Phylogenetic approach to the evolution of color term systems

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The naming of colors has long been a topic of interest in the study of human culture and cognition. Color term research has asked diverse questions about thought and communication, but no previous research has used an evolutionary framework. We show that there is broad support for the most influential theory of color term development (most strongly represented by Berlin and Kay [Berlin B, Kay P (1969) (Univ of California Press, Berkeley, CA)]); however, we find extensive evidence for the loss (as well as gain) of color terms. We find alternative trajectories of color term evolution beyond those considered in the standard theories. These results not only refine our knowledge of how humans lexicalize the color space and how the systems change over time; they illustrate the promise of phylogenetic methods within the domain of cognitive science, and they show how language change interacts with human perception.

linguistics | color | cognitive science | evolution | Australian languages

The naming of colors has long been a topic of interest in the study of human culture and cognition. It is a key case study for the link between perception, language, and the categorization of the natural world (1–4). The assumptions central to these lines of research on color naming are often linked, whether implicitly or explicitly, with the ways in which color term systems are believed to evolve. One of the most noteworthy scholarly works on color terms, both in terms of its impact on subsequent research and its clear and explicit evolutionary hypotheses, is the classification system proposed by Berlin and Kay (5) and refined in subsequent works (6–8). However, despite the very clear hypothesis in this literature that the attested range of color-naming systems in language results from evolution along highly constrained pathways, very little has been done to test these claims. Here, we directly examine the evolutionary hypotheses associated with this research tradition: principally, that as color term systems evolve languages gain but never lose basic color terms; and that the order in which color terms are added to a language's lexicon is fixed. This approach capitalizes on the different patterns we should find in the presence of strong, universal cognitive constraints on color evolution, compared with those that might result from a more relativistic view, in which every language's color term system development follows a unique path. We use Bayesian phylogenetic methods, which allow us to probabilistically reconstruct ancestral inventories and evaluate claims regarding the order in which color terms enter (and leave) the lexicon. We apply these techniques to Australia's Pama-Nyungan language family.

The Color Research Landscape

Universal Patterns in Color Naming. Berlin and Kay's 1969 influential study (5) first established the notion of a universal, cross-linguistic typology of color term systems and ascribed the limited range of systems attested in their surveys to a strict developmental pathway. The model outlined in Berlin and Kay (5) and subsequent work (6–10) makes two evolutionary claims. First, the progression through the stages of color system development is hypothesized to be unidirectional. That is,

languages gain basic color terms, but they do not lose them. Second, the order in which colors are added to a system is largely fixed.

The Berlin and Kay survey of color terms explicitly tested cross-linguistic variation in color naming, focusing scrutiny on earlier scholars' treatment of color as a canonical example of linguistic relativity (3, 9). In direct contrast to relativistic views, Berlin and Kay found that languages have no more than 11 basic color terms, and that the systems used to organize these colors occupy only a small portion of the potential design space. They found such cross-linguistic agreement in the focal points of these color categories as further evidence for universals in color semantics. Furthermore, the seven color systems they identified were hypothesized to represent natural evolutionary stages.

Berlin and Kay's basic findings have been largely affirmed by the much larger cross-linguistic sample in the World Color Survey (WCS) (8). Importantly, the 11 basic color foci of Berlin and Kay were revised to a set of six basic color foci [the lightness categories *black* and *white*, plus the Hering primary colors *red*, *blue*, *yellow*, and *green* (11)]. These foci are consistent with highly clustered "best examples" of basic colors from the WCS (12).

How Color Systems Evolve. Theories of color system evolution have themselves changed over the last several decades, as the empirical data and diversity of perspectives involved in this area of research have grown. The evolutionary process outlined in Berlin and Kay (5) comprises seven distinct stages. The most basic system involves a two-category system, with terms centered on the *black* and *white* foci. The second stage adds a color associated with the focal category *red*, followed by either *yellow* or *green* in stage III. In stage IV, both *yellow* and *green* are present, as well as *black*, *white*, and *red*. Stage V adds *blue*, followed by *brown* in stage VI. The final stage involves the addition of *pink*, *purple*, *orange*, and/or *gray*.

