
The Conservation of Unisexual Vertebrate Populations

FRED KRAUS

Department of Biology, University of Michigan, 830 N. University, Ann Arbor, MI 48109, U.S.A., email
usergf8e@um.cc.umich.edu

Ranker and Arft (1994) brought needed attention to current ambiguity in the use of the term "hybrid" and the potential confusion this ambiguity can have on the protection of allopolyploid plants under the U.S. Endangered Species Act (ESA). This legislation denies protection to hybrids under the (not explicitly stated) rationale that "hybrids" as generally understood do not constitute independent evolutionary lineages and, hence, are undeserving of protection. Ranker and Arft correctly point out, however, that the term "hybrid," denoting the F_1 progeny of interspecific matings, should not be confused with polyploid taxa that are originally of hybrid origin. The important distinction is that the former are evolutionary dead-ends that are most often sterile or have greatly reduced fertility relative to their parental species (Dobzhansky 1941; Mayr 1970), while the latter are independent lineages capable of persistence over evolutionary time scales. Ranker and Arft argue that the preclusion of protection for hybrids by the ESA pertains to the former group, while the latter, by virtue of their persistence and evolutionary independence from their parental species, qualify as species and, therefore, deserve protection under the ESA. I believe this argument to be accurate, but I would like to point out the existence among certain unisexual vertebrates of a third class of phenomena intermediate in nature to the distinction between primary, homoploid hybrids and allopolyploid species noted by Ranker and Arft. I then consider how the questionable taxonomic standing of these unisexuals affects how they fare in current protection programs and argue that a process-oriented conception of biodiversity requires inclusion of such unisexual forms in protection efforts.

Unisexual (all-female) populations of vertebrates were first described by Hubbs and Hubbs (1932) for the fish genus *Poecilia*. Subsequently, unisexual populations have been discovered in several families of freshwater fishes, salamanders, and lizards. Currently, unisexual lineages are known from at least 22 genera (see Vrijenhoek et al. [1989] for an almost complete listing), and a few of

these genera, such as *Poecilia*, *Poeciliopsis*, *Ambystoma*, *Cnemidophorus*, and *Lacerta*, are rife with unisexual taxa. In all cases that have been carefully examined, unisexual taxa/complexes have been determined to be of hybrid origin, involving two or three bisexual parental species (see Vrijenhoek et al. [1989] for references). Ploidy among these unisexuals varies from $2n$ to $5n$ (Vrijenhoek et al. 1989), with most forms being $2n$ or $3n$. Reproduction among unisexual vertebrates is variable and segregates largely along taxonomic lines. All unisexual reptiles for which information is available appear to be parthenogenetic—that is, meiotically unreduced ova develop in the absence of congeneric sperm. In the diploid unisexuals of the fish genus *Poeciliopsis*, hybridogenesis prevails. In this system, a unisexual fish has one complete haploid genome from each of two different bisexual species. Upon sexual maturity, the haploid complement of chromosomes from the male parent is eliminated prior to meiosis, resulting in the production of reduced, haploid ova bearing only the complement of chromosomes from the female parent (Schultz 1966; Cimino 1972). Upon mating with a male of the paternal species, another generation of diploid unisexuals is produced (Schultz 1969, 1977). Because the genome from the original founding female of the unisexual lineage is preserved unaltered through the generations, this form of unisexual is referred to as a hemiclinal lineage. In the remaining fish, and apparently in the salamanders, gynogenesis prevails (see Vrijenhoek et al. [1989] for references). In this reproductive mode, unreduced ova are produced that are then stimulated to develop by the presence of congeneric sperm, typically from one of the parental species. The occasional accidental incorporation of sperm in such unreduced ova can result in an elevation of ploidy in some of the offspring (Schultz 1969; Cimino 1972; Bogart et al. 1989).

The relevance of these unisexual vertebrates to the question of which organisms deserve protection under the ESA is related to the variable degree to which certain of these forms are genetically dependent upon their bisexual parental species for their continued maintenance. In the case of the reptiles and certain of the gynogenetic forms, the unisexual taxa are genetically independent of

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their parental species and, hence, clearly qualify as evolutionarily independent lineages, or species, at least under the concept of evolutionary species (Simpson 1951; Wiley 1978; Frost & Hills 1990). (Note though that the absence of bisexual reproduction in all these forms precludes their consideration under the so-called biological species concept [Dobzhansky 1941; Mayr 1970].) But how does one treat the hybridogenetic forms whose very existence involves the reincorporation of the paternal genome each generation? The hemiclinal inheritance pattern of these unisexuals indicates that something is being conserved and propagated as a lineage, but it is not a "species" as understood by the evolutionary species concept. Or consider the more complex situation seen in the salamanders of the genus *Ambystoma*. An array of unisexual *Ambystoma* is produced in the Great Lakes region, involving various combinations of two or three allochthonous genomes from a total pool of four parental species (Uzzell 1964; Downs 1978; Kraus 1985a; Kraus et al. 1991).

