What are 'good' species?

Recently in *TREE*, Mallet[1,2] argued for an operational, concept-free definition of species as 'genotypic clusters', asserting 'that species are man-made groupings'[2]. However, Mallet resorts to the traditional notion of 'good' species for final arbitration regarding what degree of variation is appropriate for the species-level taxon. This is a poor species definition for two reasons. As an operational definition it leaves us with no means for dealing with the great complexities of biological systems of descent. Moreover, the decision as to what constitutes species-level variation is based on an essentialistic perspective offered by a 'good taxonomist's or naturalist's definition'[1].

If species are, in Mallet's operational terms, 'groups that remain recognizable in sympatry because of the morphological gaps between them'[2], it is important to realize that they are nothing more than the sum of the operations that serve to identify them[3,4]. We are left with the arbitrary decision of how large these gaps must be and what frequency of intermediates would lead us to accept two species rather than one. These difficulties are problematic for the diagnosis of a 'species' under any definition or concept, due to the fuzzy nature of groups resulting from, or participating in, the evolutionary process (i.e. natural groups). However, they are more severe for a concept-free definition because we have no theoretical guideline with which to sort variation into hypotheses about natural groups. A concept-free definition of species as 'genotypic clusters' must also deal with the discrete morphological variation manifest, for example, between genders of many plants and animals. These are 'genotypic clusters' of sorts. However, neither today, nor in Darwin's time, do biologists wittingly hypothesize different species for different genders. Without an ontological context with which to sort variation in biological systems, we find ourselves perplexed by situations as straightforward as sexual dimorphism.

In stark contrast to his purely operational definition, Mallet alludes to such an ontological framework by reference to 'good' species[2]. But what are 'good' species? Mallet endorses the traditional position that, in the most difficult cases, the ultimate authority of the existence of 'good' species is the taxonomist or naturalist. The implication of this deference to the taxonomist is that 'good' species exist, but that their essential nature is hidden; a taxonomist's contribution is to reveal 'good' species through description, case by case. Thus, the notion that 'good' species can be revealed to us by taxonomic authorities is steeped in the essentialistic outlook that Mallet[1,2] (and others[5]) seek to condemn. Furthermore, the definition of a species becomes 'a group of organisms that is recognized as a 'good' species by the taxonomist or naturalist.' This is obviously undesirable. Although taxonomists may point to groups that they believe exist, species will only have objective value if the general properties of 'good' species (the species taxon) are revealed to the rest of us.

Whereas a purely operational definition causes us to forego the question, 'what is the nature of the group that we might call species?', asserting the existence of 'good' species (even if we knew their properties) demands that all groups of organisms, that we might call species, exist in the same way[6]. A definition that results in one or both of these outcomes should be avoided, particularly in studies of speciation where we are interested in all the natural groups produced by a pluralistic process of evolution. It is a step forward for students of speciation to acknowledge that different sorts of natural groups have valid claims to the term 'species'[6,7]. Similarly, it is regressive to undermine the notion that the species taxon (whatever natural group we choose for it to designate) has underlying properties that make it worth studying. One possible solution is provided by a nominalistic approach[6–9], which formulates a species definition explicitly while retaining the ontological meaning that a purely operational definition leaves behind. Such a definition would embody a statement of the necessary and sufficient properties for the diagnosis of species in any particular case. The important distinction between a nominalistic definition and Mallet's is that our avenue of inquiry would lead us to explore the nature and evolution of natural groups (as opposed to some notion of a 'good' species), with or without a coextensive relationship between such groups and 'good' species (whatever they are!).

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Reply from J. Mallet

Suppose Darwin, in *The Origin*, had used a 'phylogenetic' or 'genealogical' species concept[1–3]. Creationists would have found his argument for evolution of species both circular and false because evolution was included within the definition of species. Darwin instead proposed that there were certain morphological gaps between species that were not present between varieties or races. To debate creationists, Darwin abandoned essentialist thinking dating back to Plato and adopted a nominalist[4] definition that was independent of modes of origin. This operational definition was necessary for discussing species evolution because it avoided implicit evolutionary assumptions[5]. Some molecular evolutionists (I do not claim originality) are beginning to adopt a similar view: that species are simply genotypic clusters recognizable in sympatry. Cohan[6], for example, suggests bacterial species could be defined as DNA sequence clusters that are undergoing permanent neutral allele divergence.

