

Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis

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Matrilineal descent is rare in human societies that keep large livestock. However, this negative correlation does not provide reliable evidence that livestock and descent rules are functionally related, because human cultures are not statistically independent owing to their historical relationships (Galton's problem). We tested the hypothesis that when matrilineal cultures acquire cattle they become patrilineal using a sample of 68 Bantu- and Bantoid-speaking populations from sub-Saharan Africa. We used a phylogenetic comparative method to control for Galton's problem, and a maximum-parsimony Bantu language tree as a model of population history. We tested for coevolution between cattle and descent. We also tested the direction of cultural evolution—were cattle acquired before matrilineality was lost? The results support the hypothesis that acquiring cattle led formerly matrilineal Bantu-speaking cultures to change to patrilineal or mixed descent. We discuss possible reasons for matrilineality's association with horticulture and its rarity in pastoralist societies. We outline the daughter-biased parental investment hypothesis for matrilineality, which is supported by data on sex, wealth and reproductive success from two African societies, the matrilineal Chewa in Malawi and the patrilineal Gabbra in Kenya.

Keywords: matrilineal; pastoralism; cultural evolution; coevolution; phylogeny

1. INTRODUCTION

Phylogenetic comparative methods were developed in evolutionary biology to control for relatedness among species (Felsenstein 1985; Harvey & Pagel 1991). These methods can also be used to test adaptive hypotheses about human cultural variation (Mace & Pagel 1994, 1997). Recent developments in phylogenetic methods allow us to test the direction of change among coevolving traits, as well as test for correlated evolution (Pagel 1994). We tested the hypothesis that formerly matrilineal cultures in sub-Saharan Africa became patrilineal after they acquired domesticated cattle.

(a) *Did the spread of cattle lead to the loss of matrilineality?*

Matrilineality is a rare yet recurrent type of social organization found in all regions of the world. In the Standard Cross-Cultural Sample (SCCS), a widely used worldwide cross-cultural sample, 31 out of 186 cultures (17%) are matrilineal (Murdock & White 1969). In matrilineal societies, relatedness through females is culturally more significant than relatedness through males. Descent or group membership is traced through females and most altruistic behaviour is directed towards matrilineal kin, manifested in norms for property inheritance, political succession and residence (Schneider & Gough 1961; Flinn 1981). Matrilineality can be contrasted with patrilineality, in which group membership is traced through males (41% of cultures in the SCCS) and other cultures in which relationships through males and females have a more equal cultural significance (42% of cultures in the SCCS; Murdock & White (1969)).

Matrilineal societies tend to be horticultural, i.e. farmers without plough agriculture or large domestic

livestock. Aberle (1961) tested for ecological correlates of matrilineality in 565 cultures worldwide. Forty-seven out of 84 matrilineal societies in his sample (56%) were horticultural compared with 19 (23%) that were pastoralist or agro-pastoralist. Forty-seven out of 188 horticultural societies (30%) were matrilineal, compared with 19 out of 242 pastoralist or agro-pastoralist societies (8%). The association between matrilineality and horticulture was highly significant. Aberle (1961) concluded that, 'the cow is the enemy of matrilineality, and the friend of patrilineality' (p. 680).

However, Aberle's analysis did not control for the fact that human cultures are historically related and therefore not statistically independent (Mace & Pagel 1994, 1997). Therefore, we cannot be certain whether the ecological correlates of matrilineality that he found result from cultural adaptation or history (shared ancestry).

(b) *Phylogenetic methods and cross-cultural comparison*

Human cultures are historically related, often hierarchically. Cultural traits tend to be transmitted from older to younger generations within populations, like biological traits within species (Cavalli-Sforza & Feldman 1981; Hewlett & Cavalli-Sforza 1986; Guglielmino *et al.* 1995; Holden & Mace 1999, 2002; Hewlett *et al.* 2002). To test whether two cultural traits are functionally related, we need to know how many times two traits have independently coevolved, distinguishing between correlations due to shared ancestry and convergent cultural evolution; only the latter is evidence for adaptation. In anthropology, this is known as Galton's problem. It is similar to the problem of non-independence among species in comparative biology. Mace & Pagel (1994, 1997) proposed that phylogenetic comparative methods from evolutionary biology could be applied in anthropology, to test adaptive hypotheses cross-culturally while controlling for Galton's problem.

