

S18-2 Phylogenetic studies of plumage evolution and speciation in New World orioles (*Icterus*)

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Abstract Detailed molecular phylogenies of closely related species provide an unprecedented opportunity to study the relationship between plumage evolution and speciation. Through reconstruction of ancestral character states, phylogenies enable us to separate convergence from similarity due to shared ancestry, and gains of plumage ornaments from losses. Molecular phylogenies also provide information for inferring the details of speciation: which species split, when the splits occurred, and even whether one species is nested genetically within another. We have used these approaches in a series of studies on plumage evolution and speciation in New World orioles (*Icterus*). A genus-wide study of 44 individual plumage ornaments revealed evidence of repeated convergence and reversal. Two overall plumage types, moreover, have evolved independently in the three clades of orioles. We then conducted a detailed study focused on the “northern oriole” group. Multiple samples from throughout the ranges of the Baltimore oriole (*Icterus galbula*; eastern North America) and the black-backed oriole (*Icterus abeillei*; central Mexico) confirm that these two species are each other’s closest relatives, and that they probably split very recently. They differ from each other in many plumage traits, providing a dramatic example of rapid divergence in signal characters. In orioles, it seems likely that much of this plumage divergence occurred in allopatry. Nevertheless, lineages that have evolved plumage differences in allopatry may be less likely to remerge upon secondary contact. Such a process could account for published correlations between signal divergence and species richness.

Key words Ancestral state reconstruction, *Icterus*, Phylogeny, Plumage evolution, Speciation

1 Introduction

In recent years, molecular phylogenies based on mitochondrial DNA sequences have provided an unprecedented source of information for studying plumage evolution and speciation. Prior to this technology, phylogenies for closely related bird species were often not even attempted. For example, before our studies of the New World orioles, only one study examined the entire genus of 25+ species, and then without attempting a comprehensive phylogeny (Beecher, 1950). Although closely related species of birds often have well-marked morphological differences, these differences may involve only one or two plumage characters. Thus there are generally too few informative characters to allow construction of well-resolved phylogenies for close relatives (Omland and Lanyon, 2000). Similarly, earlier molecular methods such as DNA-DNA hybridization, allozyme electrophoresis, and nuclear coding sequences are generally not sensitive enough to position closely related species. Early phylogenies based on mitochondrial DNA restriction sites and sequences (e.g., Kessler and Avise, 1984; Zink and Avise, 1990) opened up new possibilities for studying species limits, speciation, and rapidly evolving characters such as plumage and song.

Mitochondrial DNA (mtDNA) sequences continue to provide the best estimates of phylogenies for closely re-

lated species because nuclear DNA sequences have several serious limitations. First, nuclear autosomal DNA has a larger effective population size than mtDNA, and is therefore more likely to share ancestral polymorphisms between species (Palumbi et al., 2001). Secondly, nuclear DNA does not accumulate mutations as rapidly as mtDNA, and is harder to work with than mtDNA, both in the laboratory and in the analysis stage (Avise, 2000).

Having well-resolved species-level phylogenies from mtDNA studies provides two main advantages for our understanding of plumage evolution and speciation. First, we can use phylogenies to reconstruct ancestral character states. By scoring the characteristics of present day species, we can infer the likely evolutionary changes that have taken place in the past through the principle of parsimony or maximum likelihood (e.g., Cunningham et al., 1998). For example, Fig. 1 shows a hypothetical phylogeny of two sister clades of four species each. The presence or absence of an elaborate plumage ornament is reconstructed on the phylogeny using simple parsimony (see Omland, 1997).

This reconstruction enables us to infer two key aspects of signal evolution. First of all, it provides evidence of convergent evolution of the ornament: it evolved once in species B in the left clade, and it also evolved early in the history of the right clade. Secondly, the phylogeny enables us to distinguish gains from losses. For example, if A and B

are sister species, either species A lost the ornament or species B gained it. Knowing that species C and D are unornamented sister lineages enables us to infer that there was a recent gain in species B. Similarly, parsimony reconstructs a recent loss of the feather ornament in species Y, which is nested within a group of three species that all have it.