Significance

A major question in the study of both anthropology and cognitive science is why the world's languages show recurrent similarities in color naming. Here we examine this inherently evolutionary question–the evolution of color systems in language–using phylogenetic methods. We track the evolution of color terms across a large language tree in order to trace the history of the systems. We provide further validation of phylogenetic approaches to culture, and provide an explicit history of color terms across a large language sample, the Pama-Nyungan languages of Australia. Our work is of relevance to anthropologists, psychologists, and linguists.

This core evolutionary model—unidirectional progression through color system development in a fixed order—is maintained in the revised evolutionary model presented in subsequent work (7, 8), which additionally proposes an alternative pathway through stages III and IV. Fig. 1 gives streamlined version of this model, which, like our data, is not explicit about which foci may be combined in early-stage composite categories. The row labeled A represents Kay and Maffi's "main line" of color term evolution, which accounts for 83% of the languages in the WCS.

Once a language has terms for colors, we would expect them to change over time. Major types of change in vocabulary include semantic shift, where a word extends or contracts its meaning, or is used metaphorically (13). There is no a priori expectation from language change that colors would change as a system; although we do sometimes find words changing in parallel (14), words usually change independently. We assume that cognitive constraints play a role in language change in this domain, while still allowing for normal processes of sound change, semantic shift, and lexical replacement to occur in individual color terms.

Pama-Nyungan Color Systems. The study of color system evolution in Australian languages represents a unique opportunity to evaluate claims central to the debate regarding color systems. Pama-Nyungan is a large language family that extends across approximately 90% of the Australian mainland. The internal composition of this family has been studied using both traditional (15) and phylogenetic comparative methods (16). The diversity of color-naming systems used by speakers of Pama-Nyungan languages make it an ideal case for examining the evolution of color terms. The languages range through all five basic evolutionary stages of the WCS model. This is in contrast to other large families such as Indo-European and Austronesian where languages tend to cluster in WCS stage VI, making them unsuitable for recovering evolutionary trajectories using phylogenetics.

Analysis

Color Term Data. The data for this study consist of basic color terms from 189 Pama-Nyungan languages in the Chirila lexical database (17). The basic color terms were identified based on the association of a form with at least one English translation included in the set of six basic WCS color terms, plus *brown*, the most frequent secondary color term in our sample.

Data from this sample were coded as a set of seven binary characters, each representing a color category. For each language, the character state (0 or 1) represents the presence or absence of a term representing a particular color category in that language's lexicon. (See especially Figs. S1 and S2 and Table S1.)
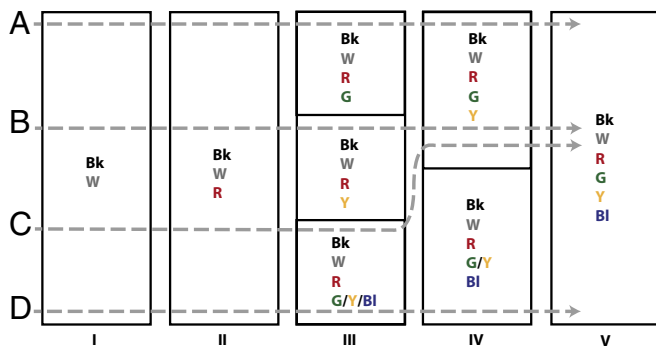

Fig. 1. Evolutionary pathways of color term systems, after WCS.

Pama-Nyungan Tree Sample. We represent the Pama-Nyungan language phylogeny using a sample of 700 trees (see Figs. S1 and S2). The trees were subsampled from a Markov chain used to derive a consensus tree summarizing relationships among Pama-Nyungan languages. The tree was compiled using basic vocabulary data (16, 18). The main clades identified in historical work on Pama-Nyungan are all recovered with high posterior probability, as are many other clades; however, some of the primary branches high in the tree receive equivocal support. We track reconstructions on nodes that have a high posterior probability (that is, that appear frequently in the tree sample), thus avoiding the problem that node reconstruction probabilities can only ever be as high as the probability of the node itself (19).

