

Hybridization and Hybrid Zones

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Hybridization is the process by which individuals from genetically distinct populations (e.g., species, subspecies) mate and produce at least some viable offspring. In nature, this occurs in areas where two genetically divergent lineages meet and interbreed, regions referred to as “hybrid zones.” Hybridization among animals was traditionally considered a rare and unusual event, but a variety of genetic studies in recent decades have shown that this phenomenon is more common than previously thought (especially between closely related species) and, in fact, has important implications in the diversification and evolutionary history of organisms. On the one hand, hybridization can break down species boundaries, eventually resulting in the loss of pure parental species. On the other, it may become a creative force to increase diversity and lead to the formation of new recombinant lineages. Hybridization may affect the genetic diversity of one or both parental taxa through introgression (i.e., the movement of alleles from one gene pool into another through admixture). The increasing use of molecular genetic and genomic approaches to study hybridization has revitalized the field of speciation research and provided examples of the importance of interspecies gene flow through hybridization during the evolutionary history of several organisms, including humans (Sankararaman et al. 2014).

Natural hybridization among primates has been well documented among cercopithecine monkeys (e.g., baboons and macaques) since the 1970s, with reports of hybridization at intraspecific, interspecific, and even intergeneric levels. The development of genetic and genomic techniques in the twenty-first century allowed genetic confirmation of natural hybridization of a larger number of primate taxa (including

examples from among all multiple primate radiations: lemurs, tarsiers, catarrhines, and platyrrhines) and has produced new awareness of the prevalence of this phenomenon within the order and its importance in primate evolution. In fact, it has been estimated that more than 10 percent of all primate species hybridize (Zinner, Arnold, and Roos 2011).

Historically, studies of primate hybridization relied on the phenotypic identification of hybrids, assuming that individuals with an admixed origin present a mosaic of features that would render them as “intermediate” in morphology or behavior compared to the parental forms. However, this is not necessarily the case (see below). Hybridization has also been detected when discordant phylogenies are found through analyses of multiple genes and gene regions. Similarly, through population genetic analyses, species may be recognized due to the presence of distinct gene pools (i.e., different allele frequencies), but populations in areas of contact may show combined mixtures of alleles due to hybridization. Current studies of hybrid zones strongly rely on genetic analyses, but the integration of morphological, behavioral, and ecological data is also needed to fully understand the mechanisms underlying this process.

Studies of Primate Hybrid Zones

Hybrid zones are geographic regions where two genetically distinct populations coexist and interbreed. They may develop *in situ* through the alteration of allele frequencies in two continuous populations due to environmental differences and as a result of natural selection (i.e., primary hybrid zones) or through the secondary contact of formerly allopatric taxa (i.e., secondary hybrid zones). Most known primate hybrid zones seem to be the result of secondary contact, when two genetically differentiated populations that formerly occupied different geographic regions expand their ranges, encounter each other, and interbreed. The offspring produced

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in the first generation (i.e., F1 individuals) have equal proportions of their genomes from each parental taxon, but after several generations of hybridization and recombination, individuals with different levels of genetic admixture will be produced. Hybridization and subsequent backcrossing with one or both parental forms can create a broad array of genotypes among individuals in the hybrid zone, ranging from those of individuals representative of parental species to individuals with precisely intermediate genotypes (F1 individuals) and individuals whose genomes heavily consist of gene variants coming from one of the parental species (e.g., highly backcrossed individuals or multigenerational hybrids). Generally, all of these animals are considered “hybrids,” although levels of admixture vary widely across individuals. The types of hybrids and their relative proportions in the population of a particular hybrid zone depend on the differences in fitness between parents and hybrids, as well as among the different types of hybrids.

To date, only a handful of natural primate hybrid zones have been studied, and the type and extent of analyses of morphology, behavior, and genetics varies considerably among them. A few primate hybrid zones have been the subject of long-term studies—the baboon hybrid zones in Amboseli National Park, Kenya (e.g., Tung et al. 2012), Awash National Park, Ethiopia (e.g., Bergman, Phillips-Conroy, and Jolly 2008), and the Kafue River Valley, Zambia (e.g., Jolly et al. 2011); the howler monkey Mexican hybrid zone (e.g., Cortés-Ortiz et al. 2007); the guenon hybrid zone in Gombe National Park, Tanzania (e.g., Detwiler 2002)—but most reports of primate hybridization constitute single accounts of the presence of hybrids. A general overview of different topics addressed to study primate hybridization and hybrid zones is presented below.