This example highlights another advantage of phylogenetic information: phylogenies can be used to pinpoint the best species for behavioral studies. For example, species B is much better than species W, X or Z in the right clade for investigating why species gain ornamentation. The right clade may well have evolved elaborate ornamentation in the common ancestor of that clade but a long time ago. A behavioral ecologist with no knowledge of the phylogeny would have a 75% chance of noticing and studying the ornament in species W, X or Z, holding him/her back from inferring the selective forces that led to its origin. Much, moreover, can be learned by studying species Y, which has recently lost the ornament. Admittedly, many explicit and implicit assumptions need to be acknowledged in such ancestral state reconstructions (Omland, 1997; Cunningham et al., 1998; Omland, 1999); yet when applied across many characters (Omland and Lanyon, 2000) or across multiple groups, ancestral reconstructions can provide a sound basis for evolutionary inference.

The other advantage of molecular phylogenies in studies of speciation and signal evolution is their provision of sound data on speciation itself. A phylogeny can tell us which taxa have speciated most recently. For example, without a phylogeny, we might assume that two parapatric taxa are each other's closest relatives, and make assumptions about how the two taxa split. This problem surfaced in the "northern oriole" group (Omland et al., 1999), as detailed below. Genetic distances among taxa can also be used to infer when two species split. Using molecular clocks to date evolutionary events may be controversial, and indeed many assumptions go into such calculations which gives rise to

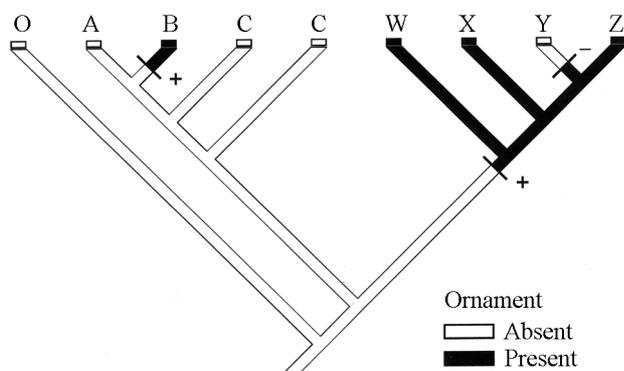


Fig. 1 Model phylogeny of nine species showing the most parsimonious reconstruction of changes in a hypothetical plumage ornament (e.g., colored wing patch or head crest) The ancestral state reconstruction suggests two convergent gains of the elaborate ornament, and one subsequent loss.

skepticism (Hillis et al., 1996; Fleischer et al., 1998). Even so, much can be learned about speciation by comparing relative levels of divergence. A well-known example of how molecular clocks have been applied to studies of bird speciation is the work of Klicka and Zink (1997), who showed that levels of divergence between putative sister species in the eastern and western US were much deeper than would be expected if speciation was caused by the most recent cycles of late-Pleistocene glaciation (cf. Avise and Walker, 1998; Arbogast and Slowinski, 1998).

Molecular data can also provide evidence of the genetic nesting of one species within another (e.g., paraphyletic species). Such findings provide a unique opportunity to study speciation and character evolution, especially because it enables reconstruction of character changes and the timing of speciation with more precision than allowed by other means. In birds, there are several cases of likely paraphyly resulting from recent speciation, involving, among others, mallards (*Anas platyrhynchos*) and the American black ducks (*Anas rubripes*) (Avise et al., 1990; Omland, 1997), though this example could also reflect hybridization (Broadsky et al., 1988).

Phylogenies are, in addition, particularly useful in research that employs the comparative method (sensu Harvey and Pagel, 1991). This paper will not present results based on the comparative method, but the discussion will address several studies that have used it to evaluate correlations between rates of speciation and plumage coloration. Rather, we simply review results of our research into speciation and plumage evolution in *Icterus*.

2 Oriole plumage reconstruction and speciation

2.1 Phylogenetic reconstruction of plumage patterns

Sexually selected characters such as plumage coloration have long been assumed to evolve rapidly and be subject to high levels of convergence (Omland and Lanyon, 2000). However, no empirical studies of all plumage traits had been conducted using a well-resolved independent phylogeny. mtDNA sequences were obtained for 45 taxa of New World orioles: all 25 recognized species and 20 additional subspecies from the genus *Icterus* (Omland et al., 1999). We obtained over 2000 base pairs of sequence from the cytochrome *b* and ND2 genes. All methods of analysis and data combinations identified three main clades, designated A, B and C (Fig. 2). Over half of the nodes on the tree received 95% bootstrap support or more. This well-resolved tree provided the phylogenetic framework for reconstructing plumage evolution (sensu Lanyon, 1993). We studied two aspects of male plumage coloration: 1) individual feather areas, and 2) overall plumage patterns.

