

KANGAROO GENETICS: IMPACTS OF HARVESTING

REPORT FOR NSW NPWS

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1. SUMMARY AND CONCLUSION

There is concern that the commercial harvest of kangaroos is selective and affecting the genetic make-up of species. These concerns relate to size, traits associated with fitness and gene diversity; that populations will be selected for smaller, less fit individuals and gene diversity will be diminished. Changes in phenotype are well known from selective breeding of domestic animals. They have also been documented in populations of wildlife subject to intensive harvesting. Whether there is genetic change in wildlife populations is likely in some cases but not clear. This study examines the likely effect of selective harvesting on size, fitness and gene diversity in kangaroos.

The response to selection depends on the heritability of the character and the selection differential. The heritability of fitness characters is likely to be low, as will their covariance with size, which is the means of selection thought to be operating in kangaroo harvesting. The characters in question are likely to be subject to balancing selection where no particular allele is dominant and the fittest individual is the heterozygote. Therefore gene frequencies under selection will change slowly. Heritability is low for correlated characters, for example those associated with body size and fitness. The response to even intense selection is slow with only a gradual change in gene frequencies. In the absence of fixation, gene frequencies will return to normal values under natural selection when the selective pressure is removed.

The selection differential, which approximates the proportion of the population in the selected group, will depend on whether the trait is inherited through one or both sexes, whether the population under selection is age structured, whether the population under selection is open or closed and the reproductive success of the portion of the population that is selected.

Gene diversity is estimated from expected heterozygosity under conditions of random mating. Comparisons of gene diversity in heavily harvested versus unharvested populations of red kangaroos and wallaroos did not show any significant differences. Genetic population structure allows an estimate of the geographic range of genetic populations and is estimated using F_{st} for allozyme data and $U-R_{st}$ for microsatellite data. Very little if any genetic population structure was revealed throughout the species range of the red kangaroo. The geographic range of genetic populations is very large, perhaps the entire species distribution, and migration of breeding individuals over large distances maintains this panmixia. Considerable genetic population structure exists throughout the species range of wallaroos. The geographic range of genetic populations is small with respect to the species range, but large with respect to the harvest range (see further). The geographic ranges of genetic populations in grey kangaroos are expected to lie somewhere between those for red kangaroos and wallaroos.

The harvest is male biased and intensive harvesting changes the age structure at particular localities. The distribution of the harvest is patchy within the range of genetic populations and within those patches the harvest is fairly uniform across adult age classes. This reduces the selection differential because a very large proportion of adult individuals is in the selected group. The harvest over the range of genetic populations is about 10%, which also lowers the selection differential. Genetic population numbers are in the millions of breeding individuals. Large males out compete small males for matings but the dominance may be weak in overall reproductive terms, because dominance of individuals is short-lived and small males may achieve significant matings after drought and as a result of greater mobility. Again this serves to reduce the selection differential.

Periodic and frequent droughts that cause widespread mortality amongst kangaroos, may enact a proportionally higher toll on larger males, and provide frequent selective sweeps to purge populations of less fit individuals. Frequent disease outbreaks following rain provide another selective mechanism to purge populations of less fit individuals. Although older males are likely to achieve proportionally more matings than younger adult males, the fitness benefits for the population may not be that marked because younger adults of breeding age have been selected for fitness by drought and pestilence. Thus the difference in fitness between younger and older males will not be great.

The effects of the commercial harvest are therefore unlikely to produce genetic changes in the population. First, the heritability of the characters in question is low. Second, the selection differential is low because differences in fitness between younger and older adult males is small, older males do not appear to monopolise matings, only a small proportion of older males are selected against (so most animals are in the selected group), and only a small proportion of the population is harvested.

2. INTRODUCTION

Concerns have been expressed about the effect of harvesting on the genetics of kangaroo species (Croft 2000). These concerns derive from the nature of the harvest, which is selective in taking larger rather than smaller animals, and takes more males than females due to size dimorphism (Pople 1996). It is argued (Croft 2000) that

larger, older kangaroos may be genetically 'fitter' because they have survived longer than younger kangaroos, and if large kangaroos are harvested selectively then the best genes in the population will be lost. Younger males with possibly a 'less fit' genetic makeup will then have an opportunity to mate due to a reduction in competition and pass on inferior genes. There is concern that consequently the species gene pool will be depleted of 'fitter' genes (Croft 2000). As well, it is thought that if larger kangaroos are selected against, then genes that produce large individuals may be depleted from the gene pool. An example cited in Croft (2000) is the increased prevalence of tusklessness in female African elephants, increasing from 10.5% in 1969 (reported incorrectly by the Guardian Weekly (October 11 1996) as 1%) to 38.2% in 1989 (Jachmann *et al.* 1995). The cause of this has been attributed to trophy hunting and poaching, both of which target elephants with large tusks. Another example is the phenotypic selection on some fish species by gillnetting, which catches larger fish and has changed the phenotype towards early maturity (Law 2000).

