Conservation Matters: Contributions from the Conservation Committee

Speciation, hybridization, and conservation quanderies: *what are we protecting anyway?*

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There are few scientific disciplines more prone to social quandaries than conservation biology. Its multidisciplinary and synthetic nature lends itself to conflicts among science, money, laws, and social values, which are encapsulated in questions like *what should you do with limited funding but seemingly endless needs?* In insect conservation, these quandaries often have an added layer of taxonomic uncertainty. When a unique population is discovered in some remnant patch of wildland, the first question is usually *is this a different species/subspecies*? A 'yes' can open the floodgates to discussions of endemism, legal protection, and conservation prioritization. What may have started as a weekend collecting trip, and the excitement of a new discovery, now involves conservation authorities, politicians, expert opinions, and land owners leery about new restrictions on their land.

In recent decades, questions about species identification and ranking have increasingly been answered with DNA-based approaches, which can provide a wealth of information and carry a lot of weight in conservation biology. Yet these genetic tools often raise as many questions as they answer - a frustrating outcome when money is on the line or timelines are urgent. For instance, what should a conservation biologist do when new genetic data fail to support the evolutionary distinctness of an endangered species that has already had millions of dollars spent toward its protection? Here, we consider two butterflies, Lange's metalmark and the Ozark swallowtail, to explore some of these questions.

Lange's metalmark

Lange's metalmark, *Apodemia mormo langei* (Figure 1), was one of the first insects to be considered *federally endangered* under the US Endangered Species Act (ESA) in 1976. It is found only in the Antioch Dunes National Wildlife Refuge (NWR) on the banks of the San Joaquin River downstream of Sacramento, California. Ecologically, Lange's metalmark is restricted to sand dunes, as its larval host plant *Eriogonum nudum psychicola* depends on this dynamic and shifting habitat. However, sand mining beginning in the early-mid 20th century destroyed the once extensive dunes of the area and reduced suitable habitat for this species to ~1.3 hectares in 1979 (Powell and Parker 1993). The Antioch Dunes NWR was established in 1980 to protect Lange's metalmark, as well as two rare plant species, and was the first NWR established with the explicit purpose of protecting rare animals or plants. Since then, extensive conservation efforts have taken place to stabilize populations of Lange's metalmark, including the establishment of a captive breeding program, planting of *E. n. psychicola*, hand-clearing/herbiciding invasive plants, and experimental grazing. Despite these efforts, population numbers are still precariously low, with competition from invasive weeds and wildfires proving to be formidable opponents.

While Lange's metalmark has a wing pattern that is distinct from most of the *A. mormo* species complex, it has little to distinguish it genetically. Using mitochondrial DNA and nuclear microsatellite markers, we found that Lange's metalmark was no more genetically distinct than any other population of the Mormon metalmark (*A. mormo*) complex in California (Proshek *et al.* 2015, *open-access article*). We observed localized patterns of genetic differentiation, as expected given the low vagility and colonial nature of this butterfly, and some populations with relatively higher genetic diversity than the population at Antioch Dunes. We also found some of the morphological characteristics that distinguish Lange's metalmark in individuals from other populations. We are following up with genome-wide single nucleotide polymorphism surveys. These methods still only sample a small fraction of the genome, but preliminary analyses of these data support and expand on the pattern

Figure 1. Adult Lange's metalmark, *Apodemia mormo langei*. Public domain, USFWS, from **https://commons.wikimedia.org/wiki/File:Dorsal_view_of_an_endangered_lange_metalmark_butterfly.jpg**

of local genetic differentiation found in our previous study (Oliver, Dupuis, and Sperling *et al. in preparation*).

Ozark swallowtail

The Ozark swallowtail, *Papilio joanae*, is a relatively unknown creature with a distribution that is localized, as its name suggests, to the Ozark Plateau of Missouri (Figure 2). Its describer, J. Richard Heitzman, spent years amassing rearing records, generating crossing lines, and observing habitat associations to form the basis of our biological knowledge of this species. In appearance, it is almost indistinguishable from *P. polyxenes*, the black swallowtail, and ecologically it uses some of the same hosts, at much the same time of year. However, it flies and selects oviposition sites almost entirely under the forest cover, a unique behavioural trait among its relatives in the Old World swallowtail (*Papilio machaon*) species group.

