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Rock-Wallaby Population Genetics and the Caughley Paradigms

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The Scene

In 1978 when Michael Onus and I carried out a survey of the wheatbelt rock-wallaby (RW) populations, it soon became apparent that there was cause for concern. One population had recently become extinct and the remaining populations had declined. Three populations consisted of fewer than 10 animals.

My initial gut feelings focused on a nutritional hypothesis as the probable cause of the decline, but this soon became untenable. By then, the predation factor had become paramount and research on fox control dominated our activities. The outcome is well known and has endured over the years.

But despite this outcome, a worrying factor has kept surfacing over the years namely, the prevailing population genetics of these five RW population-isolates.

It all started with the book *Conservation Biology: An Evolutionary-Ecological Perspective*. (Ed. by Soulé and Wilcox, 1980) and the literature on this subject has continued unabated. Soulé and his bandwagon of apostles seem to have set themselves the task of alerting the world about the plight and dire consequences of small populations. A new and ominous acronym was coined — MVP i.e., minimum viable population. Initially, we were solemnly informed that at least 50 randomly breeding animals were needed to qualify as a MVP in the short term, and that, at least 500 individuals were necessary to prevent genetic deterioration in the long term.

Apparently, when these pronouncements reached down under, Soulé was conferred the status of an oracle by some unnamed Australian wildlife biologists (no doubt from the E. States). By phone they sought his opinion on a parrot sp. whose numbers had dwindled to 48. Could the sp be saved or should they forget about it? After all it was two short of the magic number. Really, sometimes I wonder...

According to the Soulé camp (*Viable populations for Conservation*. Ed. by Soulé, Cambridge Uni Press 1987) genetic damage occurs when populations collapse into a small heap and the longer they remain so, the greater the damage. The initial guess about a MVP necessary to maintain genetic integrity has now escalated and a new threat — “mutational meltdown” — has been uncovered (presumably on a blackboard; see *Science* Vol. 270; Oct. 1995, p. 31-2; and Lynch (1996) in: *Conservation Genetics*. Ed. Avise, J.C. & Hamrick, J.L.; Chapman & Hall).

Meltdown results from the accumulation of unpurged mildly deleterious mutations that become fixed leading eventually to extinction. To counter meltdown one needs an effective population size (N_e) of »1000 (which may mean that N should be 5000-10000). Really, someone should tell those 200-odd Barrow Island rock wallabies to shape up — they should have melted away by now, and likewise, for

the Salisbury Island population, and tammars on the Abrolhos.

Given this doomsday scenario, conserving RW (and other spp in our fragmented landscape) would seem to be a futile exercise according to the Soulé School and others. Presumably, bottlenecks would have occurred by now due to the low numbers caused by predation. Moreover, predation and habitat disturbance (agricultural) would have effectively ended gene flow between populations. Such a scenario raises these questions: Is there any variation left? And if so, are the populations different?

Early on, we tried to address these questions using allozymes (blood proteins) as markers, but no variability within and between populations was found. These results were hardly encouraging, but then the sensitivity of this technique was not great. This problem was resolved years later when we were able to attack the problem again using DNA based methods. And so as a result, we now know a great deal more about the genetic diversity of rock-wallabies, not only from the wheatbelt populations, but elsewhere as well — Barrow Island and Cape Range. These studies have been made possible through a collaborative effort on the part of: Graham Hall @"CALM equivalent" Tasmania; Mark Eldridge @MacQuarie; Peter Spencer (formerly @James Cook, now @Murdoch) and Julie King (@UWA Zool.).

The Big Picture

Looking firstly at the differences between the geographically isolated populations (i.e., Barrow I., Cape Range (Ningaloo) and the wheatbelt), all were found to be genetically distinct to varying degrees. This was not unexpected and Eldridge has estimated that these populations have been isolated for a period of ranging between 6-10k years — not a bad estimate at all, in view of the fact that Barrow was isolated about 8,000 years ago.

Cape Range exhibited the greatest variability followed by the wheatbelt populations with Barrow RW coming a very distance last for a very good reason — no differences were detected! Barrow Island rock wallabies appear to be carbon copies of each other.

What does this imply? It suggests that Barrow I individuals are so similar genetically, that they may well indeed accept skin grafts from other individuals (allografts) — not that this will be ever done. Africa has its famous bottlenecked-allograft-accepting Cheetahs [but see Caughley & Gunn (1996) in *Conser Biol in Theory & Practice*. Blackwell Sci. Inc.], and it might well be that WA has its equivalent in the form of Barrow rock-wallabies.

From a management viewpoint there is a message here. Barrow RW have presumably (but, see below about methodological limitations) lost their capacity to evolve and to adapt except by an improbable fortuitous mutation. Mark Eldridge sums up the situation by stating that, the population, in evolutionary terms, is "stuffed".

This presumed lack of genetic variation does not mean that the Barrow population is under threat. After all, they have persisted on Barrow for about 8,000 years, and presumably natural selection would have fine-tuned their adaptations to this island's environment. But because they now appear to lack the capacity to adapt,

Barrow Island rock-wallabies would be an illogical choice as a source population for translocation, or for outbreeding purposes.

The Wheatbelt Situation

The four wheatbelt populations have retained a surprising amount of variation and there are some intriguing inter-population differences. At this stage our samples still too small for definitive conclusions, but Mark believes the following interpretation will hold. He calculates that there has been no gene flow during the last 100 years or so. This estimate coincides with the arrival of the fox about 80 years ago and it is hard to imagine a migrating rock-wallaby surviving a journey between sites with so many foxes about. Moreover, because depredated populations typically exist at levels well below habitat carrying capacity, conditions that trigger emigration (presumably density dependent) would no longer occur.