There is concern also that the selection imposed by harvesting will lead to a loss of 'adaptive genotypes' (Croft 2000). I interpret this term as follows; at any given genetic locus in a species there may be several alleles, so over all loci there is a lot of variability amongst individuals. This variability is not spread uniformly across all genes, but the outcome expected is that populations with high gene diversity are better able to adapt to new selection pressures as they arise. To put it another way, the population can express a range of phenotypes depending on the selective pressure applied by the environment (Cook and Callow 1999). So 'adaptive genotypes' means gene diversity and the maintenance of evolutionary potential (Moritz 1994). The definition of gene diversity that I shall use in this discussion is that of Nei (1987), which is the average heterozygosity among loci.

The questions to be discussed herein concern the amount of selection or loss of gene diversity that might occur as a result of harvesting. Is harvesting likely to affect the genetic make-up of species and their evolutionary potential? Kangaroo populations are in a state of dynamic equilibrium. They are continually subject to perturbations other than harvesting. Extreme environmental fluctuations are common in Australia and high mortality occurs in kangaroo populations as a result of climate variability. The periodic regional droughts that characterise the Australian climate can exact a large toll from kangaroo populations. Reductions by more than 50% of the pre-drought population have been recorded (Caughley *et al.* 1985, Robertson 1986, McCallum 1994, Pople 1996). The 'flooding rains' that also characterise Australia's arid areas may result in disease outbreaks that are responsible for further widespread mortality (Speare *et al.* 1989, 1990). It is important to compare the effect of these events on kangaroo population composition to the possible effect of a commercial harvest of larger kangaroos.

The influence that can be exerted on the phenotype through artificial and natural selection is well documented from selective breeding, particularly dogs and domestic livestock; eg cattle, pigs and horses. The enormous phenotypic variance among breeds of dog is evidence of the degree of phenotypic variation within a single species. The discipline of quantitative genetics enables the results of artificial or natural selection to be quantified in terms of changes in metric characters (eg, size) and gene frequencies (see Falconer and McKay 1996).

Increasing mortality rates through harvesting should reduce body size over time and alter other traits such as age at sexual maturity (Stearns 1993). However, in kangaroos the reverse has possibly occurred through reduced mortality rates as a result of dingo control (Caughley *et al.* 1980, Pople *et al.* 2000). Such effects will be diluted if there are spatial or temporal 'refuges', and the effects will be reversed following removal of the mortality agent (Stearns 1993).

In the following discussion the effect of selective harvesting of kangaroos on size and fitness, including components of fitness such as disease resistance, as well as gene diversity will be discussed, as will the effect of drought and pestilence on these characters. Other aspects of commercial kangaroo life histories and population dynamics, such as growth rate, age at maturity, dispersal and regional size variance, will be outlined in order to gain an appreciation of the intensity of the harvest in selecting for smaller body size. The gene composition of size and of fitness characters will be discussed with regard to the intensity of selection required to bring about significant and lasting changes in gene frequencies.

The discussion presented in this report is intended as a preliminary to an empirical modeling exercise. Several parameters that will be useful as variables in the model are presented for discussion. It is intended that these parameters will be incorporated into an age-structured model to assess the likelihood of genetic change in populations and species under different harvesting intensities.

Main points

- There is concern that the commercial harvest of kangaroos is selective and affecting the genetic make-up of species.
- The concerns relate to size, traits associated with fitness and gene diversity.
- Changes in phenotype are well known from selective breeding of domestic animals. They have also been documented in populations of wildlife subject to intensive harvesting. Whether there is genetic change in wildlife populations is likely in some cases but not clear.
- This study examines the likely effect of selective harvesting on size, fitness and gene diversity in kangaroos.

3. GENETIC CONSEQUENCES OF WILDLIFE HARVESTING

Quantitative genetics considerations

In quantitative genetics a metric character (a character that you can measure) is described in terms of its heritability, h^2 , which is equal to the ratio of the additive variance (breeding value of a character) to the phenotypic variance of the character (V_A/V_P). The ratio expresses the extent to which phenotype is determined by the genes transmitted from the parents (Falconer and McKay 1996). Heritability is estimated from the degree of resemblance between parents and their offspring. When expressed in terms of the correlation (or regression) between relatives, it is the observed correlation as a proportion of the correlation that would be found if the character were completely inherited.

The effect of selection is to change gene frequencies. The response to selection (R) is the difference of mean phenotypic value between the offspring of the parents selected

and the whole of the parental generation before selection. The measure of the selection, selection differential (S), is the mean phenotypic value of the parents expressed as a deviation from the population mean phenotypic value (Falconer and McKay 1996).

$$\text{Then } R = h^2 S; \text{ (E-1)}$$

The standardised selection differential, S / σ_P , is called the intensity of selection, i , where σ_P is the standard deviation of a character in the population, and 'i' depends only on the proportion of the population included in the selected group provided that the distribution of phenotypic values is normal. Selection for fitness usually operates on metric characters correlated with fitness, such as size. For a particular character x and a correlated character y , the response to selection on y is (Manly 1985):

$$R_y = h_x \cdot h_y \cdot r_A \cdot S \cdot \sigma_y / \sigma_x ; \text{ (E-2)}$$

Where:

h_x = heritability of x

h_y = heritability of y

r_A = genetic correlation of x & y

S = selection differential

σ_y / σ_x = ratio of phenotypic standard deviations of x & y before selection.

