

Review Article

A Review on Animal Hybridization's Role in Evolution and Conservation: *Canis rufus* (Audubon and Bachman) 1851—A Case Study

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Canis rufus is an example of animal whose conservational needs have been questioned because of its possible hybrid status. Control of hybridization has been defended and done in the wild to theoretically save the species. However, control of hybridization may not be the solution. Hybridization may be a phenomenon misconceived by many modern evolutionary biologists, and conservation guidelines over control on anthropogenic impacts may need revisions in order to respect the new perspectives on hybridization's role in evolution. The term “cladogamy” is being proposed to substitute “hybridization” and to refer to the crossing between two any given clades, due to difficulties from scientists and eventual arbitrary means of separating species from lower taxa.

1. Introduction

Animal hybridization is a theme often viewed as harmful to conservation [1] and to ecological/evolutionary processes [2] or at least bizarre/uncommon [3].

Mayr and the biological species concept seem to have given hybridization an unnatural image. Though botanists share a consensus on the importance of plant hybridization for their evolution, zoologists have tended to regard hybridization as an unnatural process [4].

Mayr proposed that “hybridization between species was an unusual “breakdown of isolating mechanisms”, that it was caused mainly by human-induced environmental changes, and had little importance for the understanding of species and speciation, thus adding to the impression that there was no middle ground between species and varieties”, as discussed by Mallet [5]. In fact, Mallet [4] admitted that the influence of Mayr has led to an almost eugenic view on hybridization among zoologists, in contrast with botanists. Hewitt has considered hybrid zones to be important for evolutionary studies [6] and Mallet has defended that they are natural

phenomena that require protection disregarding taxonomic status [7].

As to conservation, a notorious evidence of the strength of this almost eugenic view on hybridization is that the US Endangered Species Act of 1973 declares that hybrids are not worthy of conservation, in contrast to pure species [8]. Allendorf et al., 2001 [1], in turn, recognize that hybridization among animals may not be less natural than that in plants; still, they treat the subject as a high danger to biodiversity—especially in, but not restricted to, cases where hybridization is of anthropogenic causes.

This work intends to review the effects of hybridization amongst animal populations and infer the importance this particular phenomenon has regarding evolution and conservation.

To discuss the significance of hybridization evolution and ecology, a concise definition for it must be given. The term has a sense of a strong union of two entities that were supposed to be separated. Such is the case of electronic orbitals in chemistry—an exact science—but not of sexual organisms in biology—a nonexact science. It is difficult to apply rules

to biology, especially given that, as emphasized by Mayr himself, exact sciences and biology are of different nature [9].

Arnold et al. suggest restricting “hybrid” to matings between two different species, using “intergrade” for matings between subspecies and “cross” or “interbreed” for matings between individuals of geographically distinct populations [10]. However, there exist over 20 species concepts (22, in 1997, after Mayden [11]) and still no consensus. If one cannot define a species; one cannot define neither a hybrid nor a cross or an intergrade. Due to these difficulties, this work will not focus on the phylogenetic distance between the two lineages hybridizing.

These are the reasons why this work will propose and prefer the term “cladogamy” (clade + γάμος *gamos*, literally “clade marriage” in Late Greek) to refer to a cross between any two previously defined clades. The term also avoids the question on the natural concept of species, challenged by Darwin’s “On the Origin of Species” [12]. Cladogamy is a term that can apply to crossings between two species given any species concept and any two clades (as subspecies or varieties) distinguished by taxonomy, ecology, genetics, geography, or phylogeny.

For this reason, the *Canis rufus* case will be presented, discussed, and compared to other cases. *C. rufus* is a canid that hybridizes with *C. lupus* and *C. latrans* and has been proposed to be a hybrid species derived from these two others [13]. Conservation guidelines regard hybridization among them as a threat to biodiversity that should be controlled [14–17], and others suggest that even *C. rufus* is worthless of protection in case of recent hybrid origin [13].

2. Hybrid Origin of *Canis rufus*: Hybrid Zones and Hybrid Speciation

When nominated, the red wolf had been considered a subspecies of *Canis lupus* [18]. After mtDNA analysis by Rutledge et al., *Canis latrans* lies within the *Canis lupus* clade, being the sister taxon of the North American gray wolf lineage [19]. Together they are the sister group of the Eurasian gray wolf lineage. Even so, coyotes and wolves are classified as separated species, being reproductively isolated according to Rutledge et al. [19]. Rutledge and coworkers demonstrate that *Canis lycaon*, the eastern wolf, is a genetic bridge between *C. latrans* and *C. lupus* [20]. However, given that in the most cladistic analysis *Canis latrans* is a *Canis lupus* (paraphyletic in this case), it would not be a surprise to find out that they do directly interbreed.