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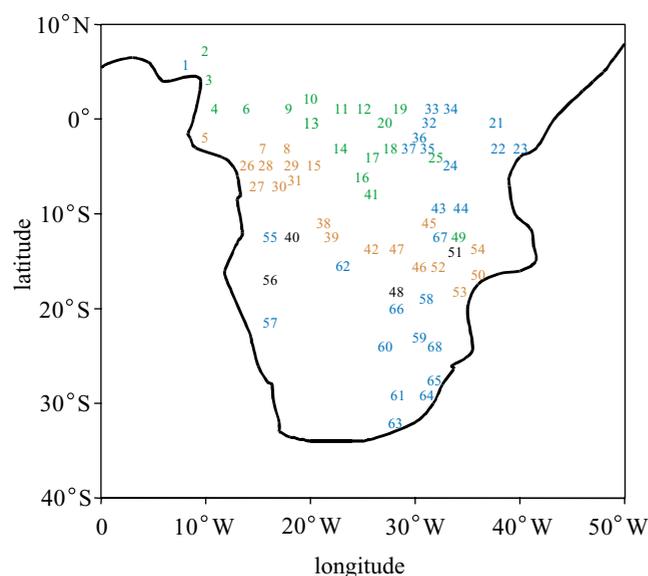


Figure 1. Map of 68 Bantu- and Bantoid-speaking cultures. Latitude and longitude were taken from Murdock (1967). Numbers correspond to column 1 in table 1, which gives the name and language of each culture. Descent rules and presence or absence of cattle are indicated by colours (green: patriliny or mixed descent, no cattle; blue: patriliny or mixed descent, with cattle; red: matriliney, no cattle; black: matriliney, with cattle).

In phylogenetic comparison, biological taxa or cultures are placed on a tree that represents past relationships among populations. Internal nodes on the tree represent hypothetical ancestral populations. Past character states are inferred from the distribution of characters in contemporary populations (at the tips of the tree). Rather than testing for a correlation between two or more variables in the sample (i.e. in modern populations), phylogenetic methods test for correlated evolution along the branches of the tree. The problem of non-independence among populations is avoided because two branches descending from a node are independent (Felsenstein 1985; Harvey & Pagel 1991).

When using phylogenetic methods in anthropology, we must assume that cultures are related in a hierarchical or tree-like way. Genetic and linguistic trees have been used as models of past relationships among cultures (Cavalli-Sforza *et al.* 1988; Holden & Mace 1997, 1999). However, the validity of using trees to describe cultural relationships has been questioned, because there is considerable interconnectedness among cultures. This has led some researchers to recommend using network rather than tree models (c.f. Bateman *et al.* 1990; Moore 1994; Gray & Jordan 2000; Bellwood 2001). We would argue that how well a tree model represents population history probably varies between regions and language groups; in some regions, a tree model may fit the data well. Holden (2002) found that a tree model fitted the Bantu languages well, probably because the Bantu linguistic radiation reflects a population expansion associated with the spread of farming (Ehret 1998, pp. 46–7; Bellwood 2001).

In a phylogenetic analysis, it is also assumed that cultural traits are mostly transmitted ‘vertically’ from older to younger generations within a population. This assumption is sometimes questioned because we know that

‘horizontal’ transmission of cultural traits between neighbouring populations also occurs (Cavalli-Sforza & Feldman 1981; Guglielmino *et al.* 1995). However, a phylogenetic approach does allow for horizontal transmission, which is treated in the same way as independent innovation. If two traits tend to be adopted *together*, this is evidence for a functional relationship between them. Moreover, previous studies have suggested that the transmission of cattle keeping and descent in Africa is largely vertical. Both cultural traits show a strong correlation with language group, an indicator of cultural ancestry (Guglielmino *et al.* 1995; Holden & Mace 2002).

In this analysis, we tested whether adopting cattle led to the loss of matriliney and/or the gain of patriliney in 68 Bantu-speaking cultures, using the phylogenetic comparative method of Pagel (1994) to control for non-independence among cultures. This method also let us test the direction of evolutionary change—did the adoption of cattle precede the loss of matriliney? In § 4 we discuss the possible adaptive function of matrilineal descent and its association with horticulture (Holden *et al.* 2003).

2. MATERIAL AND METHODS

(a) *Cross-cultural sample and tree*

We focused on Bantu-speaking populations because they provide a large cross-cultural sample for which we have a detailed language tree. Bantu is a large group of over 450 related languages found across Africa below *ca.* 5° North. We use the term Bantu in the same sense as Ruhlen’s (1991) Narrow Bantu. Bantoid is a broader language group to which Bantu belongs, and is a part of the Niger-Kordofanian language phylum (Ruhlen 1991). The sample included 68 Bantu- and Bantoid-speaking cultures for which we had both linguistic and ethnographic data (table 1). Their locations are shown in figure 1.