Using museum skins, we scored all the individual feather areas that varied among oriole species (Omland and Lanyon, 2000). We found 44 plumage areas that varied, and scored whether these areas were white, black or pigmented

with carotenoid (yellow, orange, chestnut, etc). The 44 plumage patches were then mapped on to the molecular phylogeny to reconstruct ancestral plumage changes. Forty two of the 44 plumage characters showed at least some convergence or reversal (homoplasy) (Omland and Lanyon, 2000); the two characters that did not show any homoplasy involved character states that simply united different subspecies of the same species. Most plumage characters appeared independently many times on the phylogenetic reconstruction (i.e., high levels of homoplasy). For example, Fig. 2 incorporates reconstruction of crown coloration, suggesting independent gains of colored crown feathers (e.g., orange or yellow) at least six times, and at least one subsequent reversal to black. Other less parsimonious reconstructions are possible, but clearly individual feather areas in orioles are evolving rapidly, and with high levels of convergence and reversal.

Reconstruction of overall patterns also revealed much evidence of convergence and reversal (Omland and Lanyon, 2000). We identified two main plumage types that had evolved multiple times within the genus *Icterus*. Species with the “Baltimore” plumage type have completely black heads, and consistent white edging in the secondary coverts and flight feathers. Species with the “Altamira” plum-

age type have colored heads and crowns, but black foreheads and necks, and a distinct white spot on the outer primaries. These two plumage types represent extremes in a continuum of plumage convergence values (Omland and Lanyon, 2000: Fig. 8), involving species that show greater than 8% sequence divergence and range from only 3 to as many as 37 differences in plumage. Three species that show the “Baltimore” type are found in different parts of two clades: Baltimore oriole (*I. galbula*) and Scott’s oriole (*I. parisorum*) in clade C, and orchard oriole (*I. spurius*) in clade A. Species with the “Altamira” type are found in all three clades: clade A, hooded oriole (*I. cucullatus*), clade B, spot-breasted oriole (*I. pectoralis*), and clade C, Altamira oriole (*I. gularis*) (Fig. 2).

The occurrence of both plumage types throughout the oriole tree strongly suggests convergence, but this pattern could also occur if the mtDNA phylogeny is misleading. Sequences from a nuclear intron (ODC; Friesen et al., 1999) from 10 oriole species confirm the basic structure of the mitochondrial tree, and reveal the same three main clades (E. S. Allen and K. E. Omland, unpublished data). They also verify that species within each of the two plumage types are not each others’ closest relatives, thus providing strong support for convergence and reversal in producing the two