In addition, von Holdt et al. defended that *C. rufus* is hybrid in origin, being 75% coyote and 25% gray wolf in its genome [13]. Rutledge et al. dismiss this hypothesis, supporting that the methods of von Holdt and coworkers were biased and that ethological data supports this nonhybrid hypothesis [19]. They affirm that behavior would seemingly prevent direct hybridization between *Canis lupus* and *Canis latrans* and that the alleles and haplotypes exchanged were mainly product of genetic bridging through *Canis rufus* and *Canis lycaon*. The latter is another canid considered to be of hybrid origin by von Holdt et al. [13] but not by Rutledge et al. [19].

However, cladogamy between coyotes and wolves may be more common than that Rutledge et al. assumed.

Natural cladogamy in the wild is, indeed, supported by Kays et al. [21] and also by Bohling and Waits [17], who reported a coyote-grey wolf hybrid (identified through collected nuclear DNA from scat) in North Carolina, as well as a dog-grey wolf-coyote-red wolf hybrid, by using the BAPS criterion and a dog-grey wolf-coyote hybrid utilizing the STRUCTURE-conservative criterion, among many other mixed canids. Hailer and Leonard admitted the possibility of the existence of a hybrid zone where *C. rufus*, *C. lupus*, and *C. latrans* had been historically sympatric in the past, with hybridization occurring at a low frequency [16].

This questions both the conclusion of Rutledge et al. and the taxonomic status of *Canis latrans*. It could be considered by a lumpers as a not fully speciated clade, “*Canis lupus latrans*,” depending on the species concept applied and the extant of genetic flow between wolves and coyotes. *Canis rufus*, in turn, could be considered just a lineage of admixed coyotes. This shows again why the term cladogamy will be preferred here instead of hybridization.

Therefore, this work will consider that the hybrid origin of *Canis rufus* is preferable, depending only on the accuracy of the methods of von Holdt et al. Rutledge et al.’s methods may have been different if disregarded the assumptions of strong reproductive isolation of *Canis lupus* and *Canis latrans*.

Jiggins and Mallet argued that, for being an intrinsic consequence of the long process of speciation, the appearance of hybrid zones is natural and therefore lacks reasons to be considered worthless of preservation [22]. Moreover, it may be possible that hybrid zones, instead of being just as worth of preservation as parental species, are populations that deserve special care due to their potential of creating new lineages. They may lead to what has been nominated as hybrid speciation [23]. Hybrid zones may or may not disappear after speciation has been completed. In fact, there seems to be cases in which the maintenance of the hybrid zones is only due to the absence of reproductive isolating mechanisms between two species. This seems to be the case of the hybrids of the Darwin finches *Geospiza fortis*, *G. scandens*, and *G. fuliginosa*, demonstrated by P. R. Grant and B. R. Grant. These hybrids are not fitter than the parental species, being generally a little less fit or just as fit as them [24].

Ridley (page 383) affirms that hybrids generally suffer from reduced fitness specially reflected by sterility in some cases [25]. A morphologically intermediate hybrid in the wild, even if fertile, may be unfit due to the lack of an intermediate ecological niche. The absence of such niche is also not obligate; however, if so, the fixation and evolution of hybrid lineages would never occur. Indeed, a review suggests that hybrid fitness may vary, being lower, equal, or higher (constituting the called hybrid vigor) than parental species [26].

P. R. Grant and B. R. Grant have registered that, though under normal ecological conditions, the hybrid finches are not fitter or a little less fit than the parental species, they became fitter after an ecological stressful event, the El Niño of 1983 [24, 27]. Those hybrids have survived as well as the parental species or even better than these in some cases.

In other cases, the parental species may be so well ecologically established that there is no niche left for a stable hybrid zone. A reproductive success comparison of “pure species” and hybrid males of Antarctic, subantarctic, and New Zealand fur seals reveals that, in this case, the hybrids are less fit than the parental species, which impedes the spread of a hybrid zone, though hybrids are continually produced [28].

There exists, therefore, a report on the appropriate role of cladogamy in evolution: it is a genuine, normal role, which may be beneficial, neutral, or malefic depending on the ecological circumstances. This is not different from genetic mutations arising in gametes.