We used the Bantu language tree of Holden (2002) as a model of past relationships among the 68 cultures. This language tree mirrors the spread of farming across central and southern Africa between *ca.* 3000 BC and AD 200, suggesting that it is a good model of population history for Bantu-speaking cultures (Holden 2002, 2003). Linguistic data used to build the tree were taken from Bastin *et al.* (1999). The tree was constructed using maximum parsimony, using the computer program PAUP* 4.0 (Swofford 1998). The Bantoid languages Tiv and Ejagham were used as outgroups to root the tree. Seven languages were pruned from the original tree (Holden 2002) because those cultures lacked data on descent rules or cattle.

Ethnographic data were taken from the Ethnographic Atlas, or EA (Murdock 1967). We used the Ethnographic Atlas because it includes a large number of cultures. (By comparison, the Human Relations Area Files, a more recent cross-cultural database, only included five Bantu-speaking cultures for which we also had linguistic data, compared with the 68 cultures in our sample). Using data that were previously coded by an independent researcher also ensures that the data are not biased by our expectations. Out of the 68 cultures in the sample, 24 (35%) are matrilineal and 37 (54%) are patrilineal. Cattle are present in 30 out of 68 cultures in the sample (44%). Matrilineal descent is found mostly in the ‘matrilineal belt’ of central Africa, while cattle tend to be clustered in east and southern Africa (figure 1). For the analysis, matriliney and patriliney were coded as two separate binary variables (present or absent). The relationships between matriliney and cattle, and patriliney and cattle, were

Table 1. Sixty-eight Bantu- and Bantoid-speaking cultures.

(Numbers in column 1 correspond to numbers in figure 1, where each group's geographical location is shown. Columns 2 and 3 show the language or dialect name and code (originally assigned by Malcolm Guthrie) from Bastin *et al.* (1999). Columns 4 and 5 show the ethnographic name and code from the Ethnographic Atlas (EA; Murdock 1967). Columns 6 and 7 show descent rules and presence or absence of cattle, using data from Murdock (1967).)

no.	language or dialect name	Guthrie code	ethnographic atlas name	EA code	descent type	cattle
1	Ejagham	800	Ekoi	Af18	patriliny	yes
2	Tiv	802	Tiv	Ah3	patriliny	no
3	Duala 2 d. pongo	A24/2	Duala	Ae12	patriliny	no
4	Fang 1 d. ntumu	A75/1	Fang	Ae3	patriliny	no
5	Mpongwe	B11a	Mpongwe	Ae46	matriliny	no
6	Kota 1 madungwe	B25/1	Kota	Ae41	patriliny	no
7	Teke-W5 d. lali Bouenza	B73/5	Teke5	Ac19	matriliny	no
8	Sakata	C34	Sakata	Ac24	matriliny	no
9	Lingala	C36	Ngala	Ae28	patriliny	no
10	Ngombe	C41	Ngombe	Ae39	patriliny	no
11	Mbesa	C51	Bombesa (Mbesa)	Ae36	patriliny	no
12	Likile	C57	Lokele (Likile)	Ae27	patriliny	no
13	Mongo1 d. nkundo	C61/1	Nkundo Mongo	Ae4	patriliny	no
14	Kela	C75	Kela	Ae21	patriliny	no
15	Lele 1 Mboombe	C84/1	Lele	Ac23	matriliny	no
16	Songe	D10S	Songe	Ae18	patriliny	no
17	Binja-N 1 d. Ulindi	D24/1	Songola	Ae11	patriliny	no
18	Lega 3 Mwenga	D25/3	Rega	Ae17	patriliny	no
19	Bira 2 Badiya	D32/2	Bira	Ae30	patriliny	no
20	Kumu 2	D37/2	Kumu	Ae32	patriliny	no
21	Gikuyu	E51	Kikuyu	Ad4	patriliny	yes
22	Caga 1 d. moshi kilema	E62/1	Chagga	Ad3	patriliny	yes
23	Giryama1 Goshi	E72a/1	Giriama	Ad32	patriliny	yes
24	Nyamwezi	F22	Nyamwezi	Ad20	ambilineal	yes
25	Sumbwa	F23	Sumbwa	Ad47	patriliny	no
26	Yombe 1 Zaire	H12b/1	Yombe	Ac8	matriliny	no
27	Sikongo	H16h	Kongo	Ac14	matriliny	no
28	Sundi 4 Boko	H16i/4	Sundi	Ac18	matriliny	no
29	Yaka 2 Kasongo	H31/2	Songo	Ac25	matriliny	no
30	Yaka 4 d. sud	H31/4	Yaka	Ac20	matriliny	no
31	Suku	H32	Suku	Ac17	matriliny	no
32	Hima	J13	Nyankale	Ad45	patriliny	yes
33	Ganda	J15	Ganda	Ad7	patriliny	yes
34	Soga	J16	Soga	Ad46	patriliny	yes
35	Zinza	J23	Zinza	Ad49	patriliny	yes
36	Rwanda 1	J61/1	Ruanda	Ae10	patriliny	yes
37	Rundi	J62	Rundi	Ae8	patriliny	yes
38	Ciokwe	K11	Chokwe	Ac12	matriliny	no
39	Lwena 1	K14/1	Luvale (Luena)	Ac11	matriliny	no
40	Gangela	K19	Luimbe (Ngangela)	Ac28	matriliny	yes
41	Luba-Sh	L33	Luba	Ae6	patriliny	no
42	Kaonde	L42	Kaonde	Ac32	matriliny	no
43	Mambwe	M15	Mambwe	Ac43	patriliny	yes
44	Nyakyusa 2 Mbeya	M31/2	Nyakyusa	Ad6	patriliny	yes
45	Bemba	M42	Bemba	Ac3	matriliny	no
46	Lala	M52	Lala	Ac33	matriliny	no
47	Lamba	M54	Lamba	Ac5	matriliny	no
48	Tonga 1 Zimbabwe	M64/1	Plateau Tonga	Ac30	matriliny	yes
49	Tumbuka 2 Mzimba	N21/2	Tumbuka	Ac36	patriliny	no
50	Nyanja	N31a	Nyanja	Ac38	matriliny	no
51	Cewa	N31b	Chewa	Ac10	matriliny	yes
52	Kunda	N42	Kunda	Ac37	matriliny	no
53	Sena	N44	Sena	Ac40	matriliny	no
54	Yao 2 Mbesa	P21/2	Yao	Ac7	matriliny	no