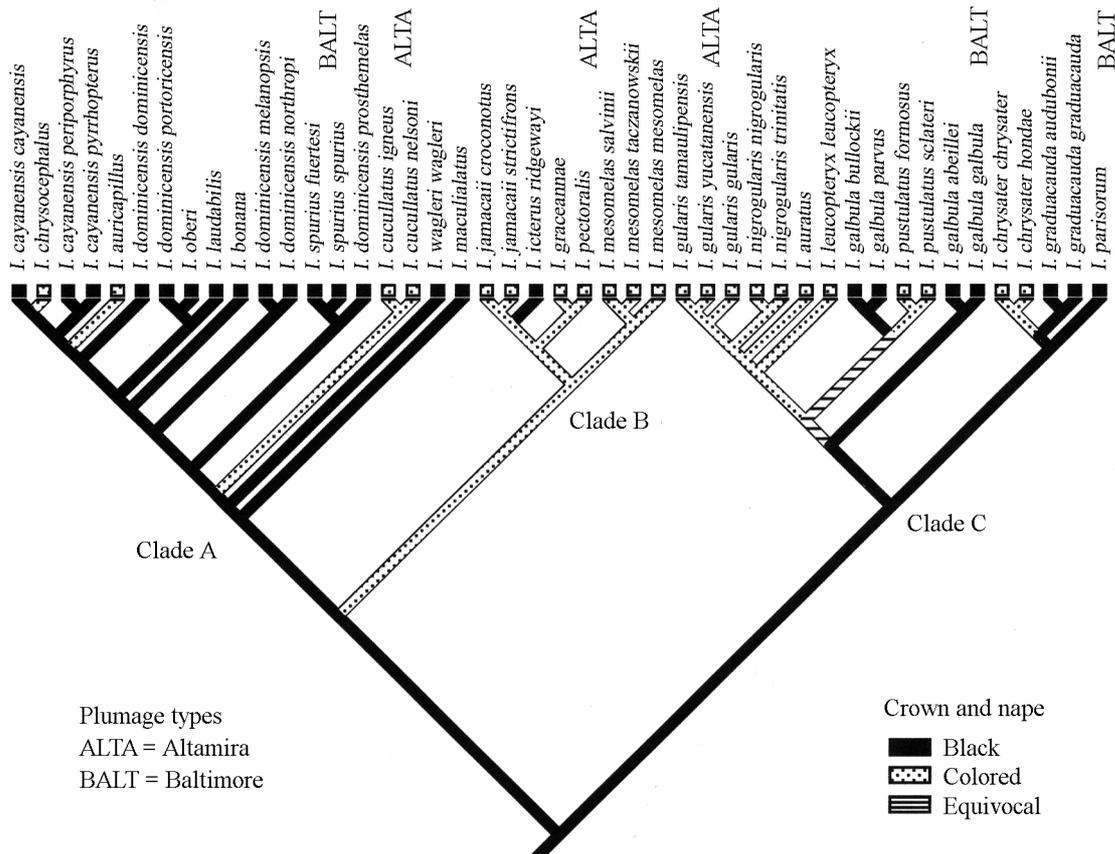


Fig. 2 Ancestral state reconstruction of crown and nape pigmentation on to the oriole mtDNA phylogeny (from Omland et al., 1999: Fig. 6)

“Colored” refers to orange or yellow coloration likely to come from carotenoid pigments. Species that exemplify the two overall plumage types are indicated above the taxon names.

main plumage types.

Our phylogenetic studies of both individual areas and overall patterns of plumage provide a much clearer picture of plumage evolution. Plumage characters are indeed changing very rapidly, probably due to sexual selection. However, the repeated convergence, reversal, and high levels of homoplasy that we found are generally not predicted by models of sexual selection (Andersson, 1994; cf. Ryan et al., 1990). Similarly, convergence would not be predicted if plumage divergence was strongly correlated with speciation. If plumage plays a major role in species recognition, then there is no reason why unrelated species of *Icterus* should be expected to evolve similar plumage areas or overall patterns. Rather, it seems much more likely that genetic or developmental processes have constrained the numbers of colors and patterns in New World orioles (Omland and Lanyon, 2000). Individual plumage patches may be changing rapidly but only according to a restricted set of character states. Convergence in overall pattern, moreover, may result from a few genes turning modular plumage elements on and off.

Price and Pavelka (1996) studied plumage patterns in Old World warblers, and also suggested the importance of developmental constraints. Such constraints may operate within many other genera that seem to have an overall plumage template with variations on that theme (e.g., Old World orioles, cardueline finches, Australasian sericornithine warblers). In contrast, other groups of birds seem much more free to vary (e.g., *Anas* ducks, birds of paradise), with nearly every species evolving novel patterns and autapomorphic ornaments. Eventually we will need genomics and other approaches to understand the genetic and developmental control of plumage coloration in birds (e.g., Theron et al., 2001). As a first step, we are using spectrophotometry and other methods to reconstruct changes in pigment types and better understand the mechanistic basis of plumage color and pattern in orioles. Some oriole species, for example, have colored patches that may not be carotenoid (C. Hofmann and K. E. Omland, unpublished data).

2.2 Speciation in the northern oriole group

The “northern oriole” group has served as the focus for more detailed studies of speciation and plumage evolution. Three taxa with distinct plumage patterns had previously been combined in one species, “northern oriole”, because of hybridization (reviewed in Rising and Flood, 1998). The eastern Baltimore oriole (*I. galbula*) has an extensive hybrid zone with the western Bullock’s oriole (*I. bullockii*) in the midwestern US. The black-backed oriole (*I. abeillei*) from Mexico was also lumped into this group because it also hybridized with Bullock’s in northern Mexico. No previous studies had suggested, however, that other Mexican species such as the streak-backed oriole (*I. pustulatus*) might be included in this species group as well.

