Large Estimates of Minimum Viable Population Sizes

In a recent paper, Reed et al. (2003) define a minimum viable population (MVP) as one large enough to ensure a 99% probability of persistence for 40 generations and conclude that "... in order to ensure long-term persistence [viability] of vertebrate populations, sufficient habitat must be conserved to allow for approximately 7000 breeding age adults." The authors assume that the population is not affected by habitat loss and that the population is discrete and isolated. Their MVP model, however, is inconsistent with an empirical, historical example of one large carnivore species that was able to persist for much longer than 40 generations with a population much smaller than 7000 reproductive individuals. The Bali tiger (*Panthera tigris balica*), which has only recently gone extinct (probably shortly after World War II), thrived on that island for at least several centuries before habitat loss and human-caused mortality drove it to extinction.

Even assuming that the whole area of Bali was suitable habitat for tigers for some time before the arrival of humans, the tiger population had an area of 5561 km^2 of available habitat. The maximum density of tigers reported in the literature for other sites is 12 individuals/100 km^2 (Karanth & Nichols 1998 and cited in Karanth et al. 2003), which means that the total population of tigers in Bali probably did not exceed a maximum of 667 reproductive individuals, far lower than the MVP estimate of 7000 produced by the model of Reed et al. (2003). Based on the maximum tiger density reported in the review by Nowell and Jackson (1996), 3.7 reproductive adults/100 km^2 leads to a considerably lower estimate of the maximum size of the tiger population on Bali.

Reed et al. (2003) also provide estimates of MVP for several individual species, including tigers. Their lower estimate for tigers is 2377 reproductive adults. For Bali this would mean a density of almost 43 tigers/100 km^2, and the overall estimate of 7000 would necessitate a density of 125 reproductive tigers/100 km^2. The authors do provide estimates of MVP sizes uncorrected for the effect of the length of the study that resulted in those estimates. For tigers these estimates of MVP size range between 329 (*P. t. tigris*) and 876 (*P. t. altaica*), which are much closer to the estimates presented above.

It could be argued that a very small tiger population on Bali persisted as a result of a rescue effect from other populations. Tigers have been reported to swim as far as 56 km across rivers and 8 km in the ocean (Nowell & Jackson 1996). These observations suggest that crossing the approximately 3 km of sea that separates Bali from Java would be an easy feat for tigers. The fact that the Bali tigers were a separate subspecies (Nowell & Jackson 1996), however, implies that immigration to the island was insufficient to prevent genetic separation. Therefore, inmigration was most likely a rare event.

Finally, the estimate of a maximum of 667 reproductive tigers in Bali assumes that all the island's area was suitable for tiger occupation. In fact, Bali has been populated for at least 1000 years. By the 1930s the human population had reached over 1 million, resulting in a human density of >180 people/km^2. Clearly, for a long period of time a great part of the island's area has not been suitable for tiger occupation. In short, the total population of tigers must have been substantially lower than 667 reproductive individuals for much longer than 40 tiger generations. Lessons from the historical record, like the one discussed here, can provide "reality checks" on models of minimum viable populations and can contribute to developing more realistic models.

So why is a single case of tigers in Bali an example worth bringing to the attention of conservation biologists? Because managers often elect tigers and other large carnivores as umbrella species. How could we justify to managers and rural people the protection of a piece of land large enough to harbor a population of 7000 large carnivores? For tigers this might mean a tract of land of 58,333 km^2. For pumas (*Puma concolor*) it would be 233,333 km^2, assuming a fairly dense population of three reproductive pumas/100 km^2 (Logan & Sweanor 2001). Perhaps the Bali population of tigers does not exemplify all large mammals, but at least it is clear that a small population of carnivores survived for much longer than 40 generations. I would rather cite empirical examples for small but viable populations than, for example, try to explain to rural people that we need to protect more than 21% of Bolivia to ensure the viability of a single population of pumas.

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Pacheco (2004, this issue) suggests that a population of the Bali tiger (*Panthera tigris balica*) may have persisted for several hundred generations at a population size of around 500 individuals. We consider this example in the larger contexts of (1) the value of single examples and (2) historical data concerning minimum viable population sizes (MVPs).

Pacheco's statement that our "... MVP model ... is inconsistent with an empirical, historical example of one large carnivore species that was able to persist for much longer than 40 generations with a population much smaller than 7000 reproductive individuals" is not accurate. Our models are not inconsistent with this example because we made no claim concerning how small a population can be and still persist for hundreds of generations. We used our models to make *probabilistic statements* about how population size affects persistence over time. Pacheco places emphasis on our MVP estimate of 7000 indivduals but ignores our claim that a 50% probability of persistence is obtained with only 550 individuals.

The concluding sentence of the 2003 paper by Reed et al. reads as follows: "Our goal in writing this paper is to stimulate a quantiative assessment of MVP approaches to conservation planning and add to the body of literature that suggests that we should be thinking in terms of several thousands—not hundreds—of individuals in our goal to maintain viable populations of vertebrates." We do not doubt that examples like the Bali tiger exist, and we find great inspiration from them. It would be rash, however, to ignore the preponderance of evidence presented in our paper on the basis of one, or a few, anomalous observations.

We concur with Pacheco that historical data on extinctions can provide "reality checks" for more theoretical treatments of MVPs. However, historical data carry their own burden of assumptions. For example, Pacheco assumes that the dispersal of tigers from Java to nearby Bali has had a negligible impact on the persistence of the Bali population. Yet subspecies status could be awarded despite considerable gene flow, and such gene flow would render the entire example moot.

Historical reality checks have been performed, as suggested by Pacheco, and in our paper we cite examples of MVPs estimated for multiple species. An example, published after our paper was submitted, is Harcourt's (2002) data for 12 species of primates on the islands of the Sunda Shelf. The median MVP for these populations was 15,750. Some populations persisted with much smaller sizes, however, and some went extinct despite being an order of magnitude larger. Simarly, there are many once-connected Indonesian islands of similar or larger size than Bali that do not have tigers on them and that presumably lost their tigers as a result of local extinction. In the models of Reed et al. (2003), median time to extinction increased with increasing carrying capacity (K) at approximately $0.474K^{0.71}$. Persistence for 500 generations, which would be "typical" for the primates examined by Harcourt (2002), yields an MVP of 18,115 individuals. When all the published data are considered, our conclusions do not seem overly pessimistic.

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