CHANGES IN POST-MARITAL RESIDENCE PRECEDE CHANGES IN DESCENT SYSTEMS IN AUSTRONESIAN SOCIETIES

Fiona Jordan
Ruth Mace
University College London
fjordan@ucl.ac.uk

Paper for EHBE 2007

*****DO NOT CITE OR CIRCULATE WITHOUT PERMISSION*****

Abstract

Descent systems express how a society organises kinship relationships. Inheritance of resources as well as rights and obligations can be traced patrilineally, matrilineally, a combination of both, or in a cognatic/bilateral fashion. Post-marital residence rules describing the kin group with whom a couple lives after marriage are often, but not always, correlated with the descent system. Murdock (1949) hypothesised that changes in the residence system would cause changes in descent, not the other way around. Here we present a Bayesian phylogenetic analysis of 67 Austronesian societies from the Pacific. These comparative methods take into account uncertainty about the phylogeny as well as uncertainty about the evolution of the cultural traits. Ancestral state reconstruction shows that unilineal residence and non-unilineal descent are the ancestral states for this group of societies. Descent changes lag behind residence changes over a 1000-year time period. Environmental or cultural change (both frequent in Austronesian prehistory) may be facultatively adjusted to via the residence system in the short term, and thus this trait may change more often.

Introduction

Murdock (1949:221-222) claimed that changes in residence patterns preceded all other types of changes in social organisation, such as descent and kin terminology, by altering the physical distribution of related individuals.

Rules of residence reflect general economic, social and cultural conditions. When underlying conditions change, rules of residence tend to be modified accordingly. The local alignment of kinsmen is thereby altered, with the result that a series of adaptive change is initiated which may ultimately produce a reorganization of the entire social structure. (Murdock 1949:17)

In its general form, this has become known as "main sequence kinship theory" (Fox 1967; Naroll 1970; Divale 1974). Thus, different patterns of post-marital residence produce different arrangements of kin: patrilocality groups fathers and brothers—termed "fraternal interest groups" by Divale (1974)—together with unrelated women, while matrilocality groups related women together with their brothers as well as their respective husbands. Whilst residence rules show some patterns of correspondence with descent rules—for example, patrilocal residence is almost always found with patrilineal descent (Coult and Habenstein 1965; Levinson and Malone 1980)—the relationship is not altogether straightforward. Many matrilineal societies have patrilocal or ambilocal forms of residence (van den Berghe 1979), such as the famously bilocal Dobu of the D'Entrecasteaux Islands (Young 1993). Driver (1956; 1969) found support for the main sequence model amongst North American societies, and identified that the sexual division of labour between the sexes was a major factor in determining residence, and thus descent. Similarly, other studies have proposed various catalysts for a change in post-marital residence, including the presence of internal versus external warfare (Ember and Ember 1971), recent migration (Divale 1974), or the sexual division of labour regarding subsistence (White et al. 1981; Korotayev 2003). However, Oceanic societies have usually been found to have no association between sexual division of labour and residence, as Alkire (1974) demonstrated for Micronesia. From a Darwinian point of view, matriliny and matrilocality may be seen as daughter-biased parental investment, allowing maternal kin (especially grandmothers) to assist with child-rearing, which has been shown to have positive effects on child survival and thus inclusive fitness (Sear, Mace, and McGregor 2000; Holden, Sear, and Mace 2003; Mace and Sear 2004). Ember, Ember, and Pasternak (1974) asked if unilocal and unilineal descent regularly co-occurred in a worldwide

sample of 42 societies. They found unilocal residence to be a "necessary but not sufficient" cause of unilineal descent, as not all unilocal societies were unilineal (1974:92), only becoming so as responses to warfare.

Main sequence theory has largely been examined with emphasis on factors that adjust residence. Alternatives to a main sequence theory seek to explain patterns of descent and residence by means of ecological factors such as horticultural subsistence and the predominant type of physical environment (Aberle 1961:668; Gough 1961:551; Service 1962:120). However, the sequence itself remains a largely untested proposition.

Testing the general model is especially important when we consider that many specific kinship models hinge on an *a priori* assumption of ancestral states as patrilineal and patrilocal (Divale 1974:77; Levinson and Malone 1980), a position frequently found in the literature (e.g. Ember 1975; Service 1966; Rodseth et al. 1991; Foley 1996). In contrast, others have suggested (Murdock 1949; Eggan 1966; van den Berghe 1979) that foraging populations were likely to have multilocal, flexible residence patterns, while Ember and Ember (1972:397) argue that "multilocality and associated features of social organization are probably recent consequences of European contact". More recently, Marlowe (2004) has re-examined foraging societies residence patterns and shown that they tend to be much more fluid and multilocal than non-foragers, with individual decisions resting on considerations of childcare and care of elderly parents. Clearly, any "ancestral" form of kinship organisation is elusive, and should rather be treated as an empirical fact to be established, whether in regional studies or in the global context.

To date, the main sequence theory has not been tested by a formal phylogenetic model that controls for the effects of shared ancestry (Galton's Problem; see for example Mace and Pagel 1994; Mace and Holden 2004). Here, we use a phylogeny of 67 Austronesian societies of the Pacific, constructed using language data and Bayesian likelihood models, as a model of population history. Comparative methods such as *Discrete* (Pagel 1994) allow us to estimate the probable direction of evolutionary change by examining the likelihood of transitions between different character states, providing a way to test Murdock's model in the Austronesian context whilst controlling for phylogenetic relationships. First, we tested whether descent and residence were co-evolving together under two coding schemes, unilineality and patrilineality. Second, we tested if post-marital residence changed first and/or changed at a higher rate when traits were evolving on a phylogeny, as would be predicted by the sequential theory.

Methods

Phylogeny estimation

Word data for 67 Austronesian languages (Figure 1) came from the *Austronesian Basic Vocabulary* (ABV), available online at http://language.psy.auckland.ac.nz/austronesian (Blust, Gray, and Greenhill, 2003–2005). This database consists of the core vocabulary terms of the Swadesh 200 word list across 467 Austronesian languages, with character data organised into binary cognate sets. *BayesPhylogenies*, which contains models of evolution that have been developed for use on language data, was used to construct trees (Pagel and Meade 2005). The Bayesian MCMC method was used to estimate a posterior probability distribution of trees. This is not a set of optimally likely trees, but rather a set of trees where topologies are represented in proportion to their likelihood.