Morphology of Hybrid Individuals

Hybrids may be morphologically similar to one of the parental species, intermediate to both species, or differ considerably from both parental forms. Differences in pelage coloration patterns are

commonly used to determine the hybrid status of individuals in primate hybrid zones. However, for most primate hybrid zones the extent of morphological variation found among hybrids and whether or not this phenotypic variation is concordant with variation in molecular characters remains unclear (see Ackermann 2010 and references therein). Only a few primate studies have combined genetic and morphological characterizations of hybrids. Results of these studies indicate that although several morphological or morphometric traits seem to have a strong genetic component, it is not always easy to rely solely on morphology to detect instances of hybridization. For example, when comparing a morphological hybrid index with the individual level of genetic admixture for baboons from the Amboseli hybrid zone, Tung et al. (2008) showed that morphology and genotype were highly concordant, but also noted that reliance on morphological features alone sometimes failed to identify individuals with low levels of hybridity (i.e., highly backcrossed animals). Similarly, a study of morphometric variation in the howler monkey hybrid zone in Mexico showed that hybrid individuals with genotypes highly biased towards one of the parental species were indistinguishable phenotypically from purebred individuals, whereas hybrids that were more evenly admixed showed a gamut of phenotypes, sometimes even outside the overall range of variation of the parental species (Kelaita and Cortés-Ortiz 2013), the result of a process known as transgressive segregation. Interestingly, another study of a recent (approximately 25–30 generations old) artificially created hybrid zone between marmoset species (Fuzessy et al. 2014) also found that extreme phenotypes outside the range of parental variation were present in that population. The generation of these extreme phenotypes may have an adaptive value, possibly serving as a source of phenotypic variation on which natural selection can operate.

Although the previous examples provide evidence for a broad range of variation in hybrid morphology in various primate taxa, it is unknown for how long morphological signatures of hybridization can persist or what genetic mechanisms underlie these phenotypic differences. Studies of captive hybrid baboons with known pedigrees by Ackerman (2010 and

references therein) have provided evidence that morphological anomalies associated with hybridization (e.g., supernumerary teeth and cranial sutural anomalies) persist through several generations of backcrossing. Genomic analyses that complement studies of morphological traits in primate hybrids will be crucial to our understanding of the identity and number of genes underlying particular morphological traits, and the genetic processes acting on the phenotype during the interactions of genomes with different levels of divergence.

Behavior in Natural Primate Hybrid Zones

Very few behavioral studies have been conducted in primate hybrid zones. Those addressing behavioral differences between hybrids and parental forms have mostly been conducted on baboons (Bergman et al. 2008; Tung et al. 2012 and references within), and only a few have been published on other taxa (e.g., Ho et al. 2014). The only behavioral studies where the degree of admixture of subjects has been confirmed genetically (the Amboseli and Awash baboon and Mexican howler monkey hybrid zones) show that some behavioral differences among individuals—particularly those related to mating strategies and social structure—are associated with ancestry and may play an important role in determining the dynamics of the hybrid zones. However, flexibility has also been observed, in which social and ecological settings influence the behavior of hybrid individuals. For example, in the baboon population in Amboseli, males' genetic background and level of genetic diversity strongly influence the probability of their establishing consortships (a behavior that strongly impacts their success at siring offspring), and assortative mating of males and females with similar levels of admixture has also been documented. Nonetheless, male dominance rank, which appears to be independent of genetic background, also had a strong effect on males' success at establishing consortships (Tung et al. 2012). For the Mexican howler monkey hybrid zone, Ho et al. (2014) found that the level of genetic admixture seen in females influenced their social behavior in ways consistent with

differences observed in pure populations outside the hybrid zone. Just as female mantled howlers are less affiliative with one another than female black howlers, hybrid females with a genetic background more similar to mantled howlers were less affiliative than those with a genetic background biased towards black howlers. However, in general, group size negatively affected the expression of female affiliative behavior, and the highly fragmented landscape in the hybrid zone seems to increase agonistic behavior in mantled howlers, but not in black howlers. Taken together, the combination of genetic ancestry and social and ecological context within the howler monkey hybrid zone may lead to a differential ability of different types of female hybrids to join groups composed of mantled-like or black-like howler individuals. The extent to which particular behaviors are affected by genetics or by social or ecological setting is unknown. Studies of behavior in hybrid zones, where genetically distinct individuals live in overlapping ecological and social settings, present a unique opportunity to unravel the effects of genetics, social setting, and ecological variables on particular behaviors. Furthermore, to understand the universality of these effects in primates requires comparative studies across hybrid zones of multiple primate taxa.

