



Review

Shedding subspecies: The influence of genetics on reptile subspecies taxonomy

Shannon M. Torstrom^{a,b,*}, Kevin L. Pangle^a, Bradley J. Swanson^{a,b}^a Department of Biology, Central Michigan University, Mount Pleasant, MI 48859, United States^b Applied Technologies in Conservation Genetics Laboratory, Central Michigan University, Mount Pleasant, MI 48859, United States

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ABSTRACT

The subspecies concept influences multiple aspects of biology and management. The 'molecular revolution' altered traditional methods (morphological traits) of subspecies classification by applying genetic analyses resulting in alternative or contradictory classifications. We evaluated recent reptile literature for bias in the recommendations regarding subspecies status when genetic data were included. Reviewing characteristics of the study, genetic variables, genetic distance values and noting the species concepts, we found that subspecies were more likely elevated to species when using genetic analysis. However, there was no predictive relationship between variables used and taxonomic recommendation. There was a significant difference between the median genetic distance values when researchers elevated or collapsed a subspecies. Our review found nine different concepts of species used when recommending taxonomic change, and studies incorporating multiple species concepts were more likely to recommend a taxonomic change. Since using genetic techniques significantly alter reptile taxonomy there is a need to establish a standard method to determine the species–subspecies boundary in order to effectively use the subspecies classification for research and conservation purposes.

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1. Introduction

The subspecies classification may reflect evolutionary relationships or only the human need to categorize, but the influence of

subspecies on other facets of biology and management demands that the factors affecting their designation be clearly understood (Starrett, 1958; Groves, 2012). The subspecies category was developed to enhance understanding of geographic variation, speciation, and to refine taxonomic distinction. However, since the establishment of subspecies there has been controversy regarding its necessity (Mayr, 1982; Patten and Unitt, 2002; Hawlitschek et al., 2012) showcased by Mayr (1970) reclassifying 315 species to subspecies,

* Corresponding author at: Central Michigan University, Brooks Hall Rm 217, Mount Pleasant, MI 48859, United States.

E-mail addresses: shtorstrom@gmail.com (S.M. Torstrom), pangl1k@cmich.edu (K.L. Pangle), swans1bj@cmich.edu (B.J. Swanson).

Table 1

List of the species concepts/criteria used in the studies evaluated in this paper.

Species concept/criteria	Concept	Reference
Biological species concept ¹	'Groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups'	Mayr (1942)
Bayesian phylogenetic and phylogeographic method ²	'This method assesses species-tree uncertainty due to the coalescent using multiple gene trees to identify independently evolving lineages'	Yang and Rannala (2010)
Cohesion species concept	'A species is an evolutionary lineage through the mechanisms that limit the populational boundaries for the action of such basic microevolutionary forces as gene flow, natural selection, and genetic drift'	Templeton (1989)
Evolutionary species concept ¹	'A species is a lineage of ancestral descent which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate'	Wiley (1978)
General lineage species concept ³	'Species are separately evolving metapopulation lineages, or more specifically, with segments of such lineages'	de Queiroz (1998)
Integrative Taxonomic Species Concept	'This concept rejects the superiority of any particular set of characters (morphological, behavioral, molecular, etc.) over others during the process of recognizing and diagnosing a species, and advocates the combined and integrated use of various such methods.'	Miralles et al. (2010)
Operational species delimitation criteria (aka. Tree Based Delimitation) ⁴	'Set of criteria for concluding if mitochondrial lineages represent species: (1) ingroup lineages must be exclusive of the outgroup (2) lineages within the species complex must be geographically exclusive of one another'	Wiens and Penkrot (2002)
Phenetic cluster criterion ⁵	'Distinguishes species by their allocation to separate clusters in multivariate analyses'	Sokal and Sneath (1963)
Phylogenetic species concept ⁶	A species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent	Cracraft (1983)

1 = From Frankham et al., 2012; 2 = Burbrink et al., 2011; 3 = de Queiroz, 2007 4 = Burbrink, 2002; 5 = Guo et al., 2009; 6 = Cracraft, 1989.

reducing the number of North American bird species by 51% (607–292).