(Continued.)

Table 1. (Continued.)

no.	language or dialect name	Guthrie code	ethnographic atlas name	EA code	descent type	cattle
55	Umbundu 1 Calusinga	R11/1	Mbundu	Ab5	dual descent	yes
56	Ndonga	R22	Ambo	Ab19	matriliny	yes
57	Herero	R31	Herero	Ab1	dual descent	yes
58	Shona	S10	Shona	Ab18	patriliney	yes
59	Venda	S21	Venda	Ab6	dual descent	yes
60	Tswana	S31	Tswana	Ab13	bilateral	yes
61	Sotho-S	S33	Sotho	Ab8	patriliney	yes
62	Lozi	S34	Lozi	Ab3	ambilineal	yes
63	Xhosa	S41	Xhosa	Ab11	patriliney	yes
64	Zulu	S42	Zulu	Ab12	patriliney	yes
65	Swati	S43	Swazi	Ab2	patriliney	yes
66	Ndebele	S44	Ndebele	Ab9	patriliney	yes
67	Ngoni	S45	Ngoni	Ac9	bilateral	yes
68	Tsonga	S53	Thonga	Ab4	patriliney	yes

tested separately. Some cultures had mixed descent systems, including dual descent (i.e. both patrilineal and matrilineal descent groups being present), ambilineal descent and bilateral kin groups (table 1). Such descent types were coded as neither patrilineal nor matrilineal since neither form was predominant.

(b) *Test for coevolution: cattle and descent rules*

We used the phylogenetic comparative method DISCRETE (Pagel 1994) to test for coevolution between cattle and matriliney, and cattle and patriliney. This is a maximum-likelihood (ML) test for correlated evolution among discrete binary characters on a tree, implemented by a computer program available from Mark Pagel (*DISCRETE*: see <http://www.ams.reading.ac.uk/zoology/pagel>).

The likelihood of the data (i.e. the character states observed at the tips of the tree) is estimated, given the tree and the model of evolution. Evolution in each character along the tree branches is modelled as a Markov process, in which the probability of change in a trait is dependent on its current state. Two models are fitted, an independent model (L_i) in which evolution in each trait is independent of the state of the other trait, and a dependent model (L_d) in which the probability of change in one trait is dependent on the state of the other trait. A likelihood ratio (LR) test was used to compare the log likelihoods of the independent and dependent models. One hundred Monte Carlo simulations were run to generate a null distribution of likelihood ratios, to test the significance of the observed LR. If the dependent model fits the data significantly better than the independent model, this indicates that the state of one trait affects the probability of change in the other, and that the two traits probably coevolve.

We tested whether evolution was punctuated or gradual by fitting the parameter κ (kappa), which estimates how far evolution is a function of branch length. Branch lengths were adjusted using κ for the dependent model (Pagel 1994; *DISCRETE: user's manual*: see <http://www.ams.reading.ac.uk/zoology/pagel>).

We tested whether the earliest Bantu-speaking populations were matrilineal or patrilineal by estimating ancestral character states using ML, treating a difference of two log likelihoods as significant. We also tested whether cattle were present or absent among ancestral Bantu-speaking populations.