Bayesian Phylogenetic Methods. To evaluate the basic evolutionary claims of the WCS theory, we use a Bayesian phylogenetic method for the study of trait evolution, implemented with the BayesTraits software package (19). These methods have previously been used in numerous studies of linguistic and cultural evolution (20–23). Modeling the evolution of cultural traits using phylogenetic comparative methods developed for biological processes is not entirely uncontroversial (24); however, arguments that these approaches are invalidated by differences in the transmission of cultural and biological material have been discussed thoroughly and largely refuted (25, 26).

The analyses presented here focus on two basic hypotheses, made explicit by Kay and Maffi (3, 7) and described above:

i) That "languages are frequently observed to gain basic color terms ..." but "languages are infrequently or never observed to lose basic color terms."
ii) That languages "gain basic color terms in a partially fixed order," which proceeds one term at a time.

To test the first of these hypotheses, we use Markov chain Monte Carlo (MCMC) comparative methods to estimate the likelihood of alternative models, given our trees and data. By computing the Bayes factor (BF) support for models that disprefer or disallow the loss of color terms compared with models that allow both gains or losses of colors (by means of their marginal likelihoods), we can evaluate whether Pama-Nyungan color system evolution is consistent with the principle that languages gain color terms but do not lose them (Figs. S3 and S4).

We examine hypothesized orderings of color term gain by applying reversible jump MCMC (RJMCMC) (22, 27) analyses to data for pairs of colors, comparing dependent and independent models of trait evolution. RJMCMC moves between models with different numbers of parameters as it searches the space of trees and transition rates, sampling models in proportion to their posterior probabilities. By representing pairs of binary traits as a single character with four possible states (00, 01, 10, 11), these analyses characterize dependencies in trait evolution in terms of eight parameters, which represent transitions between these states. Dependent RJMCMC analyses sample across models that allow separate rates for the gain or loss of each trait in the presence or absence of the other; independent analyses have separate gain and loss rates for each trait that do not depend on the other trait's state. The posterior sample of models generated by these analyses can be used to examine the support for individual parameters that represent ordered gains or losses of colors. We are thus able to assess the evidence for dependent evolution between individual color terms and to test hypotheses about the relative order in which colors are added.

Finally, we use MCMC analysis to examine the posterior probabilities for reconstructing each color to selected ancestral nodes. For ancestral state reconstructions, we implement a MCMC analysis that infers a single rate for gain transitions and a single rate for loss transitions across all seven color system characters.

This approach treats the color lexicon as a unified system as it estimates the likely ancestral color terms.

Results and Discussion

Gain and Loss of Colors. The marginal likelihoods of nested models can be used to evaluate the support for a dependent hypothesis (in this case, the hypotheses that color terms are gained but never lost), compared with a null hypothesis (here, that no such constraints act on color term systems). This is done by BF evaluation, which compares the probability of the observed data under two hypotheses represented by these nested models. Here, we use the log BFs guidelines (29), where $2logBF_{12} = 2(logL(H_1) - logL(H_2))$, with H_1 and H_2 representing the alternate and null hypotheses, respectively.

We test an unrestricted model that allows both the rates associated with color term gain and loss to vary freely. The hypothesis that color terms can be gained, but never (or almost never) lost, is represented by two models. The first sets the rate parameter for color term loss to zero. The second sets different prior distributions for each of the two rate parameters. This initializes the analysis with a bias toward gains of color terms, compared with losses, but allows for color term loss. The opposite patterns are also tested for models that are biased toward color term loss. A final alternative model restricts the rate parameters for color term gain and loss to be equal, creating a single rate model under which neither gain nor loss is prohibited and both of these processes are assumed to be equally likely.

