 1967; Kitchener 1970). Few studies have examined levels of microgeographic genetic variation in marsupials (although see Moritz *et al.* 1997; Taylor *et al.* 1997; Pope *et al.* 2000), where behavioural traits such as territoriality and mating systems may also give rise to genetic subdivision. Behavioural and morphological studies of *S. brachyurus* on Rottnest Island provide testable hypotheses for a genetic analysis of population structure. As there is some sexual dimorphism and a dominance hierarchy in males, *S. brachyurus* is predicted to have a promiscuous or polygynous mating system.

Here, I use allozyme electrophoresis to examine genetic structure at three geographic levels within *S. brachyurus*. Firstly, to compare two island populations, Bald and Rottnest Island, which have been isolated since the late Pleistocene. Secondly, to examine broad-scale population structure on Rottnest Island; Dunnet (1962) showed that *S. brachyurus* could be grouped into five fairly discrete populations, among which there was virtually no mixing of animals. If this is true, then it would be expected that there is genetic differentiation among these populations. And thirdly, to examine fine-scale group territories; within one population (West End), individuals were found to have home ranges, and groups of 25 to 150 individuals had overlapping home ranges called 'group territories' (Holsworth 1967). These group territories were stable and non-overlapping; animals rarely moved from one to another, and boundaries were generally coincident with topographic features. Kitchener (1973) suggested that *S. brachyurus* occupied the same home ranges throughout their lives, as quokkas of both sexes and a wide range of ages had died within their own home ranges, while Nicholls (1971) used radio-tracking to show that there was movement of individuals between these group territories. If the social groups observed in the field represent the breeding groups, then some genetic structure may be observed. Alternatively, if either sex preferentially mates with individuals from a different social group, little or no genetic differentiation would be observed.

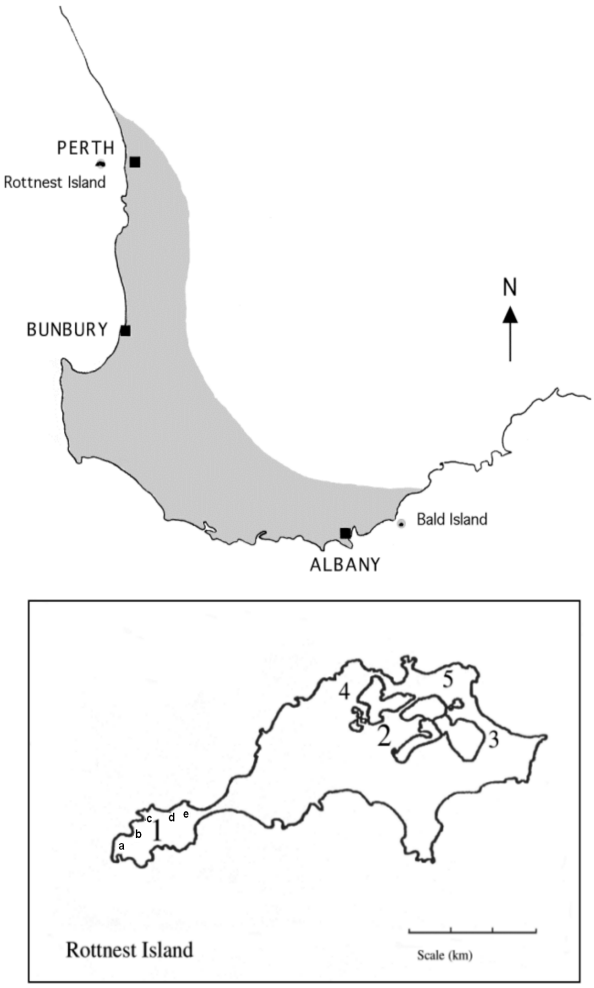

Figure 1. Map showing the distribution of *Setonix brachyurus* in south-western Western Australia (shaded) and the location of Rottnest and Bald Islands. Inset shows the sites sampled on Rottnest Island: 1) West End, 2) Rubbish Tip, 3) Government House Lake, 4) west side of Lake Bagdad, 5) Golf Course, and subsampling at West End: a) Grass Patch, b) Mabel Cove, c) Haywood Cape, d) Marjorie Bay and e) Edeline Beach.

Materials and Methods

Sampling

S. brachyurus was sampled from two continental islands off the Western Australian coastline (Fig 1). Sampling was carried out at two spatial scales on Rottnest Island, the broad-scale population level and fine-scale group territory level. For the broad-scale population level, samples were collected from five sites between July 1994 and January 1995; (1) West End (n = 47), (2) Rubbish Tip (n = 54), (3) Government House Lake (n = 50), (4) west side of Lake Bagdad (n = 49), and (5) Golf Course (n = 53). Sites were selected based on work by Dunnet (1962) and Holsworth (1967). To examine variation at the fine-scale, samples were collected from eight locations at West End. Seven individuals were excluded since these represented sites where fewer than three quokkas were captured. Sample sizes from these locations ranged between 3 and 14 for a total of 40 individuals. The sites at West End represented 5 out of the 15 group territories determined by Holsworth (1967). Twenty-one quokkas were sampled from Bald Island in November 1994.