We used a one-parameter model in which the rates of gains and losses of words are presumed to be equal (M1P, Pagel, Meade, and Barker 2004). Word meanings were allowed to evolve at different rates drawn from a gamma distribution with four rate categories (Yang 1994), and base frequencies of the character states were estimated from the data. The Formosan languages were used as the outgroup to root the tree (Pawley and Ross 1993; Blust 1999). Four Markov chains were run for between 1 x 10⁶ and 10 x 10⁶ iterations and were sampled every 1000 trees after the chain reached stationarity. Full description of the trees and phylogenetic procedures is in Jordan (2007).

Cultural data and coding schemes

Data on descent and residence for the 67 societies were obtained from (i) Murdock's (1967) *Ethnographic Atlas* as collated by Gray (1999), (ii) the *Encyclopaedia of World Cultures* (Levinson 1993), and (iii) *Ethnic Groups of Island South-East Asia* (LeBar 1975). Two different coding schemes were used (Table 1). First, societies were coded "U_D" as unilineal if they were primarily patrilineal or matrilineal, and "U_R" as unilocal if primarily patrilocal/avunculocal or matrilocal. Non-unilineal ("N_D") and non-unilocal ("N_R") societies comprised all others. Second, societies were coded as patrilineal/patrilocal or with an absence of patri-traits. This coding was to test a more specific model of the evolutionary sequence, that is, that patri-centric shifts in residence co-evolved with patri-centric descent. Patriliny

was chosen as the focus simply because it was the most common form of social organisation in the sample.

Table 1. Contingency table for unilineal descent and unilocal residence showing the number of societies classified in each trait class. Each of the cells corresponds to one of the four states in the evolutionary "flow diagrams".

Unilineal (U _D)	Non-unilineal (N _D)
44	12
6	5
Patrilineal (P _D)	Other (O _D)
32	16
1	18
	44 6 Patrilineal (P _D)

Testing correlated evolution

The framework of *Discrete* (Pagel 1994), implemented in the Bayesian context in *BayesMultiState* (Pagel and Meade 2006) was used to test for correlated evolution. *Discrete* tests for co-evolutionary change between two binary-coded characters by estimating the likelihood (*Lh*) of two models. The *Lh* is a numerical estimate of the likelihood of obtaining the data, given the tree(s) and a specific model of evolution. In Pagel's comparative method, the model is specified by a set of transition-rate parameters that indicate the probability of change from one character state to the other (see Figure 2). An independent model (I), where the two characters are free to evolve separately, is compared to a dependent model (D), where the two characters are co-evolving together. Because more parameters are required to describe the dependent model, if the independent model is true, then it will have a higher likelihood. This is because it requires fewer parameters to describe the data, as some of them will be equal. If the likelihood ratio (*LR*) of the independent and dependent model is significant, we can then reject the null hypothesis of no co-evolution

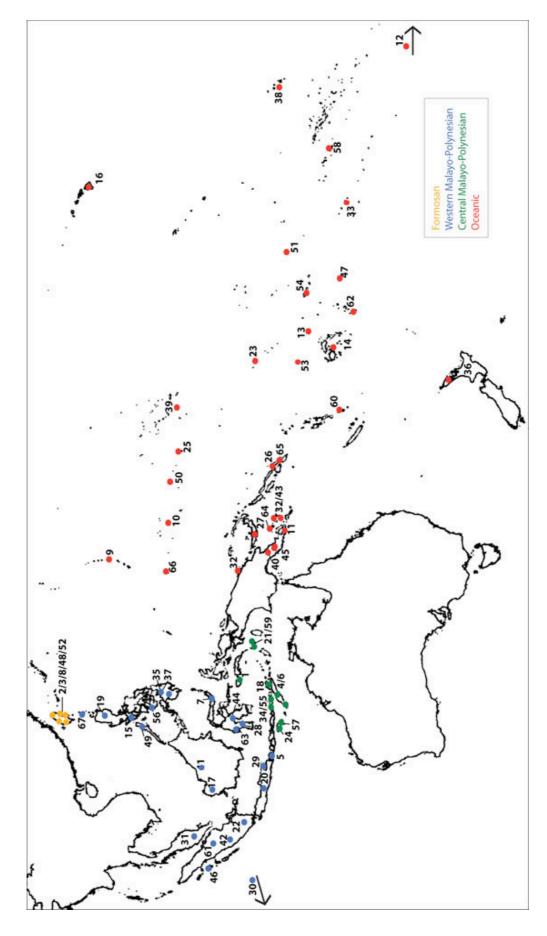


Figure 1. Geographical distribution of the 67 Austronesian societies

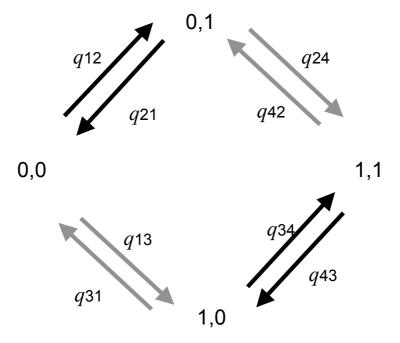


Figure 2. Transitions among four combinations of states with two binary variables in the dependent model of evolution. Transition-rates are denoted by q_{12} , q_{24} etc., and are estimated as the parameters of the model of evolution. High rates of (for example) q_{13} and q_{24} compared to all others indicates that the first trait is changing from $0 \rightarrow 1$ more often or quicker than other changes.

The Bayesian implementation of Discrete is described here in brief; readers wishing a fuller treatment of the methodologies are advised to consult Pagel et al. (2004) and Pagel and Meade (2006). Instead of conducting a comparative test for co-evolution on a single tree, the method uses a Bayesian sample of trees, so that inferences about the character co-evolution are not wedded to any particular phylogenetic hypothesis. As well as removing the effects of phylogenetic uncertainty, the method accounts for mapping (character) uncertainty by computing probability *distributions* of the four character-state combinations at each node, rather than assigning single probability values, or just single values, to each node. We can then use the posterior probability distributions of the transition-rates between these character states to investigate the degree of certainty we may have in the results.

In the Bayesian context, we do not compare two single likelihoods to test the independent versus dependent models, but rather we compare the two posterior probability distributions of the likelihoods, in which there will be variation according to the phylogenetic and trait uncertainty. We then ask which model, the dependent or the independent, accounts

for a higher proportion of the probability of the data. The harmonic (marginal) means of the likelihoods are used to compute the Bayes factor as BF = -2*(I-D), where a BF of 3–5 indicates positive evidence for the dependent model, and greater than five indicates strong evidence (Raftery 1996).