Models for which the rate parameter for color term gain or the rate parameter for color term loss is set to zero fail to converge. The incompatibility with our data of models that implement exceptionless trends of gain or loss of color categories provides evidence against a strong interpretation of the Kay and Maffi (7) model. An evolutionary explanation for color term systems must allow for at least some color term loss.

Table 1 reports the results for analyses that do converge. Two-parameter analyses all result in similar likelihoods because the gain and loss rates converge to near-identical values across all models, regardless of biases toward gain or loss introduced by priors. The unrestricted model estimates the transition rate for color term gain to be markedly higher than that for color term loss (0.95 versus 0.36, respectively). It is thus unsurprising that an analysis that forces these rates to be equal has a far lower likelihood than the unrestricted model, with BFs showing extremely strong support for the two-parameter model over this single-parameter model. In sum, the results suggest that, although a strict prohibition on the loss of color terms is not compatible with Pama-Nyungan color term system evolution, the processes by which these systems have developed have involved substantially more color term additions than losses.

Ordering of Color Term Addition: Dependent Evolution Analyses. Comparisons of dependent and independent models of evolution for each pair of colors are used to identify correlations in the evolution of color terms. Because the dependent model receives substantial BF support (BF > 2) for the majority of color pairs, we further investigate dependencies between color pairs by examining the frequency with which individual transition rates are deleted in RJMCMC (see Table 2).

We find support for evolutionary dependencies between all pairs of colors, as would be predicted by WCS, with the exception of *red/yellow* and *red/blue*. For most remaining color pairs, the BF support for the dependent model was strong. However, a correlated model of evolution between *red* and *green* receives only moderate BF support. For most pairs of colors that are added in adjacent stages along the "mainline" WCS trajectory, we find strong evidence of dependent evolution, consistent with a theory in which color terms are added in a fixed order. The exception to this is *red/green*, which receives only moderate support.

Although all pathways in the WCS model involve the addition of *red* before *green*, we find no term for *red* in 11% of the Pama-Nyungan languages that have a term for *green*. These languages can be explained either by a gain of *green* before *red* or, more likely according to our ancestral state reconstructions, a loss of *red*. Neither of these explanations is consistent with WCS theory. The lack of support for dependencies between *red* and *yellow* or *blue* is likely the result of the fact that *red* is reconstructed to the root of the tree, and lost independently across several branches of Pama-Nyungan, which vary in the likelihood of a *yellow* or *blue* category. Thus, the evolution of *red* is captured as well by one gain parameter and one loss parameter as it is by separate rates for gain and loss in the presence and absence of *yellow/blue*. Stronger support for a dependency between *red* and *brown* likely reflects the fact that *red* is found in all sampled languages that have *brown*.

The RJMCMC procedure allows the number of model parameters to vary across iterations, it provides information about the posterior probability that any parameter should be deleted, which is useful for investigating the ordering of gains and losses of colors for which dependent models are supported. To do this, we examine the percentage of iterations in which particular parameters were set to zero in the RJMCMC analysis.

We expect two categories of parameters to be frequently set to zero: parameters associated with the gain of a "later" color term in the absence of an "earlier" color term (e.g., the rate for gaining *yellow* in the absence of *red*), and those associated with the loss of an "early" color term in the presence of a "late" color term (e.g., the loss of *red* where a term for *yellow* is present, arrow (h) in Fig. 2). These two types of parameters are associated with changes that contradict the WCS theory, namely out-of-order additions of terms and losses of terms in later stages of the evolutionary trajectory. Parameters associated with color gains in the order prescribed by the WCS model (arrows *a* and *f* in Fig. 2) are expected to be deleted seldom, if ever.

Indeed, we find that parameters associated with gaining color terms in the order prescribed by the WCS "main line" (edges *a* and *f* in Fig. 2 and Table 3) are almost never deleted. The parameter for a gain of a *brown* term when a *blue* term is present is the most often deleted set to zero in 22% of models.