Three methods were used to catch *S. brachyurus*, cage trapping, hand-netting, and by hand. Juveniles and sub-adults were avoided where possible. A 1 ml blood sample was collected from the tail vein of each animal, which was then individually tagged for future identification. Animals were released at the site of capture. The blood was added to 150 µL acid-citrate-dextrose (ACD) and kept on ice in the field. The blood was centrifuged in the laboratory, and the plasma and red blood cells were stored separately at -70°C until required.

Electrophoresis

Red blood cells were lysed in an equal volume of distilled water containing 1 mg mL^{-1} NADP and then centrifuged for 5 min to remove the cell debris. Variation was examined using Titan gel electrophoresis (Helena Laboratories, USA). Standard electrophoretic procedures

were used, as outlined by Richardson *et al*. (1986). Two polymorphic loci, adenylate kinase (EC 2.7.4.3; *Ak*) and pyruvate kinase (EC 2.7.1.40; *Pk*) were examined for variation using 0.01 M citrate phosphate buffer. These were the only consistently scoreable, polymorphic loci found in an earlier survey of 28 loci across the full range of *S. brachyurus* (Sinclair 2001), and analyses are based on these two loci unless otherwise indicated.

Analysis

Variation at the two polymorphic allozyme loci was summarized by allele frequencies and observed heterozygosities using the program GENEPOP version 3.1 (Raymond & Rousset 1995). The probability test of Guo & Thompson (1992), available in GENEPOP, was used to test for locus conformity to Hardy-Weinberg equilibrium (HWE). A Markov chain algorithm was used to obtain an unbiased estimate of the exact probability. Genic differentiation (allele frequencies) and genotypic differentiation (genotype frequencies) among populations were tested using exact tests, with a Markov chain method used to generate probabilities.

F-statistics (F_{ST}) were used to determine the degree of differentiation among islands, among populations at the broad-scale population (within Rottnest Island), and fine-scale subpopulation (within West End) levels, using the program FSTAT (Goudet 1995). The method of Weir & Cockerham (1984) was used, as this corrects for small sample sizes and departures from Hardy-Weinberg equilibrium. The possible values for F_{ST} range from 0 to 1, with larger values indicating greater genetic subdivision of the sampled populations. 95% confidence limits and an exact G-test (Goudet *et al*. 1996) were used to determine whether F_{ST} values were significantly greater than zero.

Finally, genetic distances between sampled populations were estimated using Nei's (1978) unbiased distance measure. A hierarchical cluster analysis was performed using the unweighted pair-group method with arithmetic mean averaging (UPGMA; Sneath & Sokal 1973).

Results

Mean genetic variability measures were low in all populations (Table 1). Of the two polymorphic loci used in this study, each had only two alleles, of which one was generally uncommon. Three out of the five Rottnest Island populations had a frequency greater than 0.95 for the most common allele at one of the two loci. The *Ak-b* allele was more common on Rottnest Island, while *Ak-c* was the more common allele on Bald Island. A third allele, *Ak-a*, was not present in either of the island populations (Sinclair 2001). There were significant deficits in heterozygosites across all populations and across both loci. The Rubbish Tip and Golf Course populations showed deficits at the *Ak* locus; West End, Government House Lake, and West Bagdad had deficits at the *Pk* locus; while Bald Island had deficits at both loci ($P < 0.001$). Only one heterozygote was detected in the Bald Island population.

There was significant differentiation among allele frequencies and genotypes across populations for both loci ($p < 0.001$). Analysis of pairwise differentiation indicated that many of the significant values were attributed to Bald Island, however, some differences were also attributed to differences among Rottnest Island populations. F-statistics showed significant heterogeneity between Rottnest and Bald Island populations (F_{ST} = 0.288) and among the Rottnest Island populations (F_{ST} = 0.193; Table 2). The subdivision on Rottnest Island was largely due to the *Pk* locus. The Rubbish Tip population had a much higher frequency of the *Pk-a* allele than any other population. A separate analysis without this population gave an F_{ST} value nearly five times lower, 0.048, but still significantly greater than zero, indicating that there was some genetic subdivision among the four remaining populations on Rottnest Island. For an analysis of fine-scale subdivision within West End, there was very little variation in allele frequencies (Table 3), with an F_{ST} not significantly greater than zero (F_{ST} = 0.023).

