



Point of View

The nature of species: A rejoinder to Zachos et al.

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ABSTRACT

I argue strongly that the Phylogenetic Species Concept offers the only way of defining species that makes them testable, as any scientific hypothesis should be. The criticisms made by Zachos et al. (in press) are not cogent, and do not offer a means of testing species proposals. Nonetheless, their comments on species concepts in conservation do provide support to the value of the Phylogenetic Species Concept.

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Species are the units of biodiversity, of conservation, of evolution, of ecology; to such an extent are species basic to so much of biology that it is important that they be scientifically based. A scientific proposition should be testable, yet most of the species concepts that have been applied over the past half century or more do not produce “species” that are always testable.

The Phylogenetic Species Concept (PSC) does fulfil such a criterion. Species under this concept are diagnosable, that is to say they have fixed heritable differences from other species. When the available evidence indicates that two population samples differ absolutely from one another, they are ranked as separate species. If further evidence shows that they are not after all absolutely different, then the former conclusion, that they are distinct species, is falsified. This is what science is all about: hypotheses are tested, and corroborated or rejected as appropriate. I have gone through the arguments in many publications (Groves 2001a,b, 2004, 2012) and did so again, if in somewhat less detail, more recently (Groves and Grubb 2011, pp. 1–3), but I will summarise the main ones again here.

The PSC depends on evidence, not on inference. The Biological Species Concept, which held sway from the 1930s until about the 1970s and is still espoused by a significant proportion of biologists, depends on inference, maintains that species are those entities which do not interbreed; when candidates for species status are sympatric, such an inference seems reasonable on the face of it, but when they are allopatric nothing of the sort can be inferred.

The PSC does not assume that interbreeding between species is impossible, or even necessarily rare. The BSC makes this assumption, but molecular evidence shows that it is not necessarily true.

The PSC depends on whether differences between potential species are fixed, not on the degree or amount of difference between them. The Genetic Species Concept (GSC), as applied to mammals (Bradley and Baker 2001; Baker and Bradley 2006), depends on calculating an amount of difference; it maintains that distinct species show genetic distances (in cytochrome-*b*) of >2%, but there is a large “grey area” of genetic distance within which separate species status may or may not be indicated. Thus, the GSC is not so much a species concept in itself, as a recipe for detecting hitherto unsuspected cryptic species.

The PSC records the observable pattern; unlike The BSC and several other species concepts, it does not speculate on the processes by which that pattern may have arisen or may be maintained. The Cohesion Species Concept (Templeton 1989) is an interesting variant among the Process concepts. In this concept, a species is defined by the genetic and demographic mechanisms which give it its cohesion: the genetic mechanisms are those which limit its gene-flow with other species, and the demographic ones are those that constrain a species within its “fundamental niche”. Although there is not a hope of operationalising this idea, it does seem in many respects to approach the ideal of what constitutes a species’ role in nature. This is perhaps why it has frequently appealed to by mammalian taxonomists (see Hoisington-Lopez et al. 2012, for a recent example).

There is of course one inference that must be made by all species concepts: that species are populations (or aggregations of populations). There is unfortunately no escaping this; it is a lasting legacy of the Evolutionary Synthesis of the 1930s. In the case of the PSC, but of no other species concept, this is the only inference that must be

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made. Beyond this, the PSC offers falsifiable hypotheses: no other species concept does this.

Zachos et al. (in press) have recently criticised the influence of the PSC in mammalian taxonomy. They argue two cases in particular: that the PSC has frequently been inappropriately applied, and that there has often been “a naive interpretation of inconclusive available datasets”.

I will respond here to some of the points which they raise, both general and specific.

- (1) General points. They approvingly cite a book review by Avise (2000), who described how new mutations often come to differentiate regional populations: “it would be nonsensical, however, to assign species status to each such diagnosable cluster” (Zachos et al. in press, p. 2). They, like Avise himself, do not explain why it would be nonsensical, and this recalls the worry expressed by some ornithologists that certain characters differentiating phylogenetic species are “trivial” (see below). Later in this section, the authors rightly note that gene trees are not the same as species trees, but they cite no cases in which a proponent of the PSC has fallen into this error. It is not clear that this criticism is relevant.
- (2) Specific examples. Zachos et al. (in press) criticise the splitting of tigers into three species: “even the tiniest fragments of a species can be made diagnosable if the markers have enough resolution power”. This is precisely the point: if the markers have enough resolution power, and our population samples can be resolved by them, then under the PSC we will be justified indeed in proposing that we are in the presence of multiple species. If further evidence shows that they are not diagnosably different after all, then the hypothesis that they are different species has been tested and found wanting.