Given the multitude of ways used to define a species (Table 1), it is not surprising that this confusion extends down to subspecies as well; some disciplines, such as herpetology have many authors rejecting the subspecies classification (Reiserer et al., 2013) while others, like ornithology, favor the classification for understanding evolutionary divergence and conservation (Hawlitschek et al., 2012). The differences between the disciplines is evident when examining the ratio of species to subspecies within the vertebrate groups: mammals have an approximate 1:2 ratio (Reeder et al., 2007), aves is approximately 1:2.2 ratio (Lepage, 2014), while reptiles are approximately 1:0.3 ratio (Uetz, 2010). Even using the same criteria for subspecies designation could result in a different number of species if different species designations are used (Rodríguez-Robles and De Jesús-Escobar, 2000). Despite the confusion, the term “subspecies” continues to be used in many aspects of biological research and currently influences conservation efforts (Zink, 2004) and legislation (Haig et al., 2006), making it essential to identify and understand any biases in the application of the subspecies concept.

“Subspecies” replaced the term “variety” in zoology, inheriting the meaning of geographic race (variant populations of a species based on geographic location), in the late nineteenth century (Mayr, 1963). Simply replacing the term, the subspecies concept remained an ambiguous classification since species characteristics were not necessarily dependent on geographic variation (Wilson and Brown, 1953; Mayr, 1963; Mayr and Ashlock, 1991). Mayr (1963) redefined subspecies, as “an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species.” This concept, while more specific, remains ambiguous in meaning and application since “differing taxonomically” has multiple interpretations.

Repeated suggestions have been made to standardize “differing taxonomically, with statistical quantification of subspecies such as the 75% rule (Amadon, 1949). In this case, a population was considered a subspecies if 75% of the population’s morphological characteristics lay outside of 99% of the range of other populations (Amadon, 1949). The percentage, while initially accepted, was eventually argued to be too low because subspecies should be diagnostically distinct thus, the criteria then increased to 90% or

100% separation of defining characteristics between populations (Marshall, 1967; Amadon and Short, 1992). More recently, Patten and Unitt (2002) argued for a 95% rule in order to parallel the standard alpha value of 0.05 in other statistical tests.

Originally the 75% rule applied only toward morphological features using the Biological Species definition, but the “molecular systematics revolution” integrated genetics into the analysis of subspecific designation (Rodríguez-Robles and De Jesús-Escobar, 2000; Patten and Unitt, 2002). The genetic techniques altered the rules for subspecific designation by revising the traditional ranked-based taxonomy to apply a phylogenetic-based taxonomy (Mulcahy, 2008). Currently, the common methods of analysis involve sequencing mitochondrial or nuclear genes to then analyze the genetic distance between the subspecies in order to determine their genetic distinctiveness, or to evaluate the evolutionary lineages between the recognized subspecies (Burbrink, 2002; Fritz et al., 2007). If subspecies have high genetic distance values, or represent distinct evolutionary lineages, they are raised to full species rank, but if the subspecies have low genetic distance values or lack a distinct evolutionary lineage scientists either maintain the subspecies classification or collapse the subspecies to a single species with no subspecies (Burbrink et al., 2000; Fritz et al., 2007; Makowsky et al., 2010). However, the application of genetics raises additional questions about the validity of subspecies as the genetic results often disagree with the recognized subspecies based on morphological data (Ball and Avise, 1992; Burbrink et al., 2000; Phillimore and Owens, 2006). This lack of congruence can lead to alterations in the taxonomy including rejecting subspecies (e.g., Macey et al., 1998; Daniels et al., 2010), combining subspecies (e.g., Podnar et al., 2004), establishing new subspecies (e.g., Guicking et al., 2008), or elevating subspecies to full species (e.g., Leaché and Reeder, 2002; Bryson et al., 2007).

Avian subspecies have been a particular focus for genetic evaluation since Mayr’s reevaluation decreased the number of species by 51% (Mayr, 1970). More recently, Zink (2004) surveyed 41 avian species using mtDNA analyses and found that only 3% of avian subspecies qualified as distinct evolutionary entities. He found that the average bird species had only 1.9 independent evolving groups, based on DNA analysis instead of his surveyed average of 5.5 based on morphological and geographical data. Zink (2004) concluded that there were too many avian subspecies, and suggested that the number of avian subspecies should be collapsed while the

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