To run a co-evolutionary analysis, the program took two files, (i) the tree-sample of 1000 phylogenies, and (ii) for each culture, information about the state of the two traits presumed to be co-evolving. The independent and dependent model parameters were estimated from a Markov chain that ran for 100×10^6 iterations, repeatedly visiting each tree in the sample of 1000. After convergence of the chain, outcomes were sampled every 1000 iterations to avoid autocorrelation. This provided 100,000 samples with which to estimate the marginal likelihoods, posterior distributions and transition-rate parameters of the dependent and dependent models.

Using RJ MCMC to find the best models of evolutionary change

The transition rate parameters in Figure 2 give us a relative measure of which transitions occur more often. From these we can estimate the probable direction of evolution, that is, which trait changes first in a possible evolutionary pathway. We are also able to determine the significance of these changes using statistical tests. The reversible-jump (RJ) MCMC procedure directs our model-construction by using the Markov-chain device to explore the universe of possible models, visiting them in proportion to their probability (Pagel and Meade 2006:809). In this context, a "model" is described as the set of eight transition-rate parameters between the four states of character evolution, where transition-rates are sorted into classes that are functionally equivalent. For example, the model "1100000Z" denotes a situation where the transition rates of q_{12} and q_{13} are equivalent, but different to all other rates in the flow diagram, except q_{43} , which is indistinguishable from zero. In the implementation of the RJ procedure, the program reports the number of visits to each model in the sample, out of the 21,147 possible dependent models.

In order to understand the most probable evolutionary pathways in the flow diagram, we can (i) investigate the most commonly-visited model and (ii) select those models which fit our hypothesis and compare their likelihoods (using the Bayes factor) against those which do not. Comparing the dependent and independent models is the most general form of this approach.

Results

Phylogenetic trees

The final posterior probability distribution (PPD) consisted of 1000 trees sampled every 2000 iterations from one of the post-convergence chains. The PPD is a distribution containing not only topologies of trees and their likelihoods, but is also a distribution of branch lengths and the other parameters, such as transition rates, estimated by the model of word evolution (Pagel and Meade 2005). A consensus tree of this sample is used to display the results; however, this is not the single "best" tree, and comparative tests were conducted on the entire 1000-tree sample.

The consensus phylogeny showing the posterior probabilities of nodes (their certainties) is shown in Figure 3; the same tree labelled with the unilineal/unilocal coding in Figure 4, and the patrilineal/patrilocal coding in Figure 5. Both Figures 4 and 5 show that more societies have the unilocal form of residence than the unilineal form of descent. Figure 4 also has the ancestral states of unilineal/unilocal traits mapped onto the early nodes of the tree. For this coding, the program estimated the root to be unilocal ($P(U_R) = .71$) and non-unilineal ($P(N_D) = .77$) under the independent model, and similarly ($P(U_R, N_D) = .44$) under the dependent model. For the patri-coding, the estimates were less certain, with the root equivocally patrilocal ($P(P_R) = .50$) and non-patrilineal ($P(O_D) = .60$) under the independent model, and the same ($P(P_R, O_D) = .57$) under the dependent model.

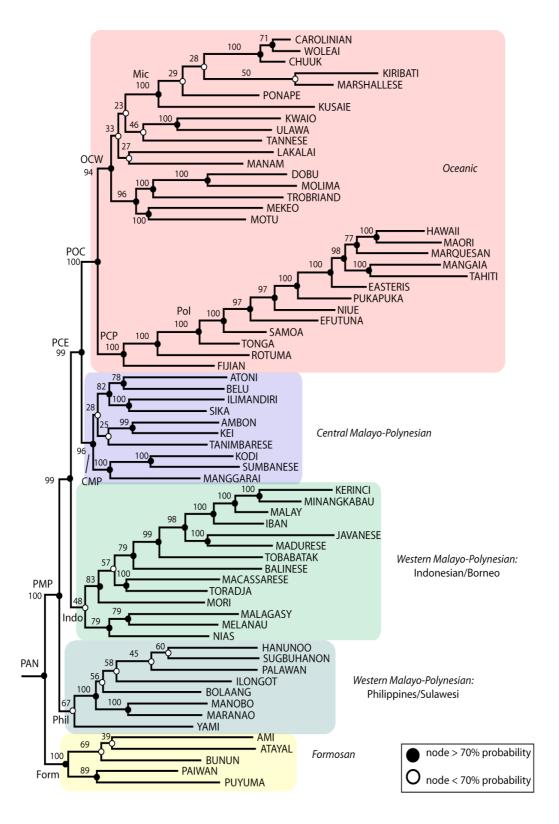


Figure 3. Consensus linguistic tree of the 1,000-tree sample, showing clades present in over 50% of the sample as well as those that do not conflict with the majority. Figures over branches correspond to the posterior probabilities of the nodes. A value of 100 indicates that a node appeared in every tree in the sample. Black circles indicate those nodes with a posterior probability distribution >0.70, a threshold for confidence in the existence of that node (Pagel 1999), while white circles indicate a *PPD* <0.70. Nodes denoting language subgroups/proto-language stages are as follows: *PAN* Proto Austronesian, *PMP* Proto Malayo-Polynesian, *PCE* Proto Central-Eastern Malayo-Polynesian, *POC* Proto Oceanic, *PCP* Proto Central Pacific, *CMP*, Central Malayo-Polynesian, *Mic* Micronesian, *Pol* Polynesian, *Form* Formosan, *Phil* Philippines/Sulawesi, *Indo* Indonesia *OCW* Oceanic-West.