Because the reproductive mechanism of these unisexual forms is apparently a leaky form of gynogenesis (Bogart et al. 1989) in which incorporation of allochthonous sperm can lead to frequent bouts of ploidy elevation, and because some recombination and introgression of alleles back into the parental species occurs at least occasionally (Kraus 1985b; Bogart 1989; Kraus & Miyamoto 1990), it appears that formation of several (and perhaps all) of the genotypic combinations (biotypes) can occur independently in a variety of ways. This extreme genomic heterogeneity led some to conclude that the unisexuals represent a complex swarm of hybrids (Bogart & Licht 1986; Bogart 1989), but this notion was rendered untenable by the observation that the unisexuals all had similar mitochondrial genomes derived from only one of the four parental species (Kraus 1989; Kraus & Miyamoto 1990; Hedges et al. 1992). This clearly showed that the tremendous genomic diversity among unisexual *Ambystoma* is within the constraints of probably only one or a few ancestral hybridization events. In this case, therefore, what is probably ultimately a single matrilineage of unisexual forms has captured enough genomic diversity from sympatric bisexual species to constitute now a diverse array of genotypes scattered throughout a large composite range. While this complex is usefully thought of in one sense as a single lineage, it clearly does not fit into any definition of a species because of its rampant remixing of allochthonous genomes.

Does this mean that such unusual biological phenomena should be discounted in efforts to preserve the planet's biological diversity? Or should we perhaps recognize that the category "species," whether of the "biological" or the "evolutionary" conception, does not encompass the total array of lineage diversity that nature presents? I would argue that such unisexual lineages and

complexes deserve protection because they represent rare and unique biological phenomena, even though they are not readily pigeonholed into one of the various definitions of species that can be constructed to accommodate much of the rest of biodiversity, whether of a bisexual, polyploid, or strictly clonal variety. Their protection is especially important because many of these unisexual clones, biotypes, and complexes have restricted ranges (Table 1), often in areas suffering heavy human disturbance. But, as far as I can determine, none is protected by public conservation programs. In many cases, these unisexual forms are abundant and, therefore, probably not in short-term danger of extinction; in other cases (some of the *Ambystoma* biotypes), they are restricted in range and sufficiently rare where found for there to be cause for concern. Despite this, they receive no consideration under state or federal conservation programs. Part of the reason for this oversight may be that the nonparthenogenetic lineages are not typically recognized with formal binomial epithets, making it easy for biologists and wildlife officials to ignore them because of the human tendency to reify preferentially those entities having names.

Also, there is a widespread tendency among those not intimately familiar with such systems to simply and incorrectly dismiss these lineages as "hybrids" (a practice followed in books intended for use by the general public as well, such as that by Conant and Collins [1991]). Reference to these unisexuals as hybrids is unwarranted, however, because they are not derived by continuous and independent mating events between the assorted parental species but, instead, persist as matrilineages through evolutionary time (though not in the cohesive fashion we've become accustomed to from bisexual species), with their own unique evolutionary fates and tendencies. Consequently, to guarantee the protection of these unisexual complexes and their underlying evolutionary dynamics may require the adoption of a more process-oriented view of biodiversity than the usual static taxonomic concepts that are acceptable for many other uses. The federal ESA (1994) provides for the protection of unique populations of organisms by adopting a fairly broad, nontaxonomic definition of species, which includes "any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." While many of these unisexual forms cannot be construed as species, the ESA's recognition that meaningful conservation may require extension of legal protection to entities below the species level may allow some opening for the protection of rare or restricted unisexual forms and the sympatric populations of parental species that support them. Some state ESA statutes may employ similar definitions and, therefore, may be equally applicable to the protection of unisexual lineages. The primary problem is for conservation professionals and government wildlife officials to recognize

Table 1. North American unisexual taxa/biotypes having geographically restricted ranges.^a