Parameters describing the gain of "late" color terms in the absence of "earlier" color terms (column *d* in Fig. 2 and Table 3) are expected to be universally deleted under the WCS theory. However, the deletion rates for this parameter are less consistently supportive of WCS hypotheses than the parameters that are associated with "main line" color gains. Percent deletion of this parameter ranges from 21% (for gain of *green* in the absence of *red*) to 100% (for gains of *blue* or *brown* in the absence of *yellow*). That is, we never find blue or brown gained without yellow. The deletion rate is also extremely high for the *green/blue* and *red/brown* color pairs. For other color pairs, relatively low deletion rates suggest that the ordering of color term gain may not be as secure as suggested by the WCS. Color pairs *green/yellow*, *green/brown*, and *blue/brown* retain the parameter associated with out-of-order color term gain in 69–74% of sampled iterations.

Table 1. BF support for color term system models

| | Harmonic mean | | |
Model	logL	2logBF	BF support
Gain/loss unrestricted	−656.73		
Gain predominant	−657.21	−0.97	Not significant
Loss predominant	−657.17	−0.89	Not significant
Gain/loss equal	−673.89	−34.32	Very strong, negative

Fig. 2. Parameters in dependent models.

Table 2. BF support for correlated evolution between color pairs

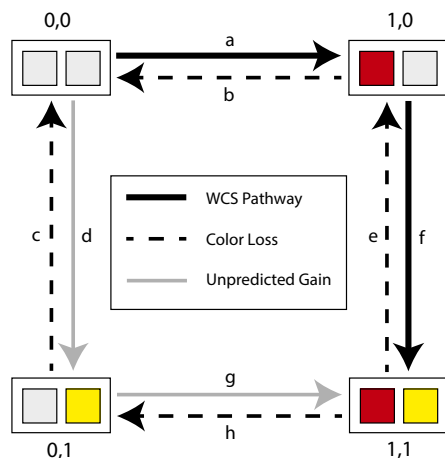| Colors	Independent	Dependent	2logBF	BF support
Red–green	−197.35	−195.70	3.29	Moderate
Red–yellow	−199.90	−200.15	−0.49	Not significant
Red–blue	−185.10	−184.12	1.95	Not significant
Red–brown	−172.20	−167.88	8.63	Strong
Green–yellow	−252.59	−233.69	37.81	Very strong
Green–blue	−232.77	−220.58	24.38	Very strong
Green–brown	−226.65	−216.018	21.26	Very strong
Yellow–blue	−236.32	−220.37	31.90	Very strong
Yellow–brown	−229.55	−220.46	18.19	Very strong
Blue–brown	−209.04	−187.35	43.38	Very strong

For *green/yellow*, this may suggest that some branches of Pama-Nyungan may evolve along an alternative WCS pathway (i.e., pathway B in Fig. 1).

The parameter associated with losses of "early" color terms in systems where "later" color terms are present (parameter *h*) is even more variable. Not only do the changes described by this parameter involve losses of color terms, they also result in systems that generally do not fit into WCS classification stages. Despite the strong expectation that this parameter should be deleted, it is retained 100% of the time for color pairs *red/green*, *yellow/blue*, and *yellow/brown* (see column *h* in Table 3). The *yellow* category would thus appear to be less resistant to loss than the WCS theory would suggest. Color pairs *red/brown* and *green/blue* are more consistent with WCS predictions, with the *h* parameter deleted 99% and 94% of the time, respectively. As a whole, the patterns of deletion for this parameter across all color pairs show clear evidence for color loss and variable resistance to loss across colors.

The posterior distribution of models produced by RJMCMC is also useful for examining alternative pathways for color term addition. Although the WCS "main line" involves the gain of *green* before *yellow*, with the addition of *blue* only after these two colors have been added, a minority of attested systems surveyed by the WCS show evidence for the addition of *yellow* before *green* or the emergence of *blue* before splitting *yellow* and *green* (8). Although the parameter for gaining *yellow* without *green* is set to zero in 29% of iterations, the parameter for gaining these colors in the reverse order is never set to zero. These results support the dominance of the *green*-first pathway in Pama-Nyungan and provides further evidence that both universal and language- or family-specific factors are involved in the evolution of color systems.