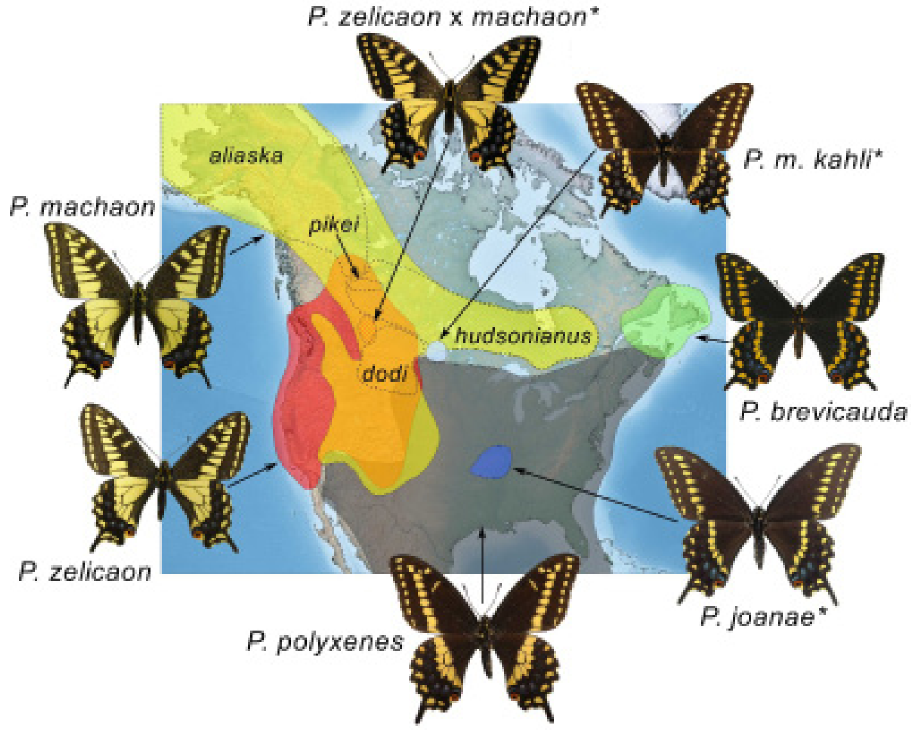

Figure 2. Generalized range map of current distributions of the *Papilio machaon* species complex in North America, from Dupuis and Sperling (2015). Putative hybrid taxa are indicated with an asterisk. Dashed lines indicate approximate ranges of *P. machaon* subspecies pertinent to Dupuis and Sperling (2015). Map image: public domain from www.simplemappr.net, *Papilio joanae* holotype (photograph by John Tewell).

Although the morphology of the Ozark swallowtail is almost identical to that of the black swallowtail, it shares several small characteristics with the Old World swallowtail, most notably a pupil connected to the margin of its hindwing eyespot. This morphological enigma served as the original impetus for investigating the genetic relationships of the group. Sperling and Harrison (1994) discovered that the Ozark swallowtail shared mitochondrial DNA signatures with the Old World swallowtail, suggesting a hybrid origin between the black and the Old World swallowtail. We recently corroborated the initial mitochondrial results, but found that nuclear microsatellite markers showed closer relatedness between the Ozark and the black swallowtail (Dupuis and Sperling 2015, *open-access article*). The mitochondrial DNA lineage of the Ozark swallowtail is shared with only a single subspecies of the Old World swallowtail, *P. m. hudsonianus*, which has a north-eastern distribution in North America (Figure 2). This makes a compelling phylogeographic story of a hybrid origin for the Ozark swallowtail during Pleistocene glaciations (Dupuis and Sperling 2015). Preliminary results using genome-wide markers for the whole species group indicate that, although most similar to the black swallowtail, at fine-scale levels the Ozark swallowtail is genomically distinct from both of its original parental species (Dupuis and Sperling *in preparation*).

Given its localized distribution, the Ozark swallowtail has been listed as "vulnerable" by some conservation organizations (Schweitzer *et al.* 2011), but as "unrankable" in other conservation prioritizations due to lack of information. There are few verified records of the species from recent years. The most recent one that we are aware of is a single individual from 2006, and before that only four individuals were recorded between 1995 and 2006. Many of the regularly-visited collection localities discovered by Heitzman have reportedly been overgrown or replaced with houses.