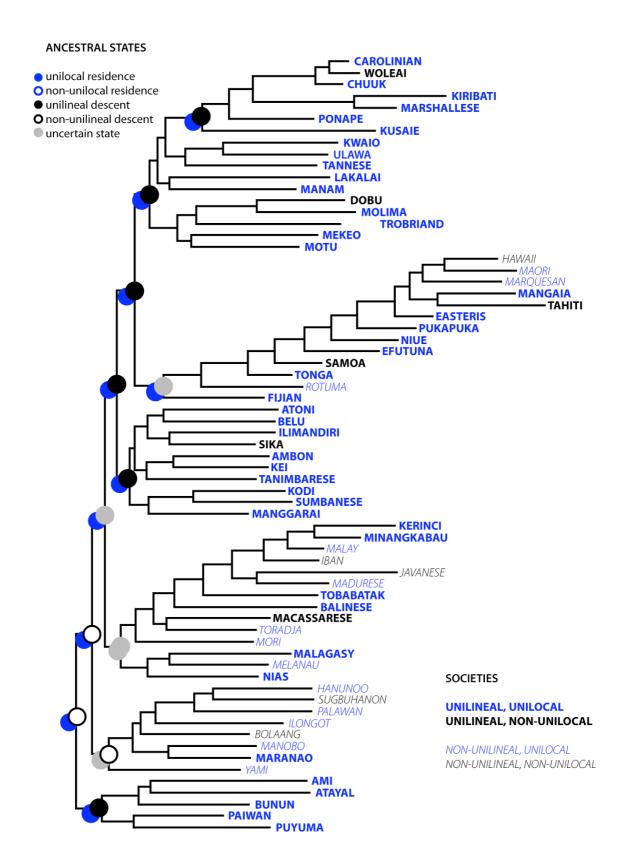


Figure 4. Consensus phylogeny of 67 Austronesian societies showing the evolution of unilineal descent and unilocal residence. Descent is denoted by font: unilineal societies appear in bold, non-unilineal societies in italics. Residence is denoted by colour: unilocal societies are in blue, non-unilocal societies are in black. Ancestral states are indicated by the coloured dots at early nodes and show that unilocal residence is more ancestral that unilineal descent.

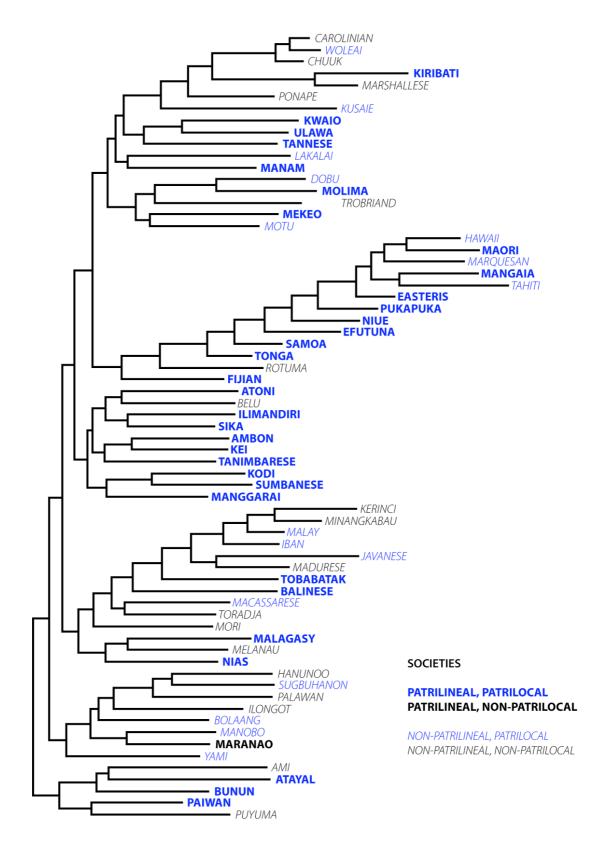


Figure 5. Phylogeny showing the evolution of patrilineal descent and patrilocal residence. Descent is denoted by font: patrilineal societies appear in bold, non-patrilineal societies in italics. Residence is denoted by colour: patrilocal societies are in blue, non-patrilocal societies are in black.

Tests for co-evolution

A chi-square test (2 x 2 with 1 *d.f.*) for the unilineal coding was not significant ($\chi^2 = 2.80$, p \leq .10). For the patri- coding there was a significant association as $\chi^2 = 20.53$, p \leq .001. Using the phylogenetic comparative method, under the unilineal coding the mean marginal likelihood of the independent model was -71.68, and the dependent model was -68.22. Using the Bayes factor calculation, BF = 6.91, indicating that the hypothesis of correlated evolution between descent and residence was positively supported. Similarly, for the patri-coded data, there was strong positive evidence for the co-evolution of the two traits (BF = 21.44).

The RJ MCMC procedure tells us if the model string found corresponds to an independent or dependent model. The dependent model should be present 413 times more than the independent for correlated evolution to be true, i.e., the independent model should represent 0.24% or less of the sample. For the unilineal coding, the independent model accounted for (exactly) 0.24% of samples, and for the patri-coding, the independent model only accounted for 0.002%. This is extra confirmation that the co-evolutionary, dependent model fits these data better than the independent model.

Descriptions of the evolutionary transitions represented by the transition-rate parameters are given in Table 2. Flow diagrams (Pagel 1997) of evolutionary change are shown in Figures 6 and 7. In testing the hypothesis of co-evolution between descent and residence, we are interested in the rates of q_{13} , q_{31} , q_{24} , and q_{42} , where a change in residence occurs before a change in descent, and especially q_{13} and q_{24} , where the transition occurs towards lineality in social organisation.

Table 2. Description of the rate coefficients as applied to residence/descent data. These descriptions can apply equally to the patri- coded data. The two transitions in italics denote pathways towards lineal descent and residence where residence changes first.

Coeffi	cent Evolutionary transition
Gains	
q ₁₂	Gain of unilinear descent system in the presence of non-unilocal residence
q ₁₃	Gain of unilocal residence in the presence of non-unilinear descent system
q ₂₄	Gain of unilocal residence in the presence of unilinear descent system
q ₃₄	Gain of unilinear descent system in the presence of unilocal residence
Losses	· · · · · · · · · · · · · · · · · · ·
q ₂₁	Loss of unilinear descent system in the presence of non-unilocal residence
q ₃₁	Loss of unilocal residence in the presence of non-unilinear descent system
q ₄₂	Loss of unilocal residence in the presence of unilinear descent system
q_{43}	Loss of unilinear descent system in the presence of unilocal residence

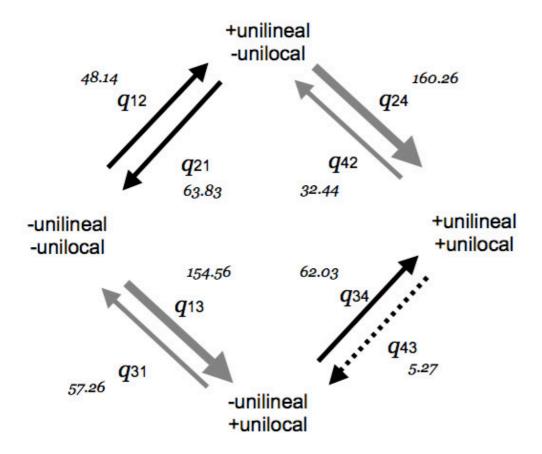


Figure 6. Evolutionary flow diagram between the four possible state of descent and residence (unilineal coding). The labels "–unilineal" and "–unilocal" refer to non-unilineal and non-unilocal respectively. Arrows show the direction of the evolutionary transition; these are annotated with the mean value of the posterior distribution for that transition rate. The larger the rate, the more probable that particular pathway of evolution. Dotted pathways are effectively zero, while large arrows indicate rates that are significantly higher. Regular arrows have equivalent rates. The pathway is taken from the most probable model under the RJ MCMC procedure (below). Changes toward unilocal residence are highly likely, no matter what the state of descent, but the loss of unilinear descent is rare if residence is unilocal.