We find further support for the WCS "main line" in the dependent model for *yellow* and *blue*. Although the parameter associated with gains of *blue* in the absence of *yellow* is always deleted, the parameter for gain of *yellow* in the absence of *blue* is never deleted. Parameters associated with losing either of these colors in the presence of the other are also almost never deleted. Thus, we find very strong support for the addition of *yellow* before *blue* in Pama-Nyungan, but poor support for the notion that these particular terms are resistant to loss.

Ancestral Node Reconstruction. Ancestral node reconstruction estimates produced by the unconstrained two-parameter analysis across all seven color categories provide further evidence regarding the evolutionary trajectories of color term systems. Fig. 3 displays histograms showing the likelihood of each color's presence at the root, ancestral nodes corresponding to well-established subgroups, and a sample of other internal nodes.

For the majority of Pama-Nyungan subgroups, the reconstructed color term categories co-occur in patterns that are consistent with the WCS typology. The Paman, Yuin-Kuri, and Durubulic subgroups, for example, both have high probabilities for *black*, *white*, and *red* reconstructing to state 1 (present) at their ancestral nodes, consistent with WCS stage II. Several other subgroups, including Karnic, Thura-Yura, and Ngayarta, have ancestral state probabilities consistent with WCS stage III, with the color categories *black*, *white*, *red*, and *green*. The alternative WCS stage III configuration, with *black*, *white*, *red*, and *yellow*, is not as well supported among ancestral state reconstructions. Only Bandjalangic shows this pattern.

Only one Pama-Nyungan subgroup, the Central New South Wales languages, could be plausibly reconstructed with the six-color system of the WCS stage V (*black*, *white*, *red*, *yellow*, *green*, *blue*). However, although the probability of reconstructing *blue* for this subgroup is fairly secure (0.89), the reconstruction of *yellow* is less certain (0.45). Regardless of whether this subgroup is reconstructed as a canonical stage V system, it represents a challenge to one of the Kay and Maffi (7) hypotheses. It also represents a rapid elaboration of the color term system, given that its parent node shows strong support for only *black*, *white*, and *red*. The pattern of *blue* and *brown* occurring without *yellow* is even more robust in the Kulin subgroup. Three of its seven languages have *blue* and *brown* terms but lack *yellow*, with probabilities of 82% and 42%, respectively, for reconstructing *blue* and *brown* but only 4% for *yellow*.

Deeper in the tree, we find evidence that basic color term systems involved small numbers of color categories for the majority of the history of Pama-Nyungan. The root shows a high probability of having *black*, *white*, and *red* color categories, with a very small probability of *green*, presumably due to the prevalence of that color category outside of the Pama–Maric languages. The ancestral node reconstructions between this root and the primary subgroups generally show a progression from three-color systems to four-color systems including

Table 3. Deletion frequencies for parameters in RJMCMC model strings, expressed as percentage