Whether *Canis rufus* is hybrid or not in origin, it seems to have historically naturally crossed with coyotes as well as the grey wolves have. The formation of hybrid zones is a consequence of noncomplete speciation between two sympatric species, and those hybrids may conquer a niche depending on the ecological conjuncture. The stability of these hybrid zones, other than potentially originating new taxa, may serve as a tool for the parental species evolution, which will be discussed in the next topic.

3. Gene Flow between *Canis rufus*, *C. lupus*, and *C. latrans* and the Potential Evolutionary Importance of Cladogamy

Hailer and Leonard admit that modern hybridization between *C. rufus* and *C. latrans* is a threat to conservation [16]. They assume, based on morphological data and on the statement that no historical data are available, that the hybrid swarm production is magnified today by recent human impacts. They follow Nowak (2002) [29], who rejects the hypothesis that *Canis rufus* is of hybrid origin. In 2011, when von Holdt et al. argued that *Canis rufus* is hybrid in origin [13], they presented results on historical inferred data. It is proposed by von Holdt and coworkers that the red wolf lineage began with crossing events between coyotes and gray wolves between 297 and 431 years ago [13].

However, if assuming, as they have, that anthropogenic ecological change caused the supposed increase of hybridization, then it must be controlled and not hybridization itself. It is intuitive that altering a natural phenomenon might not be the best conservational option.

The coyotes' alleles are already present in *Canis rufus*; there is no need of modern cladogamy events for that. If they suddenly become positive, the cladogamy between *C. rufus* and *C. latrans* would only be beneficial for it and would only speed up the process of allele alteration. If the maintenance of the 75%/25% proportion is actually the most beneficial one, then time, allied to natural selection and gametes with crossed-over chromosomes, would be in charge of fixing it.

In fact, Hedrick et al. demonstrated evidence for high balancing selection in *C. rufus* [30]. Considering inbreeding, the amount of heterozygotes in *Canis rufus* was higher than expected. This may demonstrate how susceptible to natural selection the species is.

As to the coyotes, cladogamy might be useful, since *Canis rufus* is a source of new alleles—the *Canis lupus* ones. It is

actually shown by Hailer and Leonard that a Y-chromosome haplotype typical of *C. lupus* has possibly appeared in a *Canis latrans* population via *Canis rufus* [16]. If it stuck there, disregarding other *C. lupus* genetic traits that may have had also the opportunity of becoming introgressed, it means that it was probably useful; if not, it could, at least, become so in the future. This reveals that hybridization between *Canis latrans* and *Canis rufus* was positive. They also show that coyotes have introgressed grey wolf mtDNA haplotypes as well as grey wolves have introgressed coyote mtDNA. Even so, Hailer and Leonard [16] conclude that the effects of hybridization are smaller in coyote populations due to their larger size. However, Bohling and Waits [17] report that the coyote hybridizes more than expected (with grey wolves, dogs, and red wolves) regarding its population's size, which raises questions on the mechanisms influencing hybridization. Hailer and Leonard's results were interpreted as evidence that density effects, size, and sex bias, together, are not enough to explain the pattern observed of hybridization [16]. This work suggests that the explanation for the asymmetrical pattern of alleles and haplotypes exchanges may be influenced by natural selection.

Anyway, red wolves could be actually seen by biologists as a reservoir lineage of *Canis latrans* and *Canis lupus* genes. In other words, introgression of a lineage on another one (as the one that may have resulted on the origin of the red wolf) may promote evolutionary positive events for both lineages, rather than promoting the extinction of one of them. It is possible that the removal/sterilization of *Canis rufus* × *Canis latrans* individuals has been delaying evolutionary rates of *C. latrans*.

Other cases also suggest the importance of genetic bridges. Edwards et al., in 2011, published a deep investigation on polar bear evolution that provides precious information for evolutionary biology [31]. They reconstructed a phylogeographic model of the dynamics between 242 polar bears and brown bears matrilineages through the past 120,000 years. Their results showed that, punctuated with subtle climatic changes, the two bears experienced some cladogamy events. As a conclusion, they argued that hybridization between them was an efficient mechanism of survival during those stressful ecological changes as the two bears exchanged mtDNA some various times. They did not reach a full understanding of the role of hybridization in evolution but came to the conclusion that hybrid conservation policy may need a revision in order to protect hybrids, as polar bears and brown bears are facing a new cladogamy event due to climatic changes [32]. These events have shown to be important in the past, and the polar bears as we know would not exist today had they not hybridized with brown bears, with the possibility of not even having survived to all the climatic changes in the past. Therefore, hybrid protection today may be an important conservational task especially in the case of Arctic species, against what has been proposed by Kelly et al., in 2010, [32] who stated that hybridization may actually be a threat especially in the arctic region.