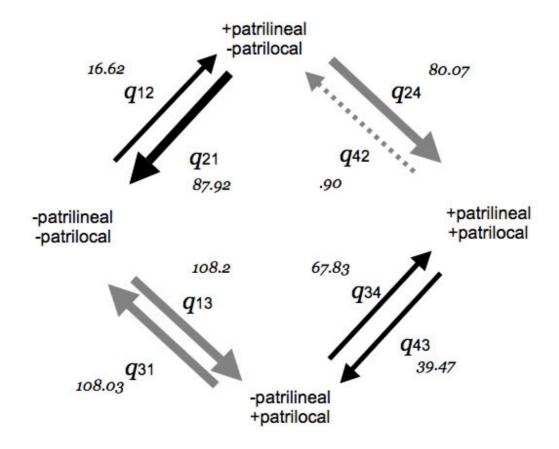


Figure 7. Evolutionary flow diagram between the four possible state of descent and residence (patri- coding). The labels "–patrilineal" and "–patrilocal" refer to non-patrilineal and non-patrilocal respectively. Arrows show the direction of the evolutionary transition; these are annotated with the mean value of the posterior distribution for that transition rate. The larger the rate, the more probable that particular pathway of evolution. Dotted pathways are effectively zero, while large arrows indicate rates that are significantly higher. Regular arrows have equivalent rates. The pathway is taken from the most probable model under the RJ MCMC procedure (below). Changes in residence are all likely, especially before descent, and when a society is not patrilineal. However, once a society is both patrilineal and patrilocal residence is unlikely to change.

Testing the directionality of change. The output of the RJ MCMC procedure gives us "model strings" which sort the transition-rates into classes, some of which may be the zero bin. Tables 3 and 4 show the most frequent models for both the unilineal and patri-coding.

Table 3. Unilineal/unilocal data showing the seven most frequent models found by RJ MCMC model-search, accounting for 55% of all the 10,000 samples. All models have two parameters, meaning they are versions of the dependent model. The flow diagram in Figure 7 is presented according to the most-frequent model.

Model string	Frequency	Cumulative frequency	No. of parameters
0101000Z	1651	0.17	2
Z010111Z	1504	0.32	2
0000111Z	651	0.38	2
0101100Z	348	0.42	2
Z000101Z	339	0.45	2
Z0Z01011	331	0.48	2
0010111Z	323	0.51	2

The first two models, which account for nearly one-third of the sample, are equivalent except for one difference, that of the transition q_{12} (gaining unilineal descent before unilocal residence) being in the zero bin as well as q_{43} . A large number of models have the parameter q_{43} set to zero, indicating this transition (retaining unilocal residence while losing unilineal descent) to be very unlikely. Taken together, these two transitions being frequently set to zero is strong evidence that residence is changing first for these data.

Table 4. Patrilineal/patrilocal data showing the eight most frequent models found by RJ MCMC model-search, accounting for 48% of all samples. Only the third most-frequent model has one parameter, equivalent to the independent model. All others are a version of the dependent model. The flow diagram is presented according the most-frequent model.

Model string	Frequency	Cumulative frequency	No. of parameters
011110Z0	9384	0.09	2
Z00100Z1	7483	0.16	2
Z00000Z0	5982	0.23	1
Z00Z00Z1	5960	0.29	2
Z00000Z1	5762	0.35	2
010110Z0	5609	0.40	2
011111Z0	5285	0.45	2
01Z110Z0	2958	0.48	2

For the patri-coding, the q_{42} parameter (representing the loss of patriliny while retaining patrilocality) is always in the zero bin, meaning that this transition is effectively zero. The q_{12} parameter, where patriliny is gained before patrilocality, is also frequently in the

zero bin or in a lower rate class than other transitions. Models where the parameters indicate that residence changes first or at a higher rate dominate the sample.

We calculate if the models presented in the flow diagram are significant by comparing the marginal means of those likelihoods to the likelihoods of an equal-sized sample of all other models. For the unilineal coding, the flow-diagram model is significant, as the likelihood was -62.38, compared to all other models whose mean likelihood was -65.30, giving BF = 5.84. This is positive evidence in support of the flow-diagram model. For the patri- coding, the flow diagram model likelihood was -68.73 and that of all other models was -70.53, giving a BF = 3.6, which is also positive evidence for the flow-diagram model. Thus, for both sets of coding, models in which residence is likely to change first and/or changes in descent are less frequent were statistically supported by the data.

Rates of change over time

Finally, we can examine the rate of cultural evolution in descent and residence by using the time scale of the Austronesian language tree to estimate the probability of a change happening over a certain number of years. To do this we first derive an approximate date for the root of the AN tree. The combination of archaeology and linguistic evidence for the Austronesian expansion suggests that pottery-making and/or agriculturalist peoples had moved from Taiwan to the Northern Philippines by at least 5500 BP and to parts of Borneo by 4500 BP (Blust 1995; Bellwood 1997). Evidence for an earlier start to the spread of Austronesian-speaking peoples has not been forthcoming, so we may date Proto Austronesian to c.6000 BP, i.e. the tree "length" from root to tips is 6000 years.

Taking the simplifying assumption that language change is proportionate to time, we derive the length of the root-to-tip distances for each of the 67 societies and average these to gain a measure of language change per year. The average tip-to-root distance was .04, meaning there was a 4% change that the character state would change over the branch. As there were 17474 lexical characters, this meant that on average 698 characters changed from the root to the tip. We use the following equation (Pagel and Meade 2005) to approximate the probability of change from $0\rightarrow 1$ on a branch of length t:

$$P(0 \rightarrow 1)_t = (\alpha/(\alpha + \beta))^*(1 - e^{-(\alpha + \beta)t})$$
 [Eq. 3]

where α and β are the transition-rate parameters between two states. Plugging the transition rates for the dependent model of unilineal/unilocal evolution into Equation 3, we obtain the

probability of change over different time periods (branch lengths), shown in Table 5 and Figure 8.