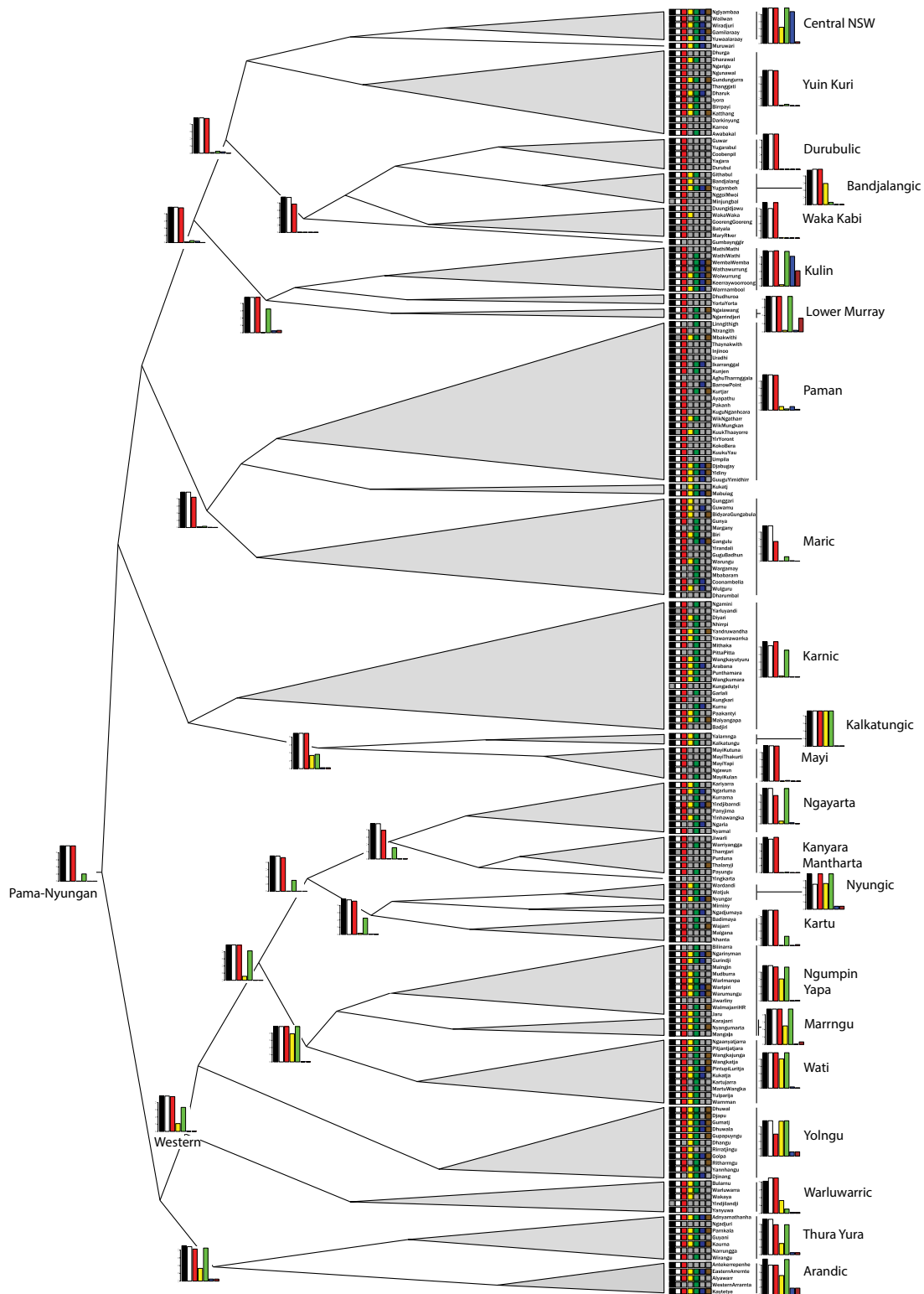| Color 1	Color 2	a	b	c	d	e	f	g	h
Red	Green	9	81	2	21	76	0	0	0
Red	Yellow	0	0	18	39	0	0	6	68
Red	Blue	0	0	1	51	2	0	29	18
Red	Brown	0	0	11	95	0	0	11	99
Green	Yellow	0	0	22	29	0	0	12	36
Green	Blue	0	0	1	98	0	0	1	94
Green	Brown	0	0	7	31	0	2	21	63
Yellow	Blue	0	0	1	100	3	0	0	0
Yellow	Brown	0	0	0	100	0	0	0	0
Blue	Brown	22	4	10	26	11	4	0	18

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Fig. 3. Ancestral state reconstructions on consensus tree.

green (WCS stage III). A transition from this four-color system to a five-color system (*black*, *white*, *red*, *green*, *yellow*/WCS IV) is also apparent within the western branch of the family, although elsewhere in the tree the likelihood of five-color WCS stage IV system is lower due to low reconstruction probabilities for *yellow*.