(c) *Testing the direction of evolution*

DISCRETE can also be used to test the probable direction of evolution, i.e. which of two cultural traits changed first. This allows us to test the hypothesis that adopting cattle preceded the loss of matrilineal descent and/or the adoption of patrilineal descent.

We tested which transitions were non-significant by deriving a 'minimum model' (Pagel 1994) showing which transition rates in the dependent model could be set to zero without reducing the overall significance of the model. First, the significance of each transition was tested by setting the rate of this transition to zero and testing whether this significantly decreased the fit of the model. All individually significant transitions were retained. In addition, at least one transition to and from each state was retained, choosing the transition with the highest rate. An LR test was used to test whether the fit of the reduced model was significantly worse than the 8-parameter model.

We also tested whether matriliney is more likely to be lost in cultures with cattle by fixing the rate for the loss of matriliney to be equal in cattle keeping and non-cattle keeping populations, and testing whether this reduced the significance of the model.

3. RESULTS

Figure 2 illustrates the distribution of cattle and descent on the tree. These cultural traits are non-randomly distributed on the tree, indicating that any test for correlation among these traits that does not control for population history is likely to give misleading results.

Using ML to reconstruct ancestral character states on the tree, neither matriliney nor patriliney was significantly more likely among the earliest Bantu-speaking populations. Cattle were absent at all deeper branches on the tree (towards the root), being adopted more recently in southwest, east and southeast Africa.

(a) *Coevolution of cattle and descent rules*

The results support the hypothesis that there was a significant negative relationship between matriliney and cattle in past Bantu-speaking cultures. When comparing matriliney with all other types of descent (including patriliney and