Our mtDNA phylogeny of the whole genus revealed some surprising relationships among these species (Fig. 2). Bullock’s oriole is not at all close to the Baltimore oriole —

the two are over 4% divergent in mtDNA coding sequence. The only monophyletic group that unites these two species also includes six other species from Mexico, South America and the Caribbean (Omland et al., 1999). The most surprising outcome was the sister relationship between black-backed oriole and Baltimore orioles. The two individuals sequenced were extremely closely related — approximately 0.5% for the combined cytochrome *b* and ND2 sequence.

Because Baltimore and black-backed orioles are so closely related, they provide an unusual opportunity to investigate when, where and how speciation may have occurred. We obtained samples of both taxa from throughout their respective breeding ranges in North America and Mexico, and sequenced cytochrome *b* and the control region. This extensive sampling revealed extremely small levels of divergence between the two taxa: there is only a single base pair substitution in cytochrome *b* (from over 900 bp sequenced) that separates the most closely related individuals of the two species (B. Kondo and K. E. Omland, unpublished). These two species provide the most dramatic example of rapid plumage divergence in *Icterus*. Baltimore and black-backed males differ in 17 individual plumage areas, and have quite different overall patterns (Omland and Lanyon, 2000), yet are about as closely related as any two oriole species can be.

2.3 Reconstructing dichromatism and delayed plumage maturation in *Icterus*

We are also using the phylogeny to reconstruct the history of sexual dichromatism and delayed plumage maturation in the genus. Rigorous scoring of female and immature plumages requires more subtle methods, including spectrophotometry. Some general trends are already emerging. Most tropical oriole species are sexually monochromatic, both males and females having contrasting and elaborate black, white and carotenoid colored patterns. It seems likely that many lineages have colonized temperate habitats through long-distance migration, and that these species have lost bright female coloration independently (K. E. Omland, unpublished data). It also seems likely that delayed plumage maturation is ancestral for the genus *Icterus*, and that a few lineages may have lost it. Studying the loss of delayed plumage maturation in these species may provide unique insights into the evolution of this paradoxical life history characteristic.

3 Discussion

New World orioles have proven to be an excellent model group for phylogenetic studies of plumage evolution and speciation. Our mtDNA phylogeny has provided a firm framework for these studies, showing that individual feather areas and overall plumage patterns are evolving rapidly and convergently. Mitochondrial data are also informing us about speciation in *Icterus*, especially in the “northern oriole” group. Baltimore and black-backed orioles have speciated very recently, and provide a well-documented

example of just how rapidly bird plumage coloration can evolve. But what role has speciation played in plumage divergence; and conversely, how has plumage divergence helped drive speciation?

During the early years of the biological species concept, many papers addressed the possible role of bird plumage coloration in species recognition (e.g., Sibley, 1957; Mayr, 1963). However, during the 1980s and 1990s this issue was largely neglected, as studies focused on the role of elaborate plumage in intra-specific mate choice (reviewed in Andersson, 1994). More recently several comparative studies have documented a correlation between various indices of plumage coloration and species richness (Barraclough et al., 1995; Owens et al., 1999; Panhuis et al., 2001). Many of these studies used dichromatism as an index of plumage coloration (e.g., Barraclough et al., 1995; Owens et al., 1999).

Yet such an index needs to be used with caution. Dichromatism may work well in groups in which many species are cryptic and monomorphic, and the most elaborately ornamented species strongly dichromatic, such as the species of *Anas* (Omland, 1997). In others, however, it may work poorly, particularly those such as the New World orioles with bright monomorphic species (e.g., Trail, 1990). Many oriole species with dramatically contrasting plumage colors are sexually monochromatic, such as the Altamira oriole (*I. gularis*). As a result, orioles would probably have a fairly low index score despite the fact that they are the most speciose genus in the Icteridae. Therefore, there is a conservative bias in the methodology of the index, which would not account for the significant correlations sometimes documented.

Early studies that pointed out a correspondence between plumage ornamentation and species richness often suggested that this relationship was driven by the need for species recognition, and invoked reproductive character displacement (e.g., Sibley, 1957). Slight differences that had arisen in allopatry would be exaggerated through reinforcement of isolating mechanisms in sympatry, thus contributing to the tremendous plumage diversity, for example, in prairie regions where many *Anas* duck species breed sympatrically (Sibley, 1957; Mayr, 1963). Under this scenario, reinforcement drives the evolution of plumage diversity. However, cases of reproductive character displacement in birds are not well established (cf. Saetre et al., 1997).