In summary, the combined study of behavior, ecology, and genetics in primate hybrid zones can provide insights into the dynamics of admixture events and into the interaction of genetic and environmental effects on the expression of behavior. For example, does behavior affect the direction and rate at which admixture occurs? Such studies require systematic long-term data collection on a number of primate hybrid systems and demand that researchers collect data on groups both within and outside hybrid zones using concordant methodologies.

The Evolutionary Consequences of Hybridization

Hybridization may be an ongoing process affecting current taxa, or it may have occurred in the past and be part of the evolutionary history of a modern single taxon. Hybridization can, alternatively, break down species boundaries and

merge formerly separated gene pools, enhance reproductive isolation of the two hybridizing species, increase the diversity found in one or both parental taxa through introgression of genes, or lead to new recombinant lineages that are distinct from parental forms. In fact, there is strong genetic evidence for the hybrid origin of one primate species, the Kipunji (Burrell et al. 2009; see also Zinner, Arnold, and Roos 2011 and references therein).

With the widespread use of genetic (and genomic) markers to infer phylogenetic relationships, it is now recognized that primate hybridization both is more prevalent than initially considered and has had profound consequences on the evolutionary history of a range of primate taxa. Discordant phylogenies are commonly found when analyzing species relationships, especially among closely related species, and often this is attributed to past hybridization events. This is because during hybridization, some parts of the genome of one taxon can move into the genome of the other (i.e., introgression), while other genomic regions never intermix. Thus if some genetic markers used for phylogenetic reconstruction are located in regions of the genome that have been exchanged between taxa, and others come from regions that have not, they can show very different phylogenetic signals. While sometimes confusing our ability to infer the phylogenetic relationship among the taxa in question, these discordant phylogenies can also help inform us about the dynamics that occurred during the period of hybridization. For example, analyses of maternal (e.g., mitochondrial) and paternal (i.e., Y chromosome) markers may produce discordant phylogenies that are the product of unidirectional bias, in which only one sex of each of the parental species contributes to genetic exchange during hybridization. In primates, several cases of past hybridization of Old and New World monkeys, apes, tarsiers, and lemurs have been detected through phylogenetic discordances among genetic markers (e.g., Tosi, Morales, and Melnick 2002; Zinner et al. 2011 and references therein), and such examples also include inferred past instances of hybridization in the human lineage (Sankararaman et al. 2014 and references therein). For example, genomic analyses have provided ample evidence that Neanderthals,

Denisovians, and other unidentified hominins interbred with *Homo sapiens*, likely shaping the ample diversity currently found in living humans (Ackermann, Mackay, and Arnold 2016 and references therein).

The study of modern hybrid zones provides the means by which we can identify the mechanisms that may have influenced the evolutionary history of modern taxa. Hybrid zones usually represent a “bridge” through which divergent genomes exchange part of their genetic material. The amount of genetic introgression that occurs between hybridizing species may depend on their level of divergence prior to establishment of the hybrid zone, as well as on the performance of exchanged loci (genomic regions) against the genetic background of the other species. A neutral gene may be exchanged with no demonstrable effect on fitness; other genes may have detrimental effects when interacting with the genome of another species and thus show little to no introgression; still other genes may provide an adaptive advantage and quickly spread through the population of the other species. The shuffling of two originally divergent genomes in hybrid zones through hybridization, backcrossing, and recombination allows selection to act on novel combinations of genes, enabling the mixture of some genomic regions while preventing other regions from intermixing. This process implies that genomes of hybridizing species are semipermeable to introgression, with permeability depending on the characteristics of different genomic regions. Understanding the genetic patterns of admixture in a number of natural primate hybrid zones will allow us to identify genomic regions associated with adaptive traits and those that play an important role in the reproductive isolation of taxa. Current research efforts in several hybrid zones (baboons, howler monkeys, guenons, marmosets, and tarsiers) are allowing us to identify the factors influencing hybridization, and the genomic regions underlying adaptive and isolating mechanisms in primates.

SEE ALSO: Amboseli; Climate Change and Primate Evolution; Evolution of the Hominoidea; Jolly, Cliff; Next-Generation Sequencing; Phenotypic Plasticity; Phylogenetic Inference; Phylogeny and Social Organization; Sympatry

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