The authors then raise the problems of humans and domestic animals. Why, they seem to be saying, are there not distinct species of humans or dogs under the PSC? The answer to the first question is that the human species is a genetic continuum. There are no points along this continuum where there are logical breaks with diagnosably distinct populations on either side; there are wide clines, but nothing resembling, for example, the hybrid zones one gets between parapatric species, and even distinctive populations formerly isolated by sea (Andamanese, Australians) overlap in character states with populations elsewhere. The question of domestic animals, such as dogs, is different; they are subject to artificial selection, not natural selection, they do not conform to any definitions applying to wild animals, and there have been arguments back and forth over what is the best way to deal with them in taxonomy and indeed in nomenclature (see, for example, Groves 1995). Domestic breeds may be ephemerally species-like, the operative word being “ephemerally”, and there are many “breed-less” populations – pariahs, village dogs, mutts and strays of all types, not to mention dogs of designated breeds which have ceased to be bred to type – which bridge the gap between the strictly maintained breeds.

The case of red deer and their relatives is cited as “a second unwarranted splitting” by Zachos et al. (in press, p. 3). Groves and Grubb (2011, pp. 94–99) divided the red deer complex into 12 species, all readily diagnosable on available evidence. Two criticisms are levelled by Zachos and his colleagues in this case: first, against the splitting as such, and secondly, at the fact that we recognised the Corsico-Sardinian red deer as a separate species *Cervus corsicanus* but failed to separate the so-called Barbary stag or North African deer from it (traditionally they have been referred to as *Cervus elaphus corsicanus* and *C.e. barbarus* respectively). In a paper published after the death of my colleague Peter Grubb, and unfortunately subsequently missed by me, Hajji et al. (2008) found that the two are indeed similar, but differed in frequencies

of certain microsatellite alleles. Interestingly, they found that both populations are genetically impoverished, as is the tiny remnant population from Mesola in northern Italy, which is perhaps the most likely ultimate source for them. All three populations have lost alleles; Mesola and North Africa have lost different sets of alleles, such that they are technically diagnosably distinct from each other, but not from Corsica plus Sardinia. Were the latter population not known, it might appear that the North African and Mesola deer are candidates for distinction at species level. There are analogous cases in which formerly quasi-continuous populations have been reduced by human agency to remnant isolates, each somewhat different, and possibly no longer sharing alleles or mitochondrial haplotypes.

Zachos et al. (in press, p. 3) regard the splitting by Groves and Grubb (2011, pp. 275–279) of klipspringers (genus *Oreotragus*) into 11 named species as “One of the most spectacular recent incidents of taxonomic inflation” and “a prime example of rash taxonomic conclusions derived from an inappropriate dataset”, because it is based on phenetics (no genetic data are available), and sample sizes are mostly quite small. In fact, were genetic information available we would have cited it, and were larger samples available we would have used them. The pelage and other differences are consistent on the available data, and our 11-species model is open to testing on the basis of further information; we see no way in which any other species concept could offer an alternative model which is testable in any way.

Groves and Grubb (2011) divided the mainland serows (*Capri-cornis*) into six species, again on the basis of phenotypic characters. This time, sample sizes are mostly much larger (pace Zachos et al. in press, who describe them as “very small”), but again no genetic data are available. Again, we put forward a testable hypothesis, and I hope that further research, when new information becomes available, will suffice to corroborate or falsify our model.

It is perhaps pertinent to note that a similar discussion is in progress in ornithology, kick-started by the classic paper of Zink and McKittrick (1995), although many of the proponents of the status quo seem to use mainly bullying arguments – “there is no clear limit to how subtle a diagnostic difference can be, which opens the door to unconstrained taxonomic inflation via character triviality” (Tobias et al. 2010, p. 726). No coherent argument can be found in such a statement.