Rather than character displacement, it seems likely that plumage differences could evolve entirely by sexual selection in allopatric populations. The extent of these differences could then play a prominent role in determining whether such forms would remerge or not upon secondary contact. Here plumage diversity helps drive speciation, rather than the reverse. New World orioles provide several case studies for considering the options involved. As discussed above, Baltimore and Bullock's orioles are over 4% different in mtDNA sequences, and differ by sixteen discrete plumage differences. Although the two species form

an extensive hybrid zone, recent research indicates that the zone is stable and quite ancient (Allen, 2002). Thus the two species show no evidence of merging, and plumage preferences may play a role in keeping the species distinct (reviewed in Allen, 2002).

In contrast, we have documented two mitochondrial clades in the Common Raven (*Corvus corax*) that also differ by about 4% in mtDNA sequence (Omland et al., 2000). Unlike orioles, however, these birds have no plumage differences, nor any other phenotypic characters that we know of, which would enable them to distinguish these two cryptic clades. In this case, we have evidence that the "California Clade" and "Holarctic Clade" exchange genes frequently throughout the west and may be reemerging (unpublished data). The contrast between orioles and ravens illustrates how it is still possible to find correlations between speciation and plumage coloration (e.g., Barraclough et al., 1995; Owens et al., 1999) even in the absence of reproductive character displacement (also see Price, 1998; Price, this symposium).

It seems likely that sexual selection in allopatry may indeed drive plumage divergence in *Icterus*, and that speciation is driven largely by geographic isolation. For example, the Jamaican oriole (*I. leucopteryx*) is largely confined to the island of Jamaica, where no other orioles are found. Nevertheless, this species has a highly distinctive appearance, and differs from other oriole species in at least seven plumage areas (Omland and Lanyon, 2000). In this and other island orioles, there is no evidence that isolated species lose their plumage differences, nor that continental species sympatric with other oriole species are more divergent in appearance, cf. *Anas* ducks (cf., Sibley, 1957; Omland, 1997). In fact, several similar-looking species with the Altamira-type pattern are sympatric throughout much of their ranges in Mexico and Central America (e.g., Altamira oriole and hooded oriole).

Nevertheless, much more work is needed to clarify the role of plumage in species recognition and reproductive isolation. Furthermore, research needs to focus on whether and how speciation drives plumage divergence, especially when considered in combination with other selective forces. There are several mechanisms that effect evolution of elaborate plumage ornamentation in birds, and there are studies that support each of them: 1) sexual selection by female choice, which has been documented in a large number of bird species (Andersson, 1982; reviewed in Andersson, 1994), including orchard orioles (Enstrom, 1993); 2) sexual selection for status signaling through male-male aggressive competition, which has never seriously been doubted, although the number of careful studies that document it is surprisingly small (e.g., Peek, 1972; Roskraft and Rohwer, 1987; Sorenson and Derrickson, 1994); and 3) the speciation process itself, which has also been supported by a few studies (Sibley, 1957), although there is really only one well-documented case of reproductive character displacement (Saetre et al., 1997). Predator avoidance and other processes

may also play a role (Dumbacher et al., 1992; Götmark, 1992).

Studies are needed that consider the continuum of mate choice decisions, from relative choices between otherwise acceptable conspecifics to threshold choices against unacceptable conspecifics, and choices that include individuals of other populations, races, or species (see Ryan, 1990). All such studies should be careful to emphasize individual fitness; there are cases when choosing to mate with heterospecifics may make the best of a bad situation (e.g., Nuechterlein and Buitron, 1998; Veen et al., 2001), or may actually lead to increased offspring fitness (Grant and Grant, 1996). Ultimately it will be valuable to know for at least some individual species, what roles female choice, male-male aggression, species recognition, and other processes have had in driving and maintaining the evolution of plumage and other signals. Similarly, it will be helpful to know the percentage of birds in which female choice, male-male aggression or species recognition has played the dominant role, and whether different mechanisms prevail over one another and in what circumstances. These are ambitious and long range goals, but now that there is good evidence for each of the mechanisms, more knowledge of their relative importance is needed, and of the interactions between them.

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