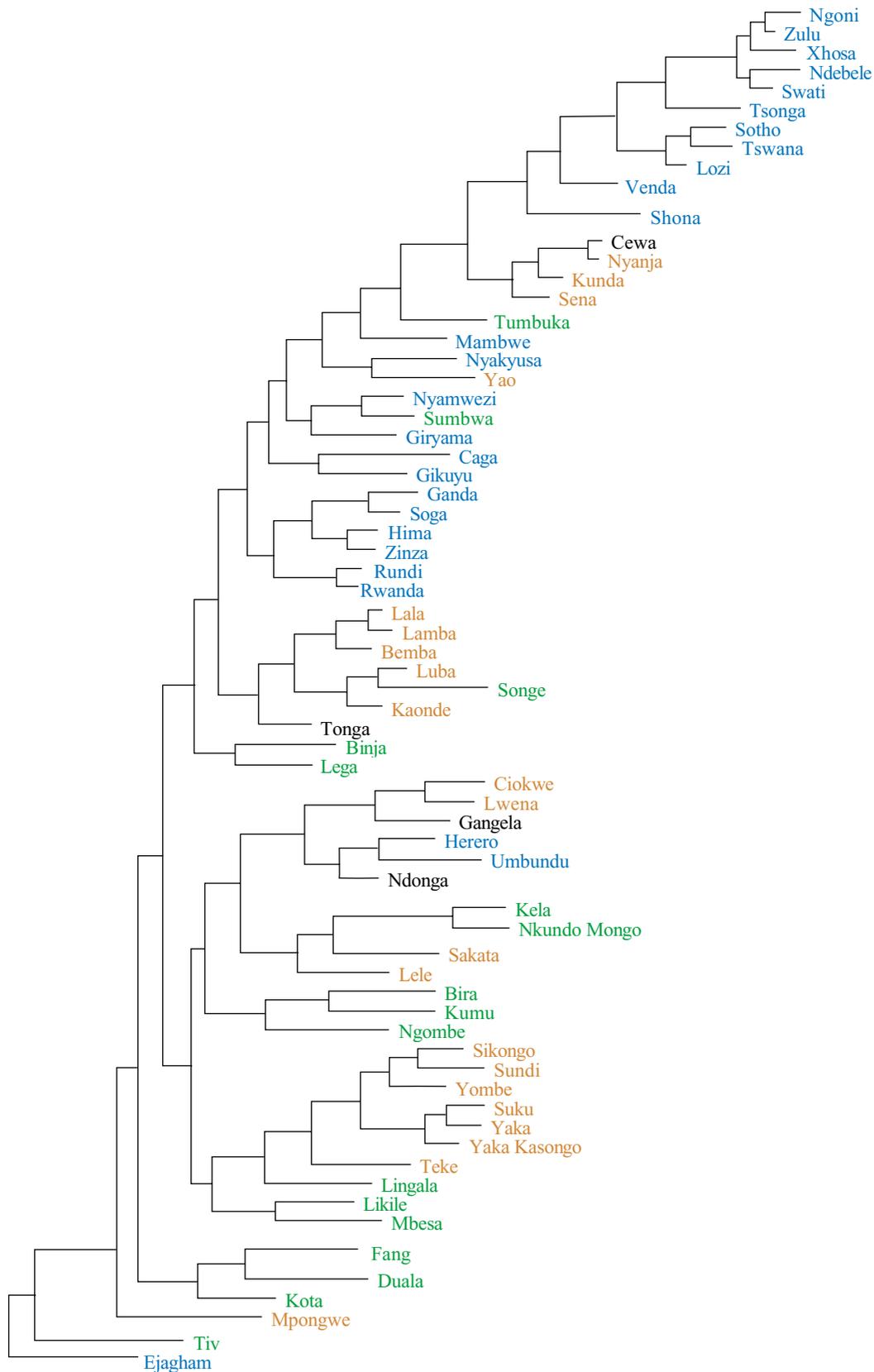


Figure 2. Bantu language tree, used to represent past relationships among the 68 cultures in the sample (modified from Holden 2002). Descent rules and the presence, or absence, of cattle are indicated by colours as listed in legend to figure 1.

mixed descent), cattle and matriliney are significantly negatively related ($L_i = -62.52$, $L_d = -56.80$, $LR = 5.72$, $p = 0.02$). However, when comparing patriliney with all other types of descent, there was no evidence that patriliney

(strictly defined) and cattle-keeping coevolved ($L_i = -69.88$, $L_d = -68.40$, $LR = 1.49$, n.s.). The independent and dependent models for the evolution of matriliney and cattle are shown in figure 3.

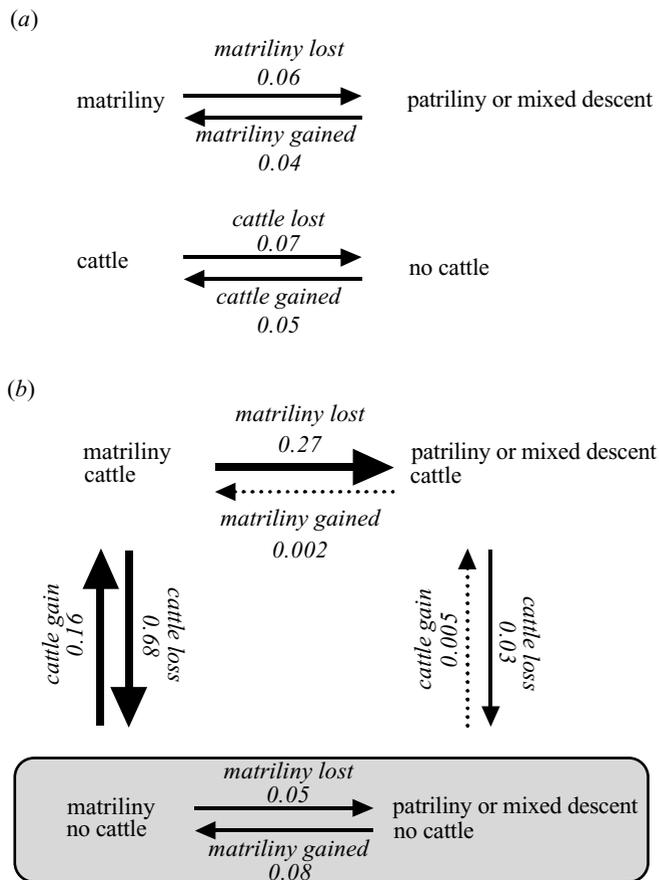


Figure 3. Transitions between character states for matriliney and cattle. (a) Independent model. The four possible transitions include the gain and loss of matriliney and cattle. (b) Dependent model. The eight possible transitions include the gain and loss of matriliney and cattle, dependent on the state of the other variable. The likelihood of the dependent model was significantly higher, indicating that cattle and matriliney coevolve ($L_a = -62.52$, $L_d = -56.80$, $LR = 5.72$, sig. $p = 0.02$). Transition rates for the unrestricted 8-parameter dependent model are shown next to each arrow. Arrow thickness indicates transition rate. Thick lines indicate rates of change 10 times higher than thin lines, and dotted arrows indicate non-significant transitions, whose rates do not differ significantly from zero. The grey area indicates the probable ancestral state for Bantu-speaking cultures: we cannot reconstruct descent rules with any certainty, but cattle were absent.

The parameter κ , which estimates how far character evolution is related to branch lengths, was estimated to be 0.45 for the dependent model for cattle and matriliney. This indicates that evolution in these cultural traits is partly a function of branch lengths, which are (arguably) related to time. The κ parameter was fitted when estimating the rates of change in each character, so that longer branches were shortened proportionately. Fitting this parameter significantly improved the fit of the dependent model.