Table 5. Probability of change in descent (top four parameters) and residence (bottom four parameters) over three time periods. Parameters are taken from the dependent model of evolution, as residence and descent show correlated evolution.

Evolutionary transition	Probability of change over x years		
	100	1000	6000
q ₁₂ Gain unilineal descent without unilocal residence	.03	.23	.43
q ₂₁ Lose unilineal descent without unilocal residence	.04	.30	.56
q ₃₄ Gain unilineal descent with unilocal residence	.04	.33	.86
q ₄₃ Lose unilineal descent with unilocal residence	.00	.03	.07
q ₁₃ Gain unilocal residence without unilineal descent	.09	.55	.73
q ₃₁ Gain unilocal residence without unilineal descent	.04	.20	.27
q ₂₄ Gain unilocal residence with unilineal descent	.10	.59	.79
q ₄₂ Lose unilocal residence with unilineal descent	.03	.15	.21

Plotting the rates for residence and descent (Figure 8) shows that while there are only small probabilities of change in both traits over 100 years, over the 1000-year period the traits diverge. Residence is more labile, with a 15–59% chance of change over 1000 years, compared to descent at 3–33%. Gains of unilocality have the highest probability in a 1000-year period. Over the whole Austronesian tree, with a time period of roughly 6000 years, the highest probability of all is the gain of unilineal descent against a background of unilocal residence, indicating this is a stable state.

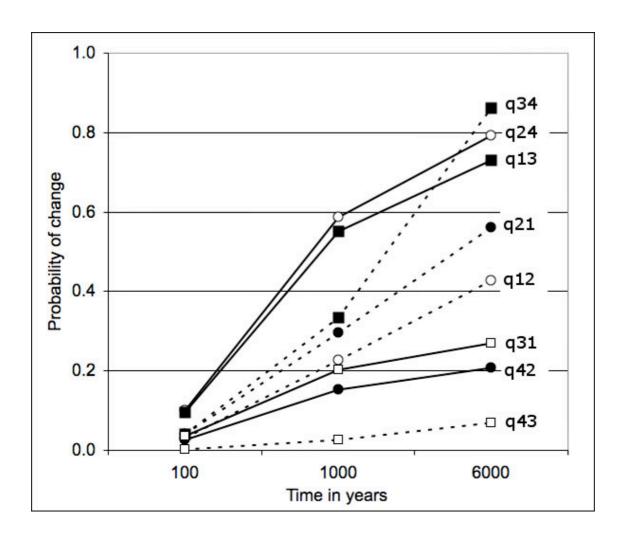


Figure 8. Probability of change over time in each of eight transitions according to the dependent model. Dotted lines indicate changes in descent, solid lines indicate changes in residence. There is a ~10% chance of change in both types of traits in the 100-year period. Changes to unilineal and –local forms are most probable over 1000 years, especially in residence, where there is a one in two chance of change. By 6000 years the traits have reached an equilibrium (i.e. probabilities add to one).

Discussion

Using a Bayesian MCMC procedure that controlled for phylogenetic uncertainty, we found that changes in post-marital residence preceded changes in descent in 67 Austronesian societies, supporting the "main sequence" theory of kinship. Relating the changes to archaeological time, both traits had a low probability of change over 100 years, but in a 1000-year period, residence had a 50% likelihood of changing form.

The most-likely scenario for the evolution of unilineal descent and unilocal residence reconstructs the root as non-unilineal (bilateral) but unilocal (possibly matrilocal, not shown; Jordan 2007). The most common transition from this state is gaining unilineal descent, as in, for example, the Formosan and Central Malayo-Polynesian societies. However, many WMP societies in the Philippines and Indonesia "lose" unilocal residence, and are bilateral and multilocal (e.g. Hanunoo, Balinese). One likely scenario for this transition is that brideprice moderates residence in the poorer strata of many Island Southeast Asian societies, for example, the Atoni of Timor (Cunningham 1967). Instead of paying a brideprice, or as well as, the husband will live with the bride's family for some period of brideservice, creating a non-unilocal residence system. Considerations of brideprice may also affect affiliation to one lineage or another in ambilineal cultures (Bellwood 1997). Indian and Islamic influences throughout Island Southeast Asia, from around 1000 BP (LeBar 1975; Denoon 1992) may also be a factor in the number of non-unilineal systems in this area, although their effects on peasant classes (until recently for Islam) are not well known (Alkire 1972). As well, many societies traditionally practised shifting cultivation and had no shortage of land, a condition likely to favour bilateral kinship e.g. the Iban of Borneo (Freeman 1981).

Unilineal descent evolves in the Proto Central-Eastern/Proto Oceanic part of the tree, and once gained in the Oceanic group, only a few Polynesian societies revert to a wholly non-unilineal form of descent, such as Hawai'i with bilateral descent groups among "commoners" (Kirch 1984). Many Oceanic societies are ambilineal or have double descent, so that both matri- and patri-lineal kin groups are present. By coding ambilineal societies as unilineal, we capture the presence of lineal descent groups—the "unbroken line" (Holy 1996)—in a society's kinship structure, but we lose the aspect of flexibility in social organisation that ambilineal societies share with cognatic and bilateral systems. This flexibility may be important in explaining the predominance of ambilineal and multilocal societies in Remote Oceania (Firth 1957; Fox 1967).

Ancestral states analyses (not shown; Jordan 2007) indicate that the root of the AN tree was probably neither patrilineal nor patrilocal. Thus, the most likely evolutionary scenario for these cultures is that patrilocality is rapidly gained and lost against the background of a non-patrilocal descent system. Lessa (1950) describes the matrilineal descent and patrilocal residence of Ulithi Atoll in Micronesia, remarking that bride-service sometimes requires residence with the bride's family. It is easy to see that in conditions like these, residence patterns, as "cultural traits", are more likely to be decisions for the individual, and are likely to have high rates of change. According to the flow diagram model, however, once patrilocality is gained, some further "push" may be required to shift the kinship structure towards patriliny. In Austronesian societies this push may be entwined with aspects of ranking, primogeniture, and status (Bellwood 1997; Kirch and Green 2001).