The UPGMA cluster analysis is shown in Fig 2. All Rottnest Island populations clustered together, reflecting a more recent common history with each other than to Bald Island. Pairwise genetic distance among populations within Rottnest Island ranged from 0.001 (West Bagdad and Goverment House) to 0.184 (Golf Course and Rubbish Tip). Distance measures between Bald Island and the five Rottnest Island populations (range = 0.290 to 0.580) were larger than the distances among Rottnest Island populations.

Table 1

Sample sizes, allele frequencies, and observed heterozygosities (Het) at two polymorphic loci for six island populations of *S. brachyurus*. Significant deficits of heterozygotes from H-W expected values: * P < 0.05, ** P < 0.01, *** P < 0.001.

Locus	Allele	Rottnest Island populations					Bald Island
		West End	Rubbish Tip	Govt House	West Bagdad	Golf Course	
	n =	47	54	50	49	53	21
Ak	*b*	0.968	0.889	0.910	0.949	0.783	0.190
	c	0.032	0.111	0.090	0.051	0.217	0.810
	Het	0.064	0.074***	0.140	0.061	0.170**	0.000***
Pk	*a*	0.160	0.537	0.100	0.031	0.047	0.214
	b	0.840	0.463	0.900	0.969	0.953	0.786
	Het	0.106***	0.481	0.080**	0.020*	0.094	0.048***
Overall Het (28 loci)		0.006	0.020	0.008	0.003	0.009	0.002

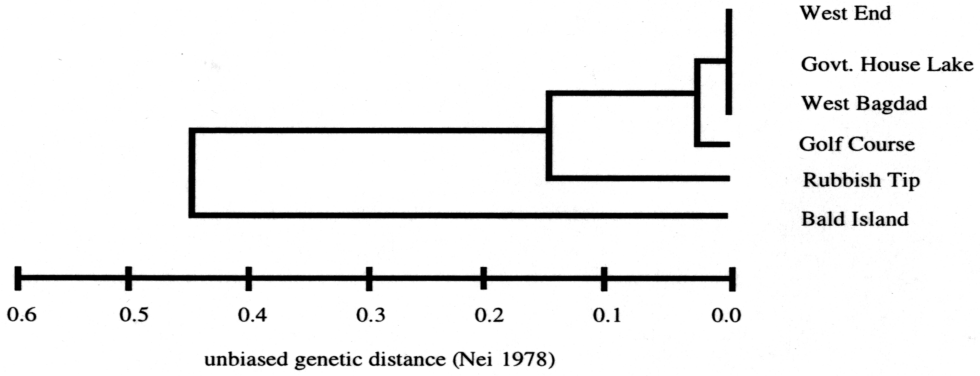

Figure 2. UPGMA cluster analysis of Nei (1978) genetic distance measure among sampled island populations of *S. brachyurus*.

Discussion

There are limitations to the use of allozyme data in examining microgeographic variation in sexually reproducing organisms, as nuclear-encoded allozyme genotypes segregate and recombine (Kessler & Avise 1985). Therefore, genotypes of the offspring can be different to either parental genotype. Population subdivision is then inferred indirectly from heterogeneity in allele frequencies. When considering small numbers of individuals in social groups, the sampling variance may be as great as the variance in allele frequencies, a problem that applies to the calculation of *F*-statistics (Chesser 1983). Also, in most studies using allozymes, *F*-statistics are calculated from more than two polymorphic loci, so the results from this study should be interpreted with some caution.

The significant heterogeneity among Rottnest Island quokka populations suggests broad-scale subdivision across the Island and hence low gene flow between populations. These genetic findings are consistent with the study by Dunnet (1962), who thought there were five fairly discrete populations on the island, among which there was virtually no mixing of quokkas. The highly seasonal conditions on Rottnest Island play an important role in the behaviour of *S. brachyurus*. While populations remain very sedentary during the winter months when food and water are abundant across the island, the drought conditions over summer force animals in the eastern parts of the island to move towards very limited food and water around lake margins (Dunnet 1962). Quokkas at West End tend to move towards the western tip, where succulent vegetation provides some moisture, but little nourishment.

The apparently high degree of subdivision may have been an artefact of the allele frequencies at the *Pk* locus in the Rubbish Tip population. However, analysis without the Rubbish Tip population indicated that there was still significant heterogeneity among the four remaining populations. The Rubbish Tip population differs from the other populations in that it has a constant food source throughout the summer months. Large numbers of *S. brachyurus* also continue to feed there during the winter months, suggesting that these quokkas may not disperse to utilise their natural food resources, as is observed in other parts of the island. If these quokkas remain at the Rubbish Tip site throughout the year, then their behaviour may limit opportunities to mix with other animals. Therefore, lower gene flow between these quokkas and the other sampled populations might be expected. Heterozygosity of the Rubbish Tip population is an order of magnitude higher than the other populations. Other Rottnest populations may undergo frequent (or seasonal) bottlenecks during the summer, leading to lower heterozygosities.