Heritability

Heritability (h^2) = V_A/V_P . The phenotypic variance (V_P) is equal to the genetic variance plus the environmental variance. For a character such as size in a wild animal, estimating the genetic variance would be difficult. There is some evidence (see further) that the environmental variance for size in male red kangaroos is large. A large environmental variance will result in a low heritability for size.

Heritability for fitness characters is generally low. Life history traits can be considered components of fitness and have heritabilities in the order of 0.26 (Mousseau & Roff 1987). In fish it is argued that heritabilities found in the wild for body size approximate those found under artificial selection in the laboratory, at 0.25 – 0.3 (Law 2000). While fitness traits have low heritability (Falconer and McKay 1996, Law 2000), stature in humans and weight in cattle have heritabilities of about 0.6 (Falconer and McKay 1996).

Selection differential.

The selection differential, S , is the proportion of individuals in the selected group. The greater S , the greater the response to selection. This proportion will depend on factors including:

- Whether the character is inherited through both males and females. Size and components of fitness, the characters of concern in kangaroos, are inherited through both parents. A harvest biased towards males will reduce S because the genes for characters will still be passed on through females.
- Whether selection is age-structured. With overlapping generations, the character may only be expressed in a small proportion of individuals (the older individuals), but present in a large proportion of the population. Kangaroo

harvesting targets older animals, and the result is to reduce S , because younger kangaroos that are not harvested (the selected group) will contain the 'preferred' genes as well as 'non-preferred' genes, having not been tested by natural selection.

- Whether the population (locality) under selection (harvest) is open or closed. To what extent does the geographic range of the population change the proportion of individuals in the selected group if the harvest locality does not include the entire population? Kangaroo harvest localities are a small proportion of the geographic range of the population (see further), which will reduce S because a proportion of the group selected against will not be harvested; there will be a higher proportion of the population in the selected group.
- The reproductive success of the group that is selected for or against. There is some information available about the relative mating success of large, older kangaroos (see further). This suggests that, while these animals may dominate matings at certain times, at other times smaller, younger males get matings (see further). If older males get a large proportion of matings, then S will be higher than if matings are more evenly distributed across the mature age classes.
- Whether the population is at equilibrium. Natural populations are not at equilibrium compared to domestic populations, and variability amongst individuals is greater than if they were. The effect is to reduce S .

Gene frequencies change slowly, even under intense selection, unless there are genes with large effects (Falconer and McKay 1996). A metric character such as size is likely to be the result of expression of a number of correlated genes that show no dominance, all with different allelic composition in different individuals. The genetic response, which is the change of gene frequencies, will therefore be only a gradual change, reducing the intensity of selection. The changes in gene frequencies for characters associated with fitness will also be slow, because these are also correlated characters.

Most characters associated with fitness are also likely to be under balancing selection where no particular allele is dominant and the fittest individual is the heterozygote (Kimura 1983, Cook & Callow 1999). Gene frequencies therefore change slowly under selection. If selective pressure is removed before variation has been lost by fixation, gene frequencies will return to their equilibrium values through natural selection, and the mean of the trait under artificial selection will revert to its original value (Falconer and McKay 1996). For example, in African elephants, if the increase in the frequency of tuskless females (Jachmann *et al.* 1995) were the result of hunting, equilibrium (pre-hunting) frequencies would result in time after cessation of this selective pressure.

The benefit of sexual selection for fitness (Andersson 1994) is that individuals carrying higher mutational load are less likely to breed. A question for selective harvesting in kangaroos is that if younger male kangaroos get a chance to breed because older animals, who would normally dominate matings, are removed from the population, then are these younger males in fact less fit than the older males they are replacing?.

The macropod immune system and fitness

Speare *et al.* (1989) reviewed the diseases of free-ranging Macropodoidea. They appear to have classes of immune response similar to those found in eutherian mammals. The genetic structure of the immune system is also similar to that of eutherian mammals (Slade *et al.* 1993). The immune system is predicted to be subject to overdominant selection, where the heterozygous state of a gene has the highest fitness (overdominance is a form of balancing selection). This idea is inferred from the presence in the immune system of numerous gene families, many genes and a high degree of polymorphism within genes. There is some direct evidence to support it: At the antigen recognition site of MHC molecules the rate of non-synonymous substitutions is greater than the rate of synonymous substitutions (Nei and Kumar 2000). This finding gives credence to a selectionist view of evolution, as contrasted to a neutralist view, where genetic polymorphism is thought to be the result of random fixation of selectively neutral or nearly neutral mutants (Kimura 1983, Cook & Callow 1999).

Main points

- The response to selection depends on the heritability of the character and the selection differential (see E-1 above). The heritability of fitness characters is likely to be low, as will their covariance with size, which is the means of selection thought to be operating in kangaroo harvesting.
- Characters are likely to be subject to balancing selection where no particular allele is dominant and the fittest individual is the heterozygote. Therefore gene frequencies under selection will change slowly.
- Heritability is low for correlated characters (see E-2 above), for example those associated with body size and fitness. The response to even intense selection is slow with only a gradual change in gene frequencies.
- The selection differential, which approximates the proportion of the population in the selected group, will depend on whether the trait is inherited through one or both sexes, whether the population under selection is age structured, whether the population under selection is open or closed and the reproductive success of the portion of the population that is selected.

4. GENE DIVERSITY AND GENETIC POPULATION STRUCTURE

Background to analytical methods.