What to do?

The fact that Lange's metalmark is not more genetically distinctive than many other of the local Mormon metalmark colonies in California raises a fundamental question - *what are we protecting anyway*? If Lange's metalmark passes the bar as a genetically distinct population entity, then perhaps we should also be protecting many other local colonies of Mormon metalmarks and other species that might be just as vulnerable to extinction (some of which are more genetically distinct than Lange's metalmark). Conservation biologists use the term "evolutionarily significant unit" to identify and delimit populations of organisms with particular evolutionary potential (see summary in Proshek *et al.* 2015), even when some of these units are not formally recognized as species or subspecies. However, invertebrates are at a disadvantage when it comes to federal protection of such unique populations, as the ESA only recognizes conservation units below the subspecies level in vertebrates. Lange's metalmark's only saving grace, as far as federal legislation goes, is its formal subspecific status, although the taxonomy of the entire Mormon metalmark complex is tenuous at best (Proshek *et al.* 2015). Because it happened to have a recognizable wing pattern, Lange's metalmark was viewed as distinct, while other populations that have no obvious identifiable traits, but are genetically distinctive, remain invisible to legal protection. In an interesting contrast, the species status of the Ozark swallowtail has done little to help gain its protection.

On the other hand, if it is a particular habitat or location that we are intending to protect with a legislated endangered species as the flagship or umbrella species (see Caro and O'Doherty 1999), then the Antioch Dunes NWR would seem to fit the bill. Lange's Metalmark serves as a culturally recognized flagship of this remnant dune habitat, along with the two endangered plants and a number of other rare species found at the Antioch Dunes (Powell 1978). But it may be instructive to critically evaluate how far conservationists are willing to go to protect such a flagship endangered species. Is the captive breeding program for Lange's metalmark an optimal use of such conservation funds if protecting the NWR habitat is really the main goal? Would conservation funding be better spent in rearing one, or several, of the other rare and unique species found in the Antioch Dunes NWR? If ecosystem preservation or ecological services are the main goals for conservation, perhaps other less "species-centric" conservation approaches would be more appropriate, cost-effective, or ecologically sound.

That leads us to ask whether we are really protecting only those biological phenomena that derive their value from the way they are perceived, rather than having intrinsic objective characteristics like genetic or evolutionary distinctiveness. Perhaps we should be more honest about the cases where we are primarily protecting cultural symbols rather than imperiled habitats. If we take this last line of thought seriously, then we would put greater emphasis on understanding, delimiting, and explaining what kinds of "endangered species" phenomena we are societally prepared to put resources into protecting. This would be a very different process, compared to the work we do to determine evolutionary significance based on, say, genetic data or habitat-based considerations. Being more open about cultural subjectivity in conservation prioritization may provide the flexibility to see conservation quandaries in a new light. There may be cases where genetic data and habitat/ecosystem considerations would only act as supporting factors in a conservation decision, rather than the primary criteria for designating endangered species.

Lange's metalmark is certainly a relic of the days before sprawling development of California's coastline. Should its flagship nature and history of conservation efforts trump the fact that it is no more genetically distinct than other nearby Mormon metalmark colonies? Does a hybrid species like the Ozark swallowtail hold the same conservation value as species that we think originated via phylogenetic divergence? Does the fact that it arose in a seemingly unusual manner (through homoploid hybrid speciation) elevate its status as an interesting biological phenomenon? How should the fact that the Ozark plateau is home to many other endemic species affect the conservation prioritization of those species? Does perceiving the Ozark swallowtail as a beautiful, mysterious entity flitting through the trees count just as much? These questions are obviously subjective ones, and we advocate no hard-and-fast answers here.

But perhaps it is time to more critically re-evaluate the motivations for our conservation efforts. These two butterflies differ considerably in their evolutionary histories, but even more so in their histories of conservation. While one is being brought back from the brink through enormous efforts and costs, we are not certain if the other has been seen in the past ten years. Conservation biology is arguably as much in our heads as it is in nature: humans have significantly altered the planet, and now want to stem losses and make amends with a small number of species. Recognizing the primarily cultural underpinnings of many of our prioritizations could lead us in some interesting directions, such as refreshing public trust and understanding of conservation biology's scientific and societal goals.

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