Deficits of heterozygotes were detected in all five populations on Rottnest Island for one of the two loci,

Table 2

Estimates of levels of subdivision as measured by F_{ST} across different sampling levels for *S. brachyurus*. The 95% confidence intervals are given; * indicates value significantly greater than zero. Results for the exact G-test are also given.

	Among Islands	Rottnest Island			Overall
Number of populations	6 450 km	All sites 5 up to 11 km	excluding Rubbish Tip 4 up to 11 km	within West End 5 < 2 km	Geographic range[1] 7 450 km
Locus					
Ak	0.328	0.043	0.065	-0.044	0.210
Pk	0.252	0.283	0.028	0.039	0.457
Over all loci	0.288*	0.193*	0.048*	0.023	0.363*
95% confidence interval	0.252 - 0.328	0.043 - 0.283	0.028 - 0.065	-0.044 - 0.039	0.210 - 0.457
exact G-test	0.0001	0.0001	0.0001	0.1530	0.0001

[1] from Sinclair (2001)

Table 3

Sample sizes, allele frequencies, and observed heterozygosities (Het) for sampled subpopulations of *S. brachyu*rus on West End. Significant deficits of heterozygotes from H-W expected values: * P < 0.05.

		West End, Rottnest Island				
Locus	Allele	Grass Patch	Mabel Cove	Haywood Cape	Marjorie Bay	Edeline Beach
	n =	14	6	7	9	3
Ak	*b*	0.964	0.917	1.000	0.944	1.000
	c	0.036	0.083	-	0.056	-
	Het	0.071	0.167	0.000	0.111	0.000
Pk	*a*	0.179	0.333	-	0.167	0.500
	b	0.821	0.667	1.000	0.833	0.500
	Het	0.071*	0.000*	0.000	0.333	0.333
Overall Het (28 loci)		0.005	0.006	0.000	0.016	0.012

and at both loci on Bald Island. These deficits may be the result of a Wahlund Effect (where homozygosity decreases as a result of sampling across more than one subpopulation), selection, or inbreeding. The F_{ST} value was not significantly greater than zero when subdivision was examined within West End, indicating that a Wahlund Effect was not responsible for the heterozygote deficits at this site. The apparent absence of fine-scale genetic subdivision within West End, however, supports radio-tracking data by Nicholls (1971). He observed frequent and extensive movement of individuals outside the group territories initially defined by Holsworth (1967). These movements may be only short visits, but enough to maintain gene flow among territories.

Inbreeding occurs as a consequence of the geographic subdivision of a population into a number of subpopulations or through the choice of mates according to phenotype or genetic relationship (Selander 1983). The limited dispersal of individuals and isolation from the mainland suggest that inbreeding may contribute to the deficit in heterozygotes. However, as the assumption is made that allozyme variation is largely neutral, one would expect that if inbreeding were responsible, then there would be deficits in heterozygotes at both loci and across all populations. Selection is unlikely to play a significant role in divergence among subpopulations as they occur over very small distances and selection pressures would be similar. None of these explanations adequately accounts for the deficits in heterozygotes of quokkas on Rottnest Island. Two further possibilities may account for these deficits, incorrect scoring of polymorphisms and X-linkage. However, genotypes from a captive bred colony (Sinclair, unpublished data) showed both loci were inherited as expected under a Mendelian mode of inheritance, that is, heterozygous males were observed. Therefore, the cause for heterozygote deficits in Rottnest Island populations could not be determined. However, highly significant deficits in heterozygotes on Bald Island for both loci are consistent with inbreeding.

Breeding group models provide the opportunity to examine which aspects of an organism's biology influence the maintenance of genetic variation (Sugg *et al.* 1996). In *S. brachyurus*, the social groups observed on West End do not show any evidence of reflecting the breeding groups, despite an apparently well maintained social group structure (Dunnet 1962; Nicholls 1971). Environmental conditions may be contributing to the homogeneity. In a study by Oliver (1986) the incidence of breeding dispersal in *Macropus rufus* and *M. eugenii* increased as environmental conditions deteriorated. A similar situation may occur in *S. brachyurus*. Both island populations of *S. brachyurus* experience extremely harsh conditions during the summer months. If group home ranges were constrained by resource distributions, and not social structure, then it would be expected that there is less structure at the fine-scale level. To examine further the microgeographic structure in both islands, the development of highly variable microsatellite markers and more extensive sampling would be required.

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