Nuclear DNA analysis (nDNA; allozyme and microsatellite loci) is used in preference to mitochondrial DNA (mtDNA) in the population genetic analyses presented here because nDNA is inherited through both parents while mtDNA is inherited through females only. Use of nDNA permits conclusions about genetic population structure and gene diversity resulting from selection on both sexes.

For red kangaroos, gene diversity and population structure are estimated from analysis of allozyme nDNA loci and microsatellite nDNA loci. Allozyme loci typically have low allelic polymorphism and low heterozygosity, while at microsatellite loci polymorphism and heterozygosity are typically higher because the mutation rate is higher. Therefore it is possible with microsatellite analysis to reveal differences in population structure that are the result of more recent ecological events.

Methods of estimating gene diversity.

Expected heterozygosity under Hardy-Weinberg (H-W) proportions (ie, the heterozygosity expected in a population under random mating) rather than allelic diversity is used to estimate gene diversity in populations (see Nei 1987, Nei and Kumar 2000)¹. With allelic diversity (number of alleles per locus) the number of alleles is dependent on sample size, and loss of alleles, perhaps as a result of intensive harvesting, will not be reflected much by loss of rare alleles. If a population were depleted of genetic diversity (called a genetic 'bottleneck') then one would expect a significant loss of heterozygosity.

Considering estimates of gene diversity made from allozyme and from microsatellite data, the interlocus variance will be large with allozymes because many loci are monomorphic. In this situation the estimate of gene diversity is not reliable. However, the use of only those allozyme or microsatellite loci that are polymorphic (0.95 criterion) will overcome this problem (Nei 1987).

Methods of estimating genetic population structure.

Allelic diversity is sometimes used to estimate differentiation between populations. It is a function of sample size and alleles at low frequency will have a disproportionate effect. The number of alleles increases with increasing sample size and this is especially the case where allelic polymorphism is high, such as at microsatellite loci. Samples must therefore be the same size. Using heterozygosity to estimate differentiation through F_{st} , alleles at low frequency hardly contribute to the estimate (Nei 1987).

Fst versus Rst. F_{st} is used in the analysis presented herein to estimate population differentiation from allozyme data (see Hartl and Clark 1989). F-Statistics are based on the infinite alleles model of mutation (IAM, Kimura & Crow 1964), with the assumptions that the mutation rate is so low that it can be ignored as a contributing factor in population differentiation, and that a new mutation erases any memory of the prior allelic state. F_{st} measures the fraction of the variance in heterozygosity between populations. For microsatellite loci the assumptions of the IAM do not hold because the mutation rate at microsatellite loci is likely to be high. Therefore the same allele in different populations may not be identical by descent. As well, an allele of large repeat number is likely to have originated from a similarly sized allele and the prior allelic state is not erased.

A new statistic has been developed to analyse population structure using microsatellite data, based on a stepwise mutation model (SMM, Ohta & Kimura 1973). Thus while F_{st} is the fraction of the variance in heterozygosity between populations, R_{st} is the fraction of the variance in allele size between populations (Valdes *et al.* 1993, Slatkin 1995). Slatkin (1995) assumes a stepwise mutation

¹ Heterozygosity (H) is the proportion of individuals within the population that are heterozygous (for particular alleles) for a given locus. $H = 1 - F$, where F is the probability of drawing a pair of alleles that are identical by descent. To estimate gene diversity in a population, the number of heterozygotes at each locus (gene) is calculated, divided by the number of individuals and averaged over all genes. Populations are in H-W proportions when they conform to the expectation of the binomial expansion (eg, $(p + q)^2$ for a 2 allele system). Hardy-Weinberg equilibrium is achieved after one generation of random mating, and genotypes from particular localities should be in H-W equilibrium for analyses of population structure.

process in developing the Rst statistic where the stepwise increment is a random variable with a mean of zero and a variance based on the mutation rate. The unbiased Rst (U-Rst) of Goodman (1997) calculates Slatkin's (1995) Rst and corrects for bias resulting from differences in population size. Data are standardised for the magnitude of the variance in allele size between loci. Estimates of population differentiation from microsatellite genotypes using U-Rst appear more reliable than those using Fst or other methods (Valsecchi *et al.* 1997).

In the analysis of gene diversity and population differentiation presented in this report, expected heterozygosity is used as a measure of gene diversity for both allozyme and microsatellite data, Fst is used to estimate population differentiation from allozyme data and U-Rst is used to estimate population differentiation from microsatellite data.

Gene diversity in large kangaroos

Gene diversity at loci such as allozymes and microsatellites should reflect gene diversity in the genome and give an indication of whether or not harvesting is affecting gene diversity. Gene diversity was assessed in and compared among populations of red kangaroos and wallaroos harvested at different localities and at different rates (Hale *et al.* in prep.).

Red Kangaroos

Gene diversity at both allozyme and microsatellite loci was estimated in red kangaroos. There was no significant difference in levels of gene diversity between populations (the genotyped individuals at each locality were found to be in H-W equilibrium and are therefore termed populations) subject to heavy levels of harvesting compared to those that were not harvested (Kruskal – Wallis test). Harvest localities are shown in Figure 1. The heavily harvested localities were near Blackall and Charleville in Queensland (harvest rates of > 30%, Pople 1996), with lightly harvested localities at Mulyungarie and Bulgunnia in South Australia and at Julia Creek in Qld (10 – 20% , Pople 1996) and an unharvested locality at Currawinya NP in SW-Qld (Pople 1996). There was also no difference in gene diversity among heavily harvested and unharvested populations.