Cladogamy has also occurred within our own species. The decoding of the Neanderthal genome and its comparison with the human one has shown that all humans outside the Sub-Saharan Africa share up to 4% more alleles with Neanderthal

than other humans [33]. That is, when *Homo sapiens* left Africa to colonize Eurasia, the colonizers crossed with Neanderthals. Today, even though they are extinct, some of their autapomorphic alleles are present in all descended from those early Eurasian human colonizers, as have been proposed earlier by some researches based on possible fossils of hybrid individuals [34]. Another hominid with which *Homo sapiens* has crossed is the Denisova hominin. Its genome shows that Melanesian and Australian aborigine people have part of their genome descended from this hominin [35]. Considering the concept of “pure species,” only in Sub-Saharan Africa the “pure *Homo sapiens*” is found. It is therefore dangerous to open debate over the conservation status of admixed canids, as a dyslogistic concept of “non-pure” would affect admixed humans as well.

Another genetic bridge was found on the hybrid zone of the crows *Corvus corone corone* and *Corvus corone cornix*, two parapatric subspecies, which were probably allopatric in the last Ice Age [36].

The report of hybridization in the exact place where P. R. Grant and B. R. Grant [24, 27] chose to work on (the Galapagos Islands) may indicate how spread the phenomenon may be when it comes to sympatric close species. The case of the hybrids of *Geospiza fortis*, *G. scandens*, and *G. fuliginosa* presented in the previous topic may show how important it may be. In the same way that cladogamy between *Ursus maritimus* and *Ursus arctos* during climatologic stressful changes has helped their survival [31], cladogamy between Darwin's finches may assure that, after the original ecological conjuncture has been established, the more successful hybrids that have survived may backcross with the parental species—which will then recover. This shows how far more complex the evolution of species is than a model in which species diverge and follow their ecological/evolutionary paths alone. Rather, it seems likely that gene flow between incipient species or between two already diverged species may be an important mechanism through which extinction is prevented. This reveals that, more than natural, the mixed canids are in need of conservation.

4. Natural Processes, Anthropogenic Processes and Need for Intervention

Canis rufus has possibly originated from a cladogamy event [13], and the former recognition of a few subspecies [29] demonstrates that it has existed for long enough to conquer an ecological niche and proceed to diversification. Through historical time, it has been sympatric with its parental species [16] and it has begun backcrossing with coyotes between 297 and 431 years ago [13]. This all would have happened before the European settlement and still the red wolf had not become extinct by introgression. Therefore, it seems very unlikely that hybridization may threaten *Canis rufus*.

Hailer and Leonard emphasized the idea that hybridization leads to species replacement in extreme cases and that observations of that phenomenon have been growing [16]. However, the very first article cited by them is one that focuses on hybridization between a local species and an alien species.

Indeed, this work considers that hybridization is one of the evolutionary mechanisms responsible for genetic variability in populations and demands conservation. However, if it must not be regarded differently from genetic mutations, then perhaps not all the cases of anthropogenic induced hybridization should receive control.

It is out of question the need of maintaining at maximum the integrity of an ecosystem, but, after its alteration, what needs to receive intervention and what does not is another conservation-related subject. For example, if ever *Raphus cucullatus* is cloned, no program for reintroduction to the wild in Maritius should be considered—not before a large enough area is restored and is free from invasive species; otherwise, its fate would most probably be to face a second extinction. In fact, *Oryx leucoryx* is an example of a species that has suffered the risk of facing a second extinction in the wild after its first reintroduction [37].

On the same way, it has never been proposed a conservation program to control the anthropogenically augmented population of *Biston betularia betularia* morpha *carbonaria* after the industrial melanism event. A threatened lineage can only evolve or perish; it cannot stay still. Even though conservationists see that this example of evolution is positive for the moths [38, 39], hybridization between *Canis rufus* and *Canis latrans* is seen as negative based on the argument that it might be anthropogenically magnified [16] or that it may threaten the red wolf integrity. If a *Homo sapiens* who might be up to 4% *Homo neanderthalensis* is not considered worthy of sterilization or elimination, then why should a *Canis rufus* × *Canis latrans* hybrid (roughly 87,5% *Canis latrans* and 12,5% *Canis lupus* genetically) be considered so?

