



Disambiguating the Minimum Viable Population Concept: Response to Reed and McCoy

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The minimum viable population (MVP) concept was originally conceived as a species-specific abundance threshold below which stochastic threats pose an unacceptable risk to an isolated population (Shaffer 1981) (i.e., the population-level definition of MVP). The concept is, however, frequently used in a much broader sense to refer to the minimum number of individuals necessary to ensure long-term persistence of an entire species (e.g., Reed et al. 2003; Clements et al. 2011) (i.e., the species-level definition of MVP). We contend that this ambiguity about the MVP concept, along with a difference in perspective on how minimum-abundance thresholds may be manipulated by adversaries of biodiversity conservation, underpins much of the apparent disconnect between Shoemaker et al. (2013) ("Reexamining the Minimum Viable Population Concept for Long-Lived Species") and Reed and McCoy (2014).

Management and recovery plans frequently specify minimum-abundance thresholds (or similarly, minimum patch area thresholds) below which discrete populations are deemed nonviable or otherwise inconsequential for meeting regional conservation goals (e.g., McCoy & Mushinsky 2007). For example, a primary objective of the recently published Range-wide Conservation Strategy for the Gopher Tortoise (USFWS 2013) was to "establish consensus . . . on what defines a viable gopher tortoise [*Gopherus polyphemus*] population across various states and habitats, for example . . . number of individuals [and] acreage." In Shoemaker et al. (2013), we presented evidence that populations of bog turtles (*Glyptemys mublenbergii*) of 15 or more adult females (30 reproductive

adults, assuming 1:1 sex ratio) may be highly resilient to stochastic threats (approximately 1% risk of extirpation) over 100 years. Our primary conclusion was that small populations deemed nonviable on the basis of widely publicized MVP rules of thumb should not be dismissed in the conservation planning process. This is more than an academic concern: population triage is a hard reality for conservation agencies faced with limited land acquisition budgets, shrinking habitats, and rising real estate prices.

The bog turtle presents a striking case in point because most extant populations are estimated to comprise fewer than 50 individuals (Rosenbaum et al. 2007). If wildlife conservation agencies adopted Reed and McCoy's recommendations (e.g., "long-term persistent populations will require thousands of individuals") or adopted similar MVP thresholds advocated in recent publications (Brook et al. 2006; Traill et al. 2007, 2010), bog turtle recovery would appear futile. Questioning MVP rules of thumb for species like the bog turtle, and thereby acknowledging that small populations can contribute substantially to regional or species-level persistence, can broaden the spectrum of options available to conservation planners. For example, protection or repatriation of small populations can promote demographic and genetic exchange among populations, thereby enhancing regional metapopulation stability and facilitating climate-driven range shifts (Mawdsley et al. 2009). Small populations located at range margins or that otherwise contribute to species-level geographic extent can play a strategic role in bet hedging under uncertainty because species that

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occur over large and diverse geographic ranges tend to be more resilient to spatially correlated threats (Boyce et al. 2002), an increasingly germane issue to conservation planners attempting to address the highly uncertain local effects of climate change (Millar et al. 2007). Finally, a reduced focus on abundance thresholds per se may permit conservation planners to redirect resources toward mitigating or offsetting pervasive deterministic threats (e.g., habitat degradation). Nonetheless, opportunities afforded by lowering minimum-abundance thresholds are accompanied by formidable liabilities; for instance, dispersal-related threats (e.g., road mortality; Roe et al. 2006) are likely intensified in small remnant populations (Andreassen & Ims 2001).

In their critique of our article, Reed and McCoy raised four primary concerns: (1) our too narrow definition of *viability*, especially with regard to the time frame of our projection models, (2) that we ignored environmental extremes and systematic environmental change in estimating MVP, (3) that we did not consider retention of genetic diversity in our MVP estimate, and (4) that low abundance thresholds might be politically dangerous and open to misuse. Regarding the first criticism, we used 100 years to represent a typical management-relevant time frame (e.g., Brook et al. 2006). Biologists tend to be wary of setting overly stringent viability targets (e.g., high probability of persistence for 1000 years or approximately 40 bog turtle generations) (Sanderson 2006). To put it another way, the changes that have occurred in the last century could not have been imagined, and environmental change in the next century will likely accelerate relative to that of the last century (Lawler et al. 2008). How does one strike a balance between pragmatism and the ease of modeling over extended time frames?

Regarding the second criticism, the MVP concept was originally intended to reflect stochastic threats in isolation, with deterministic threats assumed to be absent or otherwise held in check (Shaffer 1981). Accordingly, vital rates estimated for bog turtles in our study were characteristic of a stable population, and extirpation risk in our study reflected stochastic threats rather than the risk of a declining population vanishing within the next century. Furthermore, we clearly stated that validity of our projections hinged on environmental conditions observed during our 10-year study remaining representative of the range of conditions experienced by bog turtle populations over the simulation period. That is, by not measuring vital rates during rare environmental extremes or catastrophes, we may have underestimated long-term risk (Reed et al. 2003).

Reed and McCoy are correct in their third criticism that we did not account for genetic erosion, an omission we highlighted in Shoemaker et al. (2013). However, recent evidence suggests that fragmented turtle populations can

retain high allelic richness and genetic diversity (e.g., Rubin et al. 2001; Bennett et al. 2010; Pittman et al. 2011); slow genetic drift is likely facilitated by iteroparity and overlapping generations, multiple paternity, and long-term sperm storage (Pearse & Avise 2001). Furthermore, nearly imperceptible rates of interpopulation movement (e.g., one effective migrant every 5 years) can maintain large genetic effective population sizes for long-lived species such as turtles despite the apparent isolation of discrete populations (Shoemaker & Gibbs 2013). This evidence and our population viability results for bog turtles (Shoemaker et al. 2013) suggest that populations of turtles and other similar iteroparous, long-lived species may be highly resilient to stochastic threats, including genetic erosion, and further illustrate the perils of adhering to a generic perspective on population viability across taxa (Flather et al. 2011).

Much of the remainder of the critique by Reed and McCoy is relevant primarily in the context of species-level conservation, where our suggested minimum-abundance threshold for bog turtles would indeed be absurd for any species. To claim that a species could persist with so few living representatives would be to ignore critical (and often difficult-to-assess) risk factors such as insufficient evolutionary potential, range-wide catastrophes, systematic environmental change, and deterministic threats. In the context of species-level conservation, we suspect that minimum-abundance targets in the thousands will be required to forestall or prevent widespread loss of biodiversity in most cases. For this reason, we agree with Flather et al. (2011), who suggested a strategic objective for species-level conservation that bridges the two MVP definitions: "multiple populations totaling thousands (not hundreds) of individuals will be needed to ensure long-term persistence." In this sense, the concept that small and discrete biological populations can persist for long periods and thereby serve critically important conservation functions is consistent with the notion that species-level abundance should number in the thousands. Indeed this would appear to be the blueprint for the organization of most species in nature (Hughes et al. 1997).

We acknowledge, along with Reed and McCoy, that low MVP thresholds can be misapplied and used as a perverse justification for habitat destruction. Yet high MVP thresholds can also be misapplied and used as justification for failing to protect valuable populations and habitats (also acknowledged by Reed and McCoy, and the primary motivation behind Shoemaker et al. 2013). We contend that disambiguating the two definitions for MVP would effectively address both concerns. Population-level MVP targets would (where appropriate) provide scientific justification for conservation of small, fragmented populations that need not occur in complete genetic isolation, while species-level abundance targets would continue to buttress widespread habitat protection efforts.

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