Wallaroos

In wallaroos, harvesting is generally less intense than for red kangaroos. Gene diversity was estimated at 7 microsatellite loci among 9 localities (Fig. 2). There was no significant difference in levels of gene diversity between populations subject to moderate levels of harvesting compared to those that were harvested only lightly or not at all (Kruskal – Wallis test). Moderately harvested localities were near Jericho and Charters Towers in Qld and Brewarrina in NSW, lightly harvested localities were near Broken Hill in NSW, Warwick in QLD and Pilbara in WA while the unharvested locality was Bladensberg NP near Winton in Qld.

Modelling the effect of small population size on gene diversity.

Lacy (1987) simulated gene diversity in a 2-allele system to model the competing effects of population size, selection, immigration and mutation in small populations over time. In a population of 500 breeding individuals, 90% of gene diversity was retained after 100 generations while 60% was retained in a population of 120 breeding individuals over the same interval. For a population size of 120 individuals, immigration and balancing selection were key factors in maintaining gene diversity.

The impact of small population size on gene diversity became evident at only very small population sizes.

Genetic population structure large kangaroos.

Estimates of the geographic ranges of genetic populations (Hale *et al.* in prep.) were made from the migration rate calculated from the value for the pairwise differentiation between populations obtained in the F_{st} (for allozyme data) and $U-R_{st}$ (for microsatellite data) analyses. Sample localities are shown in Figures 1 & 2.

Red kangaroos

Genetic population structure was compared amongst six localities for the allozyme analysis (all those in Fig. 1 except Western Australia) and nine genetic loci were analysed. Genotypes at each locality were in H-W equilibrium. The F_{st} analysis showed Mulyungarie to be significantly differentiated from each of the other five localities. For the microsatellite analysis all seven localities shown in Figure 1 were compared and four genetic loci were analysed. Genotypes at each locality were in H-W equilibrium. The $U-R_{st}$ analysis showed no significant differentiation between any of the localities analysed.

It is interesting that Mulyungarie alone is differentiated from the other five populations in the allozyme analysis. Although significant, the effect size is small (mean pairwise $F_{st} = 0.052$) and could be due to a weak selective effect at one or more of the allozyme loci used in the study. The lack of significant differentiation in pairwise comparisons involving Julia Creek and Bulgunnia (Fig. 1), over the largest distances analysed (Fig. 1), suggests that this is an inconsistent result.

Based on these results, migration for red kangaroos appears sufficiently high to maintain panmixia among all localities tested. The geographic range of genetic populations of red kangaroos is certainly very large and may well encompass the entire species range.

Wallaroos

Genetic population structure for wallaroos was compared amongst nine localities throughout Australia (Fig. 2). Genotypes from all nine localities were in H-W equilibrium. Thirty six pairwise $U-R_{st}$ estimates of genetic differentiation ranged in value from 0 to 0.472. Comparisons Jericho-Winton and Thargominda - Winton (Fig. 2) were not significantly different to zero at $p < 0.05$, while Jericho - Thargominda was barely significant at this level, with the Bonferroni sequential correction applied. All other pairwise $U-R_{st}$ values were significant.

A Mantel test of matrix correspondence between log geographic distance and log $U-R_{st}$ (Nm values) for all $U-R_{st}$ pairwise comparisons showed a significant negative regression ($r[z] = -0.664$, $p = 0.003$), suggesting that gene flow in wallaroos is the result of isolation by distance. The regression coefficient was still significant when the Pilbara locality in Western Australia was removed from the analysis.

The small amount of differentiation identified between Thargominda, Winton and Jericho (Fig. 2) is non-significant or barely significant. This suggests an upper limit to the geographic range of genetic populations. Other localities in close pairwise proximity were significantly differentiated (CLN - WIN, BRE - WAW, CHT - WIN;

Fig. 2). The area of Central Qld bounded by Thargominda, Winton and Jericho sees the highest offtake of wallaroos in the study area. Wallaroos here concentrate uncharacteristically in open country (Pople *et al.* 1998). It has been suggested that the reason for this is the removal of predation by the dingo fence and the resulting ability to disperse in open country without risk of predation (Pople *et al.* 1998). The large geographic range in this area may therefore be anomalous, and the natural range may be less, as suggested by the results for other pairwise comparisons. The results show that the geographic range of the genetic population in this region would be no more than 200,000 sq. km. In other parts of Eastern Australia geographic ranges are likely to be smaller.

Grey kangaroos

Studies of home range tell us that dispersal distances and home ranges of grey kangaroos lie between those of red kangaroos and wallaroos (Dawson 1995). Without any analysis, one might expect that the geographic ranges of genetic populations for grey kangaroos would be somewhere between those for red kangaroos (very large) and wallaroos (small).