Once a society is both patrilineal and patrilocal it is unlikely to shift away from this state. If it does, it will most certainly not shift to a different residence system first. Service (1962) observed that patrilocality occurs in so many different ecological and cultural contexts that no clear patterns can emerge to explain its global predominance. However, as evidenced by its prevalence worldwide (~70%, Levinson and Malone 1980), patriliny may "stick" in many cases as it conforms to some basics of evolutionary biology (Hartung 1976; Alexander 1979). That is, the greater reproductive variance of males as opposed to females means that if resources are available to be transferred, it makes more sense to invest them in males: "a daughter's reproductive success is less affected by poverty than a son's" (van den Berghe 1979:96). On this model, in those Austronesian societies where individuals may acquire heritable wealth, patriliny may become common, as is the case in Bantu-speaking populations in Africa (Mace 1996; Holden and Mace 2003). This may be the situation for the Manggarai of Flores, in the "patrilineal" CMP clade, who keep buffalo and horses for prestige and for brideprice payments (LeBar 1975). In this respect, however, they are unlike many Austronesian societies (especially those in the Remote Pacific) who do not have large domestic livestock or similar forms of transferable wealth.

Rates of cultural evolution

By calibrating the language tree with archaeological estimates of the age of the Austronesian language family, we were able to estimate rates of cultural evolution. Two points are of note. First, different dynamics of change are at work over different time periods. The probability of change to unilocal post-marital residence over a 1000-year period was much more than the probability over 100 years, but was less than a linear relationship with time would suggest.

This indicates that there may be limits on the rate of cultural change, or, that some form of equilibrium where societies can switch their residence pattern back and forth is reached. Second, rates of cultural change are not homogenous for all traits. For these societies, change to unilocal residence had a much higher probability (and more variation) of change over the 1000-year period than did descent, indicating that of the two it may indeed be the more labile trait. Goodenough (1956) found that residence patterns in Chuuk, as recorded in census data, could fluctuate throughout a decade. We would expect this to follow from the main sequence hypothesis, if it is the underlying conditions causing residence change, rather than descent, which act first. In addition, Divale (1974) estimated that some societies had unilocal residence for up to a thousand years without developing a unilineal form of descent, so whatever benefits are to be gained by unilocal residence, they do not necessarily cause an immediate transition to unilineality. From an evolutionary perspective, localising one type of kin (male or female) may have benefits that are not to do with inheritance of resources/material wealth, but concern aspects of kin investment through childcare and time allocation.

Conclusion

Using cutting-edge Bayesian comparative methods, we tested a simple but influential anthropological model of kinship change. The Bayesian framework removes the dependence on any single phylogenetic hypothesis, and the comparative test becomes "tree-free". Integrating transition-rates over a tree sample also makes explicit the uncertainty about culture change that so worries many skeptics of the phylogenetic approach.

A phylogenetic comparative method is crucial when testing cross-cultural hypotheses, demonstrated by conventional chi-square tests of association that returned results counter to the phylogenetic analyses. Researchers relying on non-phylogenetic statistics must control for Galton's Problem, not simply because their conventional tests may find an association when the data do not support one, but because they may also fail to detect a real association in the data. Even if we are skeptical of a phylogenetic comparative approach (e.g. Boyd et al. 1997; Borgerhoff Mulder 2001; Nunn et al. 2006), the non-phylogenetic alternatives are extremely unsatisfactory. In contrast, a Bayesian approach allows us to account for uncertainty about population history, estimate the uncertainty in adaptive hypotheses, and develop illuminating models of evolutionary relationships.

Acknowledgements

We wish to thank Russell Gray and Simon Greenhill for their hard work on the ABV database and for generously making it available to us.

References

- Aberle, D. F. (1961). Matrilineal descent in cross-cultural perspective. In Schneider & K. Gough (Eds.), *Matrilineal Descent* (pp. 665-727). Berkeley, CA: University of California Press.
- Alexander, R. D. (1979). *Darwinism and Human Affairs*. Seattle: University of Washington Press.
- Alkire, W. H. (1972). Concepts of order in Southeast Asia and Micronesia. *Comparative Studies in Society and History, 14*(4), 484-493.
- Alkire, W. H. (1974). Cultural adaptation in the Caroline Islands. *Journal of the Polynesian Society*, 123-150.
- Bellwood, P. (1997). *The Prehistory of the Indo-Malaysian Archipelago (2nd Edition)* (2nd ed.). Honolulu: University of Hawai'i Press.
- Blust, R. (1995). The Prehistory of the Austronesian-Speaking Peoples a View from Language. *Journal of World Prehistory*, *9*(4), 453-510.
- Blust, R. (1999). Subgrouping, circularity and extinction: some issues in Austronesian comparative linguistics. In E. Zeitoun and P. Jen-kuei Li (Eds.), *Selected Papers from the Eight International Conference on Austronesian Linguistics* pp. 31-94. Taipei: Academica Sinica.
- Blust, R., Gray, R. D., & Greenhill, S. (2003-2005). Austronesian Basic Vocabulary. Retrieved September, 2005, from http://language.psy.auckland.ac.nz/index.php
- Borgerhoff Mulder, M. (2001). Using phylogenetically based comparative methods in anthropology: more questions than answers. *Evolutionary Anthropology*, *10*, 99-111.
- Boyd, R., Borgerhoff-Mulder, M., Durham, W. H., & Richerson, P. J. (1997). Are cultural phylogenies possible? In P. Weingart, S. D. Mitchell, P. J. Richerson & S. Maasen (Eds.), *Human By Nature: Between Biology and the Social Sciences.* (pp. 355-386). New Jersey: Lawrence Erlbaum Associates.
- Coult, A. D., & Habenstein, R. W. (1965). *Cross tabulations of Murdock's world ethnographic sample*. Columbia: University of Missouri.