(b) Direction of evolution

Results support the hypothesis that adopting cattle leads to the loss of matriliney. Six parameters were retained in the minimum model (figure 3b). The two non-significant transitions were as follows. (i) Cultures without cattle with

patrilineal or mixed descent did not gain cattle directly. Instead, they first became matrilineal, then acquired cattle, and then became patrilineal. (ii) Cultures that have cattle and patrilineal or mixed descent do not become matrilineal. Patrilineal or mixed descent with cattle appears to be a stable cultural state, rarely lost once achieved.

If we set the transition rates for losing matriliney to be equal in cattle-keeping and non-cattle-keeping cultures, this reduces the fit of the model. This indicates that matriliney is significantly more likely to be lost in cultures that keep cattle, compared with cultures without cattle.

4. CONCLUSION AND DISCUSSION

(a) Matriliney and cattle in the prehistory of Bantu-speaking populations

Our results support the hypothesis that acquiring cattle led to the loss of matriliney in Bantu-speaking cultures. We can reconstruct the following scenario in the prehistory of Bantu-speaking populations, which is also supported by historical linguistics and archaeological evidence (Vansina 1990; Ehret 1998; Marshall 2000; Smith 2000; Van Neer 2000).

It is thought that the earliest Bantu-speaking populations lived in the rainforests of equatorial Africa. It is uncertain whether they were matrilineal or patrilineal, but we know that they lacked cattle. The reason why we cannot infer descent rules among early Bantu-speakers with certainty is probably because descent rules are highly variable across equatorial African populations today, and also change relatively rapidly (figures 1–3). However, our uncertain result is also consistent with independent evidence from historical linguistics, using which Vansina (1990) argued that kinship and social organization among Bantu-speaking cultures in equatorial Africa was originally bilateral rather than matrilineal or patrilineal (c.f. Ehret 1998, pp. 149–155).

Using ML, it appears that cattle were absent at all deeper nodes on the tree but were later acquired in southwest, east and southeast Africa. This is consistent with archaeological and linguistic evidence that cattle were absent among early Bantu-speakers in central Africa (Vansina 1990; Van Neer 2000). Both matriliney and patriliney later developed in central Africa, although cattle were not adopted for ecological reasons (Vansina 1990, pp. 92, 106–114, 152–155; figure 1). Factors other than cattle must be responsible for the variation in descent in central Africa, which is probably why there are significant transitions between matriliney and patriliney among Bantu-speaking cultures that do not keep cattle (figure 3b).

In our sample, cattle were found mostly in east and southern Africa (figure 1), so transitions relating to cattle only apply to these regions. Linguistic and archaeological evidence suggests that the earliest Bantu-speakers in east and southern Africa were Early Iron Age farmers, who practised mixed farming with an initially small number of livestock, mostly sheep (Phillipson 1993; Ehret 1998; Holden 2002; Mitchell 2002). Cattle later became more important in subsistence in some parts of southern Africa, notably in the Toutswe culture in modern Botswana from the 7th century AD (Phillipson 1993, pp. 194–195; Mitchell 2002, p. 275) and in east Africa after 1000 AD

(Oliver 1982; Phillipson 1993, pp. 225–240). As discussed above, our results suggest that patrilineal cultures did not gain cattle directly (figure 3*b*). This suggests that Bantu-speaking cultures in east and southern Africa were matrilineal before they acquired cattle, and then become patrilineal. We infer that matriliney may have been more widespread among Early Iron Age Bantu-speaking farmers than it is in east and southern Africa today.

This inference is also supported by evidence from historical linguistics. Ehret (1998, pp. 149–155) has reconstructed vocabulary items relating to kin institutions in the early Bantu-speaking communities of east and southern Africa. He argues that these societies had both matrilineages and patrilineages—i.e. dual descent—but that matrilineages were originally more important in their social organization. He also states that Bantu-speaking societies in the East African Lakes region, which are mostly patrilineal today, were originally matrilineal, as shown in their feminine metaphors for ‘lineage’, which include ‘belly’ and ‘house,’ both items that are associated with women (Ehret 1998, p. 153).

(b) *Why are matriliney and cattle negatively correlated?*

Using a behavioural ecological approach, matriliney and other aspects of human social organization can be seen as flexible, adaptive responses to the environment. We have proposed elsewhere that matrilineal descent might arise from daughter-biased investment by parents and/or grandparents (Holden *et al.* 2003). Wealth inheritance to daughters is adaptive if the marginal benefit of wealth to sons does not compensate for the risk of non-paternity in sons’ offspring. We suggested that, for parents, the benefits of wealth inheritance to sons and daughters are equal if

$$B_S/B_D = 1/P,$$

where B_S is the benefit of wealth to a son, B_D is the benefit to a daughter, and P is the probability of paternity. If $B_S/B_D > 1/P$ then it is adaptive to transmit wealth to sons; if $B_S/B_D < 1/P$ then it is adaptive to transmit it to daughters.