Main points

- Gene diversity is estimated from expected heterozygosity under conditions of random mating, genetic population structure is estimated using F_{st} for allozyme data and $U-R_{st}$ for microsatellite data.
- Comparisons of gene diversity in heavily harvested versus unharvested populations of red kangaroos and wallaroos did not show any significant differences.
- Very little if any genetic population structure was revealed throughout the species range of the red kangaroo. The result indicates that the geographic range of genetic populations is very large and migration of breeding individuals over large distances maintains this panmixia.
- Considerable genetic population structure exists throughout the species range of wallaroos. The geographic range of genetic populations is small with respect to the species range, but large with respect to the harvest range (see further).
- The geographic ranges of genetic populations in grey kangaroos are expected to lie somewhere between those for red kangaroos and wallaroos.

5. KANGAROO POPULATION DYNAMICS

Maturation and body weight

Large kangaroos live for 15 – 20 years (Dawson 1995). Male red kangaroos are sexually mature from 2 – 4 years, while females mature from 2 - 3 years of age. Males weigh 20-30 kg at onset of maturity and reach 40kg near 5 years of age (Dawson 1995, Pople 1996). A 2-3 year old male red kangaroo will double in weight before he is fully-grown at about 15 years. Onset of maturity varies with pasture condition, being delayed during drought (Dawson 1995). Male western grey kangaroos mature at about 2.5 years of age weighing about 25kg while eastern grey kangaroos mature at about 4 years (Dawson 1995). Kangaroo shooters prefer animals at about 25kg or more (Pople 1996).

Maximum body weights (MBW) for male and female red kangaroos vary among localities. For males in the Blackall region MBW (52kg) are similar to those at Currawinya NP (52kg) and Bladensburg NP (53kg). Those at Julia Creek (72kg), Mulyungarie (65kg) and Bulgunnia (78kg) are markedly larger. For females the differences follow the same trend but are not as marked (Pople 1996 Fig. 7.1 & unpublished). These results indicate that maximum body weight has a large phenotypic variance. The results from the population genetic structure analysis in the previous chapter reveal that there is little if any genetic structure among these populations. It seems therefore that a large component of the phenotypic variance can be explained by the environmental variance. The response to selection (R , Equations E-1 & E-2) will be smaller if the heritability for the character is small, which it appears to be because the environmental component is large

Dynamics of the harvest

Pople (1996) examined age structure in harvested and unharvested red kangaroo populations. In unharvested (Currawinya NP) and harvested (Blackall region) localities the age structure was revealed by a random shot sample of the population. Not surprisingly, in harvested populations there are less of the older, larger animals in the sample, particularly males. Harvesting in the Blackall region is very high on particular properties, up to 50% / annum (Pople 1996). In Table 1 the harvest on one property is proportioned into sex and age classes. The data show that shooters take a larger proportion of male than female kangaroos. They also take a large proportion of kangaroos from the younger age classes, and the reason is that kangaroos in the younger age classes are of adequate size to be harvested commercially (2 - 3 year old males weigh 20 – 30 kg) and they form a larger proportion of the population than older males.

Table 1: Proportion of red kangaroos shot in each of 4 age classes on a property near Blackall, 1991-3 (from Pople 1996).

Age class (years)	Propn (%) males	Propn (%) females
1	1.5	0.5
2	19	8
3	22	11
4+	31	7

The age structure of the harvest shown in Table 1 reveals an aspect of shooter behaviour that has important implications for the selection differential (S in E-1 & E-2). Shooters will target an area that is accessible and take smaller kangaroos rather than range widely to target only large males. Thus on a broad scale selection by the shooter against large individuals is weak, or selection for smaller individuals is weak and the intensity of selection for small body size imposed by the harvest is weaker than if large males were particularly targetted.

Harvest distribution, quotas and population size.

The commercial harvest of all species of kangaroos is patchy and depends primarily on access. As discussed, a shooter will harvest where there are sufficient kangaroos of adequate size to be taken at minimal cost. Therefore shooters tend to frequent particular localities that are not necessarily localities of high kangaroo density or of a high proportion of large kangaroos (Pople *et al.* 1998). This has important

implications for the intensity of selection imposed on genetic populations. The geographic ranges of genetic populations are much larger than the harvest areas, so harvesting within the range of a genetic population is patchy. One would therefore expect immigration into the harvest locality from localities outside where the age structure has not been impacted by harvesting. The age structure in the population will rapidly return to normal (ie, stabilise) after cessation of harvesting in about one generation or six years (Pople 1996). However, the age structure of an arid zone population of kangaroos will rarely stabilise due to environmental fluctuations. Pople (1996) noted large males among red kangaroos at Idalia near Blackall within two years of cessation of long-term harvesting. It is likely they were immigrants.

The annual commercial quotas for all 4 species of kangaroos are set by the States at 10-20% of the population estimate. Population densities are estimated from aerial surveys. For example in Queensland during the early 1990's it was estimated that there were 3 - 5 million red kangaroos and the quota was 5 - 600,000. The highest harvest densities (>5/sq.km.) occur in the Blackall region. The Queensland population of eastern grey kangaroos is estimated at 5 - 10 million and the quota 0.8 - 1.5 million, with highest harvest densities in the Roma / St George / Charleville region. Wallaroos are harvested at low densities (0.01-1/sq.km.) except in the Blackall region. The estimated population size has been 1 - 2 million and the quota about 200,000 (Pople *et al.* 1998). Looking at harvest distribution maps for red kangaroos, wallaroos and eastern grey kangaroos (Pople and Grigg 1998) the patchy nature of the harvest is evident. From the population density estimates for these species obtained from aerial surveys (Caughley and Grigg 1982), it is evident that some areas of high kangaroo density are not harvested intensively. Recent helicopter surveys conducted with parallel ground - truthing have revealed that population estimates for wallaroos are still underestimates (Clancy *et al.* 1997).