<i>Taxon/biotype</i>	<i>Range</i>	<i>Reference</i>
<i>Poeciliopsis monacha-lucida</i> ^b	Ríos Fuerte, Mocorito, & Sinaloa, Sinaloa.	Schultz, 1977
<i>P. monacha-latidens</i>	Ríos Fuerte, Mocorito, & Sinaloa, Sinaloa.	Schultz, 1977
<i>P. monacha-occidentalis</i>	Sonora.	Schultz, 1977
<i>P. 2monacha-lucida</i>	Ríos Fuerte & Sinaloa, Sinaloa; Río Mayo, Sonora.	Schultz, 1977
<i>P. monacha-2lucida</i>	Río Fuerte, Sinaloa.	Schultz, 1977
<i>P. monacha-lucida-virtosa</i>	Río Mocorito, Sinaloa.	Schultz, 1977
<i>Poecilia formosa</i>	Brownsville, Texas to Tuxpan, Veracruz.	Darnell & Abramoff, 1968
<i>P. formosa-latipinna</i>	Lower Río Grande basin, Texas.	Rasch & Balsano, 1989
<i>P. formosa-mexicana</i>	Río Tuxpan basin, Veracruz.	Rasch & Balsano, 1989
<i>P. formosa-"Imantouri"</i>	Río Soto la Marina basin, Tamaulipas.	Rasch & Balsano, 1989
<i>Menidia clarkhubbsi</i> complex	Coastal areas from Copano Bay, Texas, to Mobile Bay, Alabama.	Echelle et al., 1989
<i>Fundulus heteroclitus-diaphanus</i>	Two sites in Nova Scotia.	Dawley, 1992
<i>Ambystoma laterale-texanum</i>	NW Ohio, SE Michigan, Pelee Island, Ontario.	Downs, 1978; Kraus, 1985b; Bogart et al., 1985
<i>A. 2laterale-texanum</i>	NW Ohio, SE Michigan, Pelee Island, Ontario.	Downs, 1978; Kraus, 1985b; Bogart et al., 1985
<i>A. laterale-2texanum</i>	NW Ohio, SE Michigan, Pelee Island, Ontario.	Downs, 1978; Kraus, 1985b; Bogart et al., 1985
<i>A. laterale-texanum-tigrinum</i>	Kelleys Island, Ohio.	Kraus, 1985a
<i>A. laterale-texanum-jeffersonianum</i>	NW Ohio, SE Michigan.	Kraus et al., 1991
<i>A. laterale-jeffersonianum-tigrinum</i>	Hillsdale Co., Michigan.	Kraus et al., 1991
<i>A. laterale-2jeffersonianum-texanum</i>	Vermillion Co., Illinois.	Morris & Brandon, 1984
<i>Cnemidophorus cozumela</i> complex ^c	Yucatan Peninsula.	Fritts, 1969
<i>C. dixoni</i>	Hidalgo Co., New Mexico, Presidio Co., Texas.	Scudday, 1973
<i>C. opatae</i>	Opoto, Sonora.	Wright, 1967
<i>C. laredoensis</i>	Laredo, Texas.	McKinney et al., 1973
<i>Lepidophyma flavimaculatum</i>		
<i>obscurum</i>	Costa Rica to central Panama.	Bezy, 1989
<i>L. reticulatum</i>	Pacific versant to Costa Rica.	Bezy, 1989

^aAs far as I can determine, the forms listed in this table receive no protection in any national or state endangered species program. Unisexual vertebrates occur on other continents as well, though relatively few have been studied intensively.

^bThe convention used in naming most of the nonparthenogenetic unisexuals is to designate the parental genomes present in the unisexuals separated by a hyphen (Schultz, 1969). Multiple genomic dosages present from one parental species are prefixed by a numeral indicating the number of contributed haploid complements.

^cMost of the parthenogenetic taxa have formal binomials applied to them, although considerable clonal structure is often hidden within these taxa. Under evolutionary species concepts stressing the independent derivations of species (e.g., Frost & Hillis, 1990), many or all of these clones would be considered separate species. Hence, many of the widespread unisexual *Cnemidophorus* of the southwestern United States and northern Mexico (not listed here) would be divided into a number of species and the numbers of unisexual taxa having restricted geographic ranges would increase relative to that here.

that not all organismic diversity comes in neat little packages of bisexual species and that populations of unisexual organisms represent distinct evolutionary phenomena deserving of protection, whether or not their products are recognized by formal binomial names. This, in turn, necessitates that the biologists advising these people are aware of the problem themselves. It would be desirable for biologists in regions containing such fauna to recognize and highlight the existence and uniqueness of these unisexuals so that, when necessary, they may receive the same degree of legal protection (such as it is) accorded the remainder of biological diversity.

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