Zachos et al. (in press) make some further points with which one can only agree. Their first point is that taxonomy attempts to reflect the process of evolution, but was never designed to do so, so that there will be examples of incipient speciation which are hard to deal with under any species concept. A second point that in the modern conservation crisis many formerly continuous, clinically varying populations have been divided by extinction of intermediate populations into restricted isolates, at least some of which may be characterised by fixed heritable differences: the red deer case cited above is almost an example, in which two of the three isolates appear to be diagnosably different from each other, but not from the third.

The third cogent point which they raise is this: in agreeing that there probably are indeed more mammalian species to be described than are at present recognised, they note that a taxonomic arrangement which does not split finely enough may have a detrimental effect on conservation activities – “when a threatened taxon is lumped together with a non-threatened one” – and I can only agree. A lack of critical examination of whether a supposedly non-threatened species is indeed a homogeneous entity, and does not actually consist of two or more threatened species, is an example of the baleful effects of unexamined taxonomic “lumping”. And indeed there has been considerable discussion in recent years over the implications of the PSC for conservation: see, for example, Agapow et al. (2004), who emphasise that we must not

use any perceived problems with the PSC as a reason to reject it. To reiterate the point which I made recently (Groves 2012): the biological world is much more diverse, much richer than we had imagined, and we must get used to it.

References

- Agapow, P.M., Bininda-Emons, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C., Purvis, A., 2004. The impact of species concept on biodiversity studies. *Quart. Rev. Biol.* 79, 161–179.
- Avise, J.C., 2000. Cladists in Wonderland. *Evolution* 54, 1828–1832.
- Baker, R.J., Bradley, R.D., 2006. Speciation in mammals and the genetic species concept. *J. Mammal.* 87, 643–662.
- Bradley, R.D., Baker, R.J., 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. *J. Mammal.* 82, 960–973.
- Groves, C.P., 1995. On the nomenclature of domestic animals. *Bull. Zool. Nomenclature* 52, 137–141.
- Groves, C., 2001a. *Primate Taxonomy*. Smithsonian Institution Press, Washington.
- Groves, C., 2001b. Why taxonomic stability is a bad idea, or why are there so few species of primates (or are there?). *Evol. Anthropol.* 10, 192–198.
- Groves, C., 2004. The what, why and how of primate taxonomy. *Int. J. Primatol.* 25, 1105–1926.
- Groves, C., 2012. Species concept in primates. *Am. J. Primatol.* 74, 1–5.
- Groves, C.P., Grubb, P., 2011. *Ungulate Taxonomy*. Johns Hopkins University Press, Baltimore.
- Hajji, G.M., Charfi-Cheikerouha, F., Lorenzini, R., Vigne, J.-D., Hartl, G.B., Zachos, F.E., 2008. Phylogeography and founder effect of the endangered Corsican red deer (*Cervus elaphus corsicanus*). *Biodivers. Conserv.* 17, 659–673.
- Hoisington-Lopez, J.L., Waits, L.P., Sullivan, J., 2012. Species limits and integrated taxonomy of the Idaho ground squirrel (*Urocitellus brunneus*): genetic and ecological differentiation. *J. Mammal.* 93, 589–604.
- Templeton, A., 1989. The meaning of species and speciation: a genetic prospective. In: Otte, D., Endler, J. (Eds.), *Speciation and its Consequences*. Sinauer Associates, Sunderland, MA, pp. 159–181.
- Tobias, J.A., Seddon, N., Spottiswoode, C.N., Pilgrim, J.P., Fishpool, L.D.C., Collier, N.J., 2010. Quantitative criteria for species delimitation. *J. Mammal.* 152, 724–746.
- Zachos, F.E., Apollonio, M., Bärmann, E.V., Festa-Bianchet, M., Göhlich, U., Habel, J.C., Haring, E., Kruckenhauser, L., Lovari, S., McDevitt, A.D., Pertoldi, C., Rössner, G.E., Sánchez-Villagra, M.R., Scandura, M., Suchentrunk, F. Species inflation and taxonomic artefacts – a critical comment on recent trends in mammalian classification. *Mamm. Biol.*, <http://dx.doi.org/10.1016/j.mambio.2012.07.083>, in press.
- Zink, R.M., McKittrick, M.C., 1995. The debate over species concepts and its implications for ornithology. *Auk* 112, 701–719.