The large population sizes in regions of genetic panmixia (free interchange of breeding individuals) is evident. Loss of gene diversity and fitness are problems encountered commonly when population sizes are small. Fixation of alleles leads to loss of gene diversity and fixation of deleterious alleles leads to loss of fitness (Lacy 1987, Hauser *et al.* 1994). Population sizes in these situations are in the order of a few hundred breeding individuals. Population sizes of large kangaroos are in the order of millions of breeding individuals.

Behavioural ecology and mating success

Male size and age has a role in sexual selection in kangaroos (Moss 1995, Walker 1995). In the species harvested there is a large size dimorphism between the sexes. Females may prefer bigger males because they are less likely to be injured during copulation and because copulation is more likely to be completed (Walker 1995). Experience in males may be more important than size. Bigger males can win fights with smaller males, but this may be a function of experience as well as size (Moss 1995). Other research has shown that larger males are indeed more likely to achieve dominance, but only for short periods (Walker 1995). The ability to range widely may also be a positive factor in mating success (Andersson 1994). For example, genetic studies have revealed that in koalas mating success of adult males that range widely is significantly higher than of adult males with well-defined home ranges (Ellis *et al.* 2000 & in press). Younger male kangaroos are apparently more likely to disperse than older animals (Dawson 1995). After drought younger males may get more

opportunities to mate because there is a pulse of ovulation in females (Pople 1996), delivering plenty of mating opportunities for subordinate individuals (Moss 1995, Brooks & Kemp 2001). There is debate over the fitness benefits to females from mating with males with particular traits such as large body size. Large males may have 'good' genes, possibly conferring such things as greater disease or parasite resistance (Brooks & Kemp 2001).

Effect of drought.

Caughley *et al.* (1985) considered drought and its consequent mortality to be intrinsic to kangaroo ecology. The sizes of populations are reduced during drought, sometimes dramatically, and the reduction is not density dependent (Pople 1996). Local droughts occur almost every year and regional droughts about once every 10 years. There is a moderate ($r = 0.4 - 0.5$) increase in numbers when good conditions return (Caughley *et al.* 1985). One question to be considered here is whether there is a differential mortality among age classes.

Large size in mammals carries with it a greater metabolic load. Robertson (1986) found more males than females and more old males than young males in carcass surveys of red kangaroos that had died during drought, suggesting that mortality amongst old males was more likely during drought. Pople (1996) studied the age distribution of kangaroos during a drought at Currawinya NP. Data was obtained on the age distribution of the population over three years from 1991 going into a severe drought. The findings suggest that adult males are lost in higher proportions than females from the population but did not show a differential effect on larger versus younger males.

Droughts occur regularly every few years. Both local and regional droughts kill the very young or the less fit in the population. Small, younger males and females surviving to age ten will have experienced two or three droughts to test their fitness. By the time males reach an age where they are socially capable of breeding (Moss 1995, Walker 1995), drought will have helped remove the less fit individuals.

Effect of pestilence

In central-western Queensland at least, epidemics among kangaroos occur about every 2-10 years (Kirkpatrick 1985, Speare *et al.* 1989). They are associated with heavy rain or flooding, and deaths occur over a 1-2 week period. When considering the possible selective effect of disease on kangaroo populations, the studies of Clancy *et al.* (1990) and Speare *et al.* (1991) on post 1990 flood die-off in south-western Queensland are informative. A helicopter survey identified large numbers of dead kangaroos, with numbers of dead kangaroos declining with increasing distance from the Thomson-Barcoo-Cooper Creek waterway and numbers of live kangaroos increasing. The mortality coincided with a large-scale outbreak of blackfly (*Austrosimulium pestilens*), and reduced the local population by two-thirds. Speare *et al.* (1991) suggested that based on autopsy evidence an arbovirus epizootic was responsible for the majority of deaths.

The effect of pestilence will be as that for drought. By the time males reach an age where they are socially capable of breeding, pestilence will have helped remove the less fit individuals.

Main points

- The harvest is male biased and intensive harvesting changes the age structure at particular localities
- The distribution of the harvest is patchy within the range of genetic populations and within those patches the harvest is fairly uniform across adult age classes.
- The harvest over the range of genetic populations is about 10%.
- Genetic population numbers are in the millions of breeding individuals.
- Large males out compete small males for matings but the dominance may not be marked, because dominance is short-lived and small males may achieve significant matings after drought and as a result of greater mobility.
- Periodic and frequent droughts cause widespread mortality amongst kangaroos, may enact a proportionally higher toll on larger males, and provide frequent selective sweeps to purge populations of less fit individuals.
- Frequent disease outbreaks following rain provide another selective mechanism to purge populations of less fit individuals.
- Although older males are likely to achieve more matings than younger adults, the fitness benefits for the population may not be that marked because younger adults of breeding age have been selected for fitness by drought and pestilence.