It has been carefully estimated that, given only the dynamics of crossing between red wolves and coyotes, red wolves would fast become extinct by introgression [15]. However, the permanence of coyote hybridization would not provoke changes in the red wolf gene pool—if given the action of natural selection in a suitable environment (original or restored) and given the parallel crossing with *C. lupus* (which was sympatric to the other two, in historical Texas, e.g., [16]). Unless, of course, the selection pressure over hybrids would change for any reason. These reasons could be natural or anthropogenic changes. However, if anthropogenic, should conservationists stop it? In fact, the selection of *Biston betularia betularia* morpha *carbonaria* after the industrial melanism event was, supposedly, anthropogenically induced. Anyway, it was beneficial to the moths. It is equally possible that, all of a sudden, even if due to the anthropogenic alteration of the ambient, it would become rather positive for *Canis rufus* to alter the proportion of *C. latrans*/*C. lupus* alleles than keeping that relation still. The difference between that hypothetical frame and the alteration of the distribution of *carbonaria* morpha alleles in the moths is none. Stating all at once—without deeper investigation (which might be impossible)—that hybridization is necessarily negative is a eugenic position. If it happens with *C. rufus*, it would certainly neither be the first nor the last case of nonpurposeful artificial selection. Another case, which seems to be malefic to diversity, would be the decrease in the size of African elephants' tusks [40]. The poaching—an

anthropogenic factor—has created a selective pressure over smaller tusks, so that today, in some parts of Africa, the majority of bulls have short tusks, despite sexual selection. In a similar way, bighorn sheep bulls in Canada have today shorter horns, due to excessive trophy hunting in the past [41]. Only the elephants with smaller tusks and bighorn sheep with smaller horns would have the highest survival rates. This way, the original allele proportion has changed through time, but it has guaranteed their survival. They have evolved.

There is a reported case of hybrids between a local and an invasive species of salamanders that are fitter than the parental species [42]. It is certainly a threat to biodiversity; however, this may be the only way through which the native species lineage may survive the human impact. The solution to this case would be the removal of the invasive species. In contrast, *Canis rufus* is a lineage that naturally crosses with other canids; therefore, “hybridization” is not what needs to receive control on this case.

The human impact in nature invariably provokes changes in the proportions of alleles’ frequencies in the genomes of wild populations (i.e., nonpurposeful artificial selection). Even though this might change the gene pool and even the general phenotype of those populations, this might be what saves their wild existence in spite of human impacts. The alteration of those adaptations might provoke the extinction of the lineages suffering from that artificial selection. Ideally, the natural pressure should be maintained as near as possible from the original one. If not possible, then the response to the altered pressure—be whatever it is, which includes cladogamy—is what preserves the threatened lineages, and it is not to conservationists to control. What conservationist efforts should focus on is the maximum possible restoration of natural selective pressures.

5. Conclusion

The only anthropogenic threat to the alteration of *C. rufus* gene pool would be ecological alterations creating new selection pressures allied to defalcation of the cladogamy process. In other words, the problem of *C. rufus* crossing with *C. latrans* would be balanced if they could still cross with *C. lupus*. If these three *Canis* had been naturally sympatric and naturally crossing, it is not conservational at all to separate them and forbid them to cross. Hybridization is a process underestimated by modern conservational biology. There are cases, indeed, where introgression may diminish biodiversity in a short term, but natural processes are what they are—natural. Cladogamy is a natural way through which a lineage can evolve or perish, as is any other evolutionary mechanism. Cladogamy seems to play a role no different from mutations when it comes to a lineage in the struggle of evolution versus extinction, as becoming obvious in the cases such as the one of the polar bear.

Therefore, cladogamy is a natural process, a consequence of the complexity of sexual reproduction. Cladogamy is involved in the following:

- (1) birth of new lineages recognizable as new taxa,

- (2) creating profitable genetic bridges between the parental species that can result in increasing fitness of (or even helping the survival of) a parental species,
- (3) natural extinction through introgression with fixation of some beneficial alleles in the new cladogametic clade.

The reproduction between *Canis rufus* and its progenitor species, *Canis lupus* and *Canis latrans*, is not supposed to be stopped. This event arose naturally and may be important for *Canis* evolution in North America and to local ecology, being the red wolf a genetic bridge and occupying its own niche. *Canis rufus* is threatened by its low population size and habitat loss, and conservational measures to save this canid must focus on that.

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