Although the general trend suggested by ancestral node reconstruction probabilities is consistent with WCS evolutionary pathways, a more detailed examination of the results reveals evidence for patterns that contradict Kay and Maffi (7). Reasonably strong evidence for color term loss can be found in languages like Wayilwan (with only *black*, *white*, *green*) within the Central New

South Wales subgroup (with a probable reconstruction of *black*, *white*, *red*, *green*, *blue*). We also find a reasonably high probability for a *green* category in Western Pama-Nyungan nodes ancestral to the Kanyara–Mantharta subgroup, although the probability of *green* in Kanyara–Mantharta itself is very low (0.01). This decrease in the probability of a *green* category along the branches leading to the Kanyara–Mantharta subgroup can reasonably be interpreted as a likely loss of that color.

Comparative Reconstruction of Terms. Linguistic reconstruction using traditional comparative methods (30) reveals only a small number of color terms in that may be inheritances from Proto-Pama-Nyungan or high nodes within the Pama-Nyungan phylogeny. The forms *kara and *maru, both meaning *black*, are found in a number of distant subgroups across the tree, suggesting that these items may reconstruct to Proto-Pama-Nyungan. However, if these forms do reconstruct to the root, they must have been independently lost in most branches. Other explanations, such as a parallel semantic shift in several branches, cannot be excluded but are not evident from the available data.

Several obvious sources for color terms are evident. Northern Karnic *tyimpa *black*, for example, occurs in Thura–Yura with the meaning "ashes." Terms for "ashes" are also recruited to express the color category *white*, as in Yolŋu *gaywaraŋu. In other instances, we see polysemy (that is, where a color term has multiple meanings, including both color and noncolor terms). Polysemy between *white* terms and the concepts "shining" and "clean" are evident. *Red* terms are frequently polysemous with or derived from items meaning "blood" (e.g., Biri *kuma*) or "red ochre" (e.g., Bandjalangic *kutyin). Proto-Pama-Nyungan *kurnka ("raw" or "unripe") is used to refer to the *green* color category in a number of languages. *Green* terms also come from "leafy" meanings (e.g., Ngayarta *palharra) or "tree" meanings (e.g., *yukiri in many Western languages).

The instability of color terms in Pama-Nyungan is comparable to that in the Indo-European family, where the basic color terms show numerous innovations. In Indo-European, we likewise find color terms that relate to salient objects bearing that color. For example, compare the English loanword *orange*, Latvian *melns* "dirty" (cognate with Greek *mélas* "black"), English *black* (cognate with Greek *phlégo* "burn, blaze"; Latin *flagrāre* "flame, burn") (ref. 31, p. 1055). However, Indo-European shows an additional pattern, whereby cognate color terms appear in different branches of the family in different meanings. They remain their status as color terms but refer to different portions of the color spectrum. English "yellow" is cognate with Greek *khlo:rós* "green," and Old Irish *gel* "white." In addition, we also see semantic narrowing and broadening, where terms for specific colors (such as in Sanskrit) derive from a word meaning colored more generally. For example, Sanskrit *rakta* "red" is from the past participle of the root *raj* "be colored." In this last shift, we see a parallel in the Australian data, where Yolŋu *miku* "red" also means "colored."

Conclusions

Our work shows an application of Bayesian phylogenetic methods to data that bridges linguistics, cultural anthropology, and cognitive science. Color term systems show themselves to be appropriate to Bayesian reconstruction techniques. We find general support for the WCS model of color term development, but with more nuance, including variability across color categories in the level of support for individual components of the WCS evolutionary theory. We also find exceptions to their predicted patterns, such as the loss of color terms in multiple subgroups. These exceptions are not easily explained by looking at the individual histories of color terms, nor do the linguistic mechanisms associated with color term change in Pama-Nyungan differ from those found in well-studied families like Indo-European. The principles outlined in the WCS evolutionary theory do play a substantial role in the development of color term systems, but that further study from an evolutionary perspective can refine our understanding of the interaction of cognitive constraints and language change in shaping lexical systems.

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