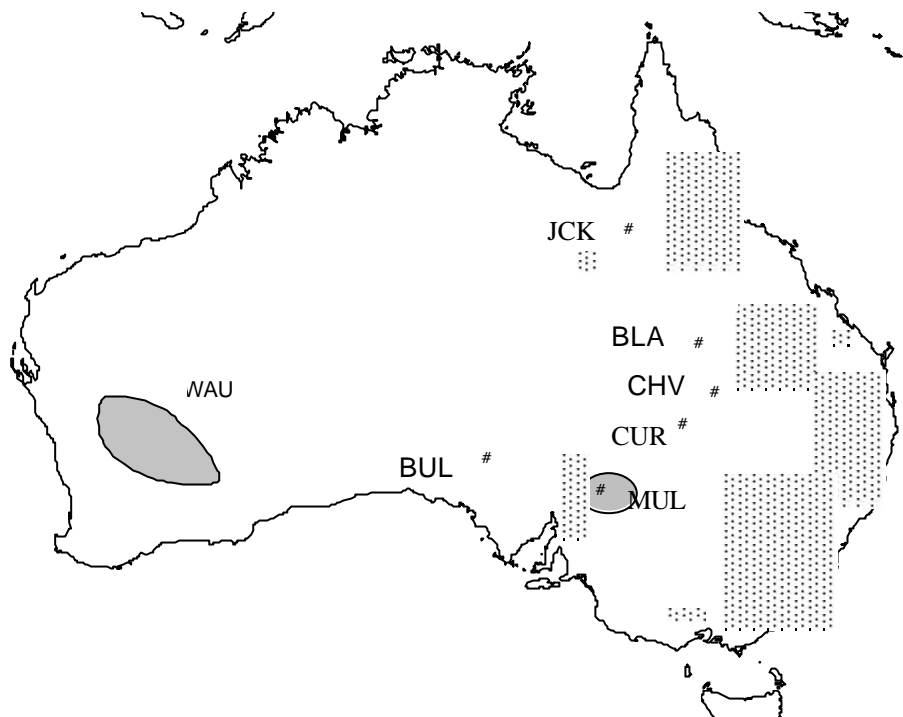


Figure 1. Map showing the location of sampling localities for the red kangaroo allozyme and microsatellite analyses. BLA, Blackall; BUL, Bulgunnia; CHV, Charleville; CUR, Currawinya; JCK, Julia Creek; MUL, Mulyungarie; WAU, Western Australia. Cross-hatching denotes sampling area in Western Australia. Light shading denotes areas of elevation greater than 300 m in eastern Australia. Dark shading denotes the distinct genetic population identified at MUL in the allozyme analysis.

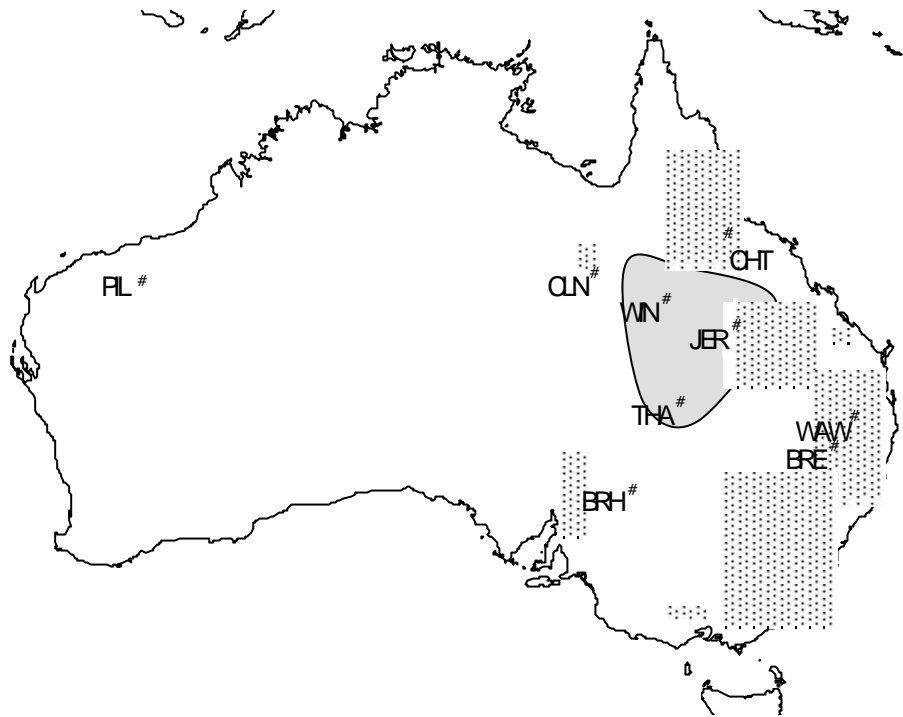


Figure 2. Map showing the location of sampling localities for the wallaroo microsatellite analysis. BRE, Brewarrina; BRH, Broken Hill; CHT, Charters Towers; CLN, Cloncurry; JER, Jericho; PIL, Pilbara; THA, Thargominda; WAW, Warwick. Light shading denotes areas of elevation greater than 300 m in eastern Australia. Heavy shading denotes area including the three localities that showed no differentiation in genetic population structure.

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