Kerry Shaw complains that I say a 'good' species is what a good taxonomist says it is. To some extent, this is true: I used the term 'good' species several times meaning that people generally agree that 'the blue whale' and 'the fin whale', for example, are species, even though these and many other plant and animal species both hybridize and, in parts of their genomes, evolve reticulately[7]. Unless taxonomists are mad, there is something reasonable about such species (though 'goodness' itself was not my definition). If Darwin could argue with creationists about species origins, the term 'species' must to some extent be independent of evolutionary assumptions. What do we mean by 'species', then? I have already given examples of *Anopheles* sibling species identification using allozymes[7,8], and of species detection in *Heliconius* butterfly hybrid zones, based on colour pattern genes[8]. Here, I give two examples based on allozyme data from hybrid zones. In Fig. 1a, a local population in a hybrid zone contains a single-peaked distribution along a hybrid index. There is only one genotypic

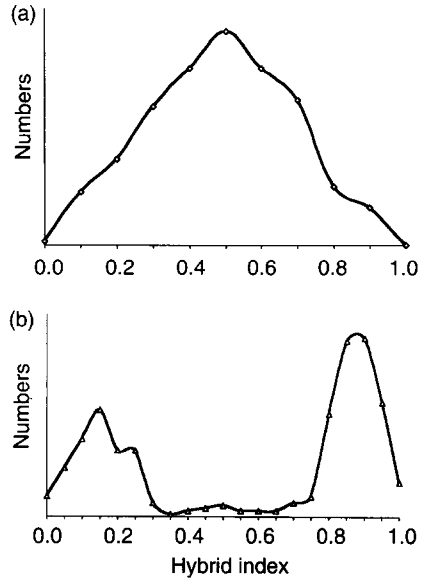

Fig. 1. Plots of hybrid index scores in two hybrid zones. (a) Distribution of hybrid index scores in a population at the centre of an intraspecific hybrid zone. (b) Distribution of hybrid index scores in a population in the centre of an interspecific contact zone. These graphs represent the kinds of data produced in allozyme analyses of, for example, (a) *Bombina bombina* × *B. variegata* hybrid zones[9], and (b) *Heliconius erato* × *H. himera* hybrid zones[8,10].

Hybrid indices are calculated as follows: take loci that are divergent in frequency between hybridizing taxa I and J; make a raw score for each individual by summing the numbers of J-associated alleles over all divergent loci; correct the hybrid index so that it has a maximum of one by dividing the raw score by the total number of alleles sampled. Any polymorphic marker can be used; non-divergent loci will simply change the scale.

cluster, and therefore a single species. Taxa like those that form hybrid zones, as in Fig. 1a, are the same species in that separate genotypic clusters dissolve where the two forms overlap. In the European toads *Bombina bombina* and *B. variegata*, which inspired Fig. 1a, the names are highly informative about ecology, behaviour, physiology and morphology in allopatry[9]. Yet the two *Bombina* forms, which have undergone separate genealogical divergence for 2–7 million years (My), have failed to speciate. In contrast, in Fig. 1b, individuals within a different kind of hybrid zone mostly belong to one of two genotypic clusters with a thin smear of intermediates (putative 'hybrids') between them. *Heliconius erato* and *H. himera* hybrid zone populations produced hybrid indices similar to those in Fig. 1b. These two tropical butterflies are only about 1.5–2.5 My old, yet they never fuse into a single cluster where they overlap[8,10]: *erato* and *himera* have speciated. This species definition is exactly that of Avise and Ball[11]. It is difficult to obtain genealogical information from allozymes, so their method does not actually test for 'genealogical concordance' as claimed[11], but instead checks for genotypic clusters in sympatry[7]. Shaw claims that genotypic clusters will cause confusion because of an ambiguous dividing line between species and races or morphs. But the dividing line is clear; given a continuum between hybrid index scores like the extremes in Fig. 1, there will be an intermediate situation in which a single-peaked distribution becomes two-peaked. A more complex hypothesis of two species can be tested against the null hypothesis of a single species[7]. Species 'concepts', on the other hand, which require comparison with evolutionary or genealogical ideals, provide no dividing line. How much cohesion, genealogical concordance or reduced gene flow is required to give separate species? It is unclear.