- Cunningham, C. E. (1967). Soba: An Atoni village of West Timor. In Koentjaraningrat (Ed.), *Villages in Indonesia* (pp. 63-89). New York: Cornell University Press.
- Denoon, D. (Ed.). (1997). *The Cambridge History of the Pacific Islanders*. Cambridge: Cambridge University Press.
- Divale, W. (1974). Migration, external warfare, and matrilocal residence. *Behavior Science Research*, *9*, 75-133.
- Driver, H. E. (1956). *An Integrational of Functional, Evolutionary, and Historical Theory by Means of Correlations*. Bloomington, IN.: Indiana University Publications in Anthropology and Linguistics Memoir 12.
- Driver, H. E. (1969). *The Indians of North America* (2nd ed.). Chicago: University of Chicago Press.
- Eggan, F. R. (1966). *The American Indian: perspectives for the study of social change*. Chicago: Aldine.
- Ember, C. R. (1975). Residential variation among hunter-gatherers. *Behavior Science Research*, *3*, 199-227.
- Ember, C. R., Ember, M., & Pasternak, B. (1974). On the Development of Unilineal Descent. *Journal of Anthropological Research*, 30, 69-94.
- Firth, R. (1957). A note on descent groups in Polynesia. Man, 57, 4-8.
- Foley, R. (1996). The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness. *Evolutionary Anthropology*, *3*(6), 194-203.
- Fox, R. (1967). Kinship and Marriage. Harmondsworth, Middlesex: Penguin.
- Goodenough, W. H. (1956). Residence Rules. Southwestern Journal of Anthropology, 12, 22-37.
- Gray, J. P. (1999). A corrected Ethnographic Atlas. World Cultures, 10(1), 24-136.
- Hartung, J. (1976). On Natural Selection and the Inheritance of Wealth. *Current Anthropology*, 17(4), 607-622.
- Holden, C. J., & Mace, R. (2003). Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 270(1532), 2425-2433.
- Holden, C. J., Sear, R., & Mace, R. (2003). Matriliny as daughter-biased investment. *Evolution And Human Behavior*, *24*(2), 99-112.
- Holy, L. (1996). Anthropological Perspectives on Kinship. London: Pluto Press.
- Jordan, F. M. (2007). *A Comparative Phylogenetic Approach to Austronesian Cultural Evolution*. Unpublished PhD Thesis, University College London, London.

- Kirch, P. V. (1984). *The Evolution of the Polynesian Chiefdoms*. Cambridge: Cambridge University Press.
- Kirch, P. V., & Green, R. C. (2001). *Hawaiki, Ancestral Polynesia*. Cambridge: Cambridge University Press.
- Korotayev, A. (2003). Division of labor by gender and postmarital residence in cross-cultural perspective: A reconsideration. *Cross-Cultural Research*, *37*(4), 335-372.
- LeBar, F. M. (Ed.). (1975). *Ethnic Groups of Insular Southeast Asia* (Vol. 2). New Haven: HRAF Press.
- Lessa, W. A. (1950). The ethnography of Ulithi Atoll. Washington, D.C.: CIMA.
- Levinson, D. (Ed.). (1990). Encyclopedia of World Cultures. Boston: G. K. Hall.
- Levinson, D., & Malone, M. J. (1980). *Toward explaining human culture: a critical review of the findings of worldwide cross-cultural studies*. New Haven, CT: HRAF Press.
- Mace, R. (1996). Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioral Ecology And Sociobiology, 38*(2), 75-81.
- Mace, R. M., & Sear, R. (2004). Are humans cooperative breeders? In E. Voland, A. Chasiotis & W. Schiefenhoevel (Eds.), *Grandmotherhood: the Evolutionary Significance of the Second Half of Female Life*. Piscataway: Rutgers University Press.
- Mace, R., & Holden, C. J. (2005). A phylogenetic approach to cultural evolution. *Trends In Ecology & Evolution*, 20(3), 116-121.
- Mace, R., & Pagel, M. (1994). The Comparative Method in Anthropology. *Current Anthropology*, 35(5), 549-564.
- Marlowe, F. W. (2004). Marital residence among foragers. *Current Anthropology*, 45(2), 277-284.
- Murdock, G. P. (1949). Social Structure. New York: MacMillan.
- Murdock, G. P. (1967). Ethnographic Atlas. Pittsburg: University of Pittsburg Press.
- Naroll, R. (1970). What Have We Learned from Cross-Cultural Surveys? *American Anthropologist*, 72, 1227-1288.
- Nunn, C. L., Mulder, M. B., & Langley, S. (2006). Comparative Methods for Studying Cultural Trait Evolution: A Simulation Study. *Cross-Cultural Research*, 40(2), 177-209.
- Pagel, M. (1994). Detecting Correlated Evolution on Phylogenies a General- Method for the Comparative-Analysis of Discrete Characters. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *255*(1342), 37-45.
- Pagel, M. (1997). Inferring evolutionary processes from phylogenies. Zoologica Scripta,

- *26*(4), 331-348.
- Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology*, 48(3), 612-622.
- Pagel, M., & Meade, A. (2005). Bayesian estimation of correlated evolution across cultures: A case study of marriage systems and wealth transfer at marriage. In R. Mace, C. J. Holden & S. Shennan (Eds.), *The Evolution of Cultural Diversity: A Phylogenetic Approach* (pp. 235-256). London: UCL Press.
- Pagel, M., & Meade, A. (2006). Bayesian Analysis of Correlated Evolution of Discrete Characters by Reversible-Jump Markov Chain Monte Carlo. *American Naturalist*, 167, 808-825.
- Pagel, M., Meade, A., & Barker, D. (2004). Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology*, *53*(5), 673-684.
- Pawley, A., & Ross, M. (1993). Austronesian Historical Linguistics and Culture History. Annual Review of Anthropology, 22, 425-459.
- Raftery, A. E. (1996). Approximate Bayes factors and accounting for model uncertainty in generalised linear models. *Biometrika*, 83(2), 251-266.
- Rodseth, L., Wrangham, R. W., Harrigan, A. M., & Smuts, B. B. (1991). The Human Community as a Primate Society. *Current Anthropology*, *32*(3), 221-254.
- Sear, R., Mace, R., & McGregor, I. A. (2000). Maternal grandmothers improve nutritional status and survival of children in rural Gambia. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 267(1453), 1641-1647.
- Service, E. R. (1962). *Primitive Social Organization: An Evolutionary Perspective* (2nd ed.). New York: Random House.
- Service, E. R. (1966). *The Hunters*. Englewood Cliffs, NJ: Prentice Hall.
- van den Berghe, P. (1979). *Human Family Systems: An Evolutionary View*. New York: Elsevier.
- White, D. R., Burton, M. L., & Dow, M. (1981). Sexual division of labor in African agriculture: A network autocorrelation analysis. *American Anthropologist*, 83(4), 824-849.
- Yang, Z. H. (1994). Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: Approximate methods. *Journal of Molecular Evolution*, 39(3), 306-314.
- Young, M. (1991). Dobu. In D. Levinson (Ed.), *Encyclopaedia of World Cultures*. New Haven: HRAF Press.