Any resource that benefits sons more than daughters will tend to increase male-biased parental investment, if paternity uncertainty remains constant. In many African societies, livestock are used for bridewealth, a marriage payment from the groom or his family to the bride’s family that enables men to marry. Herds may allow men to support several wives, a human form of resource-holding polygyny. They also require defence against raiders. Therefore, livestock tend to be transmitted to sons, promoting patriliney (Orians 1969; Lancaster 1976; Hartung 1982; Mace 1996). In this analysis, we have focused on cattle, because they are the only large livestock found in our sample. However, we would expect similar high marginal benefits for sons to be associated with other large, valuable livestock such as camels.

In contrast to livestock, the fitness benefits of land under horticultural farming may be more similar for sons and daughters. Therefore, in horticultural societies, daughter-biased land inheritance, leading to matriliney, may be an adaptive parental investment strategy because of the risk of paternity uncertainty in sons’ children (Holden *et al.* 2003).

This hypothesis was supported by a study comparing the effects of wealth on fertility for men and women in two African societies, the Gabbra and the Chewa. The Gabbra are camel herders in Northern Kenya, who are patrilineal with son-biased wealth inheritance. They speak a non-Bantu language and keep camels rather than cattle, but share many similarities with the Bantu-speaking cattle owners in our sample, notably using livestock for bride-wealth, polygynous marriage and raiding. The Chewa are horticulturalists in Malawi who are matrilineal, transmitting land from mother to daughter. We found that in the Gabbra, the benefit of wealth (camels) to sons was 2.98 times higher than to daughters, so son-biased wealth inheritance would be adaptive unless $P < 0.36$. In the Chewa, the benefit of wealth (land) for sons was only 1.069 times higher than to daughters, so daughter-biased investment would be adaptive if $P < 0.94$ (Holden *et al.* 2003). A further research question would be to test whether cattle have a similarly high marginal benefit to sons in Bantu-speaking populations.

(c) *Methodological issues*

This analysis has shown how recent advances in phylogenetic comparative methods can be used to test adaptive hypotheses in cultural evolution.

We used a maximum-parsimony language tree to model population history. Maximum-parsimony language trees have several advantages compared with either traditional linguistic trees or lexicostatistical trees. Parsimony methods use a computer-implemented algorithm to search for the best tree according to an explicit optimality criterion (Gray & Jordan 2000; Holden 2002). The resulting tree(s) is bifurcating, with branch lengths proportional to the number of linguistic innovations. Unlike lexicostatistical trees, which are based on a measure of overall similarity among languages, parsimony methods only use derived characters or shared innovations to define descent groups. In principle, ML could also be used to construct language trees (Pagel 2000*b*), although computing constraints led us to use parsimony here. We anticipate that the next generation of language trees will see the incorporation of a ML approach to tree construction.

It is controversial how far branch lengths on language trees are related to time (Swadesh 1971; Blust 2000; Pagel 2000*a*). However, branch lengths on maximum-parsimony trees probably provide a better estimate of time than traditional linguistic trees that assign equal lengths to all branches (which is equivalent to specifying a punctuated model of evolution) or lexicostatistical trees, whose topology is affected by unequal rates of linguistic evolution across the tree (Blust 2000).

We used a ML comparative method to test for correlated evolution among cultural traits. Branch lengths on the tree were used to estimate the rate of cultural evolution in descent rules and cattle keeping. The branch-length scaling option in DISCRETE was used to test how far cultural evolution is a function of branch length, with branch lengths adjusted accordingly. The results showed that cultural evolution in matriliney and cattle-keeping is related to branch lengths, and thus probably to time.

In ML comparative methods, transition rates are estimated individually for each possible character change. This allows us to test the direction of evolutionary change

in correlated traits even when the two traits change on the same branch of the tree (Pagel 1994). The results of this analysis supported the directional hypothesis that acquiring cattle led to the loss of matriliney in Bantu-speaking cultures (figure 3b).

Cultural evolution is often thought to occur faster than biological evolution. A ML approach permits high transition rates to be estimated for labile characters, unlike parsimony methods, which minimize character change, assuming it to be rare. We can assess the assumption that cultural traits are labile by examining the estimated rates of character change. The results of this analysis showed that all types of cultural transition involving the gain and loss of matriliney and cattle occur (figure 3b). However, some transitions are much more likely than others, for example, matrilineal cultures with cattle are far more likely to adopt patrilineal or mixed descent than the other way round, whereas cattle-owning cultures with patrilineal or mixed descent rules rarely, if ever, become matrilineal.

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