One final comment about the wheatbelt situation: I was surprised to learn that the variability found for both Nangeen Hill and Sales' Rock was lower than Mt. Caroline or Tutakin. The latter two sites were carrying smaller populations (» 7-10 RW) when we arrived on the scene. This suggests that, in the past, both Nangeen and Sales may have experienced a more severe bottleneck, but a larger sample size needs to be analysed to confirm this.

Conservation and Population Genetics: The Caughley Paradigms

Caughley & Gunn (Ibid) challenged the Soulé establishment by asserting that "no instances of extinction by genetic malfunction has been reported". They went on to propose that we should recognise two distinct paradigms in conservation biology. The first is "the small population paradigm" where one should focus on the negative consequences inherent in being a small population. Here one needs to be concerned with environmental stochasticity and catastrophes, demographic stochasticity and genetic deterioration.

Caughley labeled his second approach "the declining population paradigm". This paradigm requires one to establish the cause of smallness and to find a cure. Smallness in this case is due to deterministic factors such as overkill, habitat destruction and fragmentation, impact of introduced spp and chains of extinction.

The Caughley view provoked a quick response from the Soulé camp (Hedrick et al. 1996; *Conser. Biol.* 10(5), 1312) who accused him of stirring i.e., of being divisive; of polarising the debate; of constructing a false dichotomy, and of simply being, too simplistic. Additional supporting papers (including the 48 parrot story) from the Soulé camp can be found in the same issue.

Who should we believe? My own view favours Caughley's pragmatic approach. His 'declining' paradigm seems to me to be just plain common sense. Its not an original idea as any student of Prof. Bert Main would acknowledge. Bert's message was this: Species become conservation problems when there is a change in the their distribution and abundance. These changes, which can be an increase, but more commonly a decline, are the key indicators and are causes for concern. The problem then becomes as Caughley aptly expresses it: "determine the cause(s) and find a cure" — if a cure is feasible of course.

Clearly, the message coming from conservation genetics is not to be ignored, but I believe the Soulé School in particular have overstated their case. In defending their case, they accuse Caughley of being divisive, and of fueling controversy when a united front is needed to promote conservation. There is irony here for their original blackboard message, which they trumpeted far and wide, was this: small populations are doomed to suffer genetic deterioration with irreversible and fatal consequences. If one accepts this view, then species conservation for many vertebrates in a fragmented landscape would seem to be a lost cause. But if this threat is so inevitable, and cause for so much immediate concern, then why do we still find small flourishing populations of macropods living on islands having done so for thousands of years? We can take some comfort from this.

It seems to me that we should continue to apply the Caughley paradigms by identifying causes and seeking cures where possible for this will arrest and hopefully reverse the decline. Then we should spread the risk by creating and fostering as many populations as possible.

But this strategy raises difficult questions about what do we do about genetic variation? Theory tells us that genetic impoverishment is inevitable and indeed, our DNA based markers may well signify the same. However this information may well be misleading because we do not at this stage understand what the molecular markers are really telling us. If for example, our molecular markers uncover a low level of heterozygosity, then this suggests that there has been a parallel loss of heritable variation. This would seem to be a reasonable inference, but there are exceptions as is the case of the endangered cotton-top tamarin. Genetically, it is another cheetah with little detectable variation, but it still exhibits a high level of heritability for body weight (Lynch 1996).

Nevertheless, despite this correlative lapse between molecular markers and a quantitative trait, one cannot help but feel more comfortable when our measuring techniques uncover variation in a population. But, it is still a matter of faith to use such information as a course of action; conservation genetics will become a predictive science, and a vital tool, when the marking system can truly measure the amount of adaptive-genetic variation for relevant traits of interest. In the final analysis, a species ability to respond to novel challenges is proportional to the existing additive genetic variance (VG) for any selected trait (Lynch 1996). We need to be able to measure VG .

Wheatbelt rock-wallaby Genetics: What to do?

My views and reasons are as follows:

Caughley says we first should identify the proximate cause of the decline and implement a cure. He argues that, its pointless to address the genetics, if you do not know the cause of the decline.

We claim we have i.e., predation — though he strongly disputed this.

We have partial cure at least — control predators.

Having done this, should we mix them up? Should we start tinkering with their genetics?

No, not yet.

Indeed, why not? Simply because all populations have increased in response to predator control. This signifies that all have retained an appreciable level of fitness.

Would fitness increase, or would long term survival be enhanced by mixing? Theory urges us to so, but experimentally, this would very difficult to test especially the latter benefit; we don't have a reliable crystal ball.

Moreover, mixing could well be counter-productive. If mixing is proposed, then it should be done using translocated individuals at new site. This approach would avoid any possibility of a genetic disaster resulting from genomic divergence. Lynch (1996) describes some of the potential pitfalls awaiting the intrepid advocate of gene flow.

To conclude, my understanding of the genetic scene leads me to recommend a cautious, conservative approach. Such an approach does not mean that we should ignore or dismiss this aspect of wildlife management. We should, however, disregard the small-numbers-doomsday-scenario and one hopes that in Australian management circles, that the gene responsible for the 48 parrot story has not become fixed in too many conservation organisations, or in the minds of scientific advisors.

Being cautious does not mean that we should not continue to determine and monitor the genetic constitution of our populations. From our first look at RW populations, we have acquired useful information. During our next census, we will gain a great deal more for a small investment on our part. In the field, thanks to PCR, its simply a matter of using an ear punch to collect a tiny disc of tissue for analysis.

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