Shaw also claims that species as genotypic clusters are arbitrary because morphological and genetic gaps between males and females are similar to those between species. But all inherited differences are quantized, whether resulting from single base pairs, genes or whole chromosomes. There are gaps between *any* genotype and all others differing at one or more point mutations. It would be futile to use quantum differences alone to detect species, and I didn't suggest it. We should use multilocus *arrangements* of discrete differences, rather than the discreteness or even size of each genetic difference. Compare X-linked and autosomal loci of a Y-bearing male to homologous loci in other individuals of both sexes, and you will find that his genotype is rather average for his species. The whole Y chromosome must be counted as a single genetic element because it is inherited as a block. Other chromosomal polymorphisms, such as chromosomal inversions that trap strong differences should be treated likewise. Similarly, species will be impossible to detect on the basis of mtDNA alone because the whole mitochondrial genome must be treated as a single allele[11].

Weighing down species definitions with evolutionary assumptions, such as binary branching or reproductive isolation, which we know to be fallacious in many actual cases, creates indistinct boundaries, is illogical, specific to certain groups, and constrains hypotheses about origins. In contrast, viewing species as sympatric genotypic clusters is a simple, clear, useful and general way of cataloguing the diversity of life, and, I argue, an unbiased initial step needed in testing hypotheses of species evolution.

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What is 'the paradox of the lek'?

Turner's[1] article in the December 1995 issue of *TREE* suggested that a resolution may have been found for 'the paradox of the lek'. Males of many species have exaggerated traits probably used by females in mate choice. In many (most obviously in lekking species), males play no direct role in offspring provision or care. In an important recent paper, Pomiankowski and Møller[2] reviewed the available evidence for the existence of genetic variation in sexually selected traits, and found that they typically have relatively high levels of additive genetic variation, probably more than broadly equivalent non-sexually-selected traits in the same organism. This contrasts with expectations that male traits subject to strong selection from female choice should show reduced levels of genetic variation as advantageous alleles are fixed, thereby removing one of the more perennial criticisms of some models of sexual selection. So, by choosing males with long tails, females are likely to pass this attribute on to their offspring. Pomiankowski and Møller (and Turner) consider this a resolution of the lek paradox.

I write to ask for clarification of what exactly constitutes the paradox we are concerned with? In their influential review, Kirkpatrick and Ryan[3] state the paradox is 'Why should females have evolved such strong preferences when they seem to receive no tangible benefit from their choice?'. Andersson[4] states that it is because female choice is often conspicuous 'and the heritability of the father's fitness is probably low.' I think there is a possibility of confusion arising from the presentation of Pomiankowski and Møller's findings, as in fact they do not address this latter question, which is the true heart of the paradox. Pomiankowski and Møller have shown that signals are heritable (and presented novel, plausible and testable ideas why this may be so), but this leaves open the whole question of whether or not these signals are reliable indicators of quality.

Equilibrium models of sexual selection imply that the male trait involved can become exaggerated to a limit where the sexual benefit of the trait is balanced by countervailing viability costs associated with it. It is perfectly possible (indeed, essential) for the trait to be heritable, in which case there would be no net benefit to females choosing on the trait so random mating may be as successful as choosiness. This is one possible paradox. Perhaps in such cases arbitrary choice processes such as copying would make some sense, and we are still some way short of knowing exactly which processes of mate choice do occur during mate choice on leks or even in more conventional mating systems[4]. In contrast, 'good genes' or 'viability indicator' models require that the trait is heritable and also that it is positively correlated with alleles conferring high viability. Plausible mechanisms exist that could maintain such genetic variation, but studies suggesting that indicator traits, including apparently expensive ones, are positively correlated with high fitness are few and far between[5–8]. Pomiankowski and Møller's review simply did not address this issue.

In my opinion we are still a long way even from proving that this paradox commonly exists in species with strong sexual selection, never mind 'resolving' it. More studies are needed showing positive fitness consequences of female mate choice based upon exaggerated traits. Finding that there is substantial heritability for fitness and that it is positively associated with expensive traits would indeed provide a challenging paradox.

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