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Scars for survival: high cost male initiation rites are strongly associated with desert habitat in Pama-Nyungan Australia

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ABSTRACT

Costly ritual behaviours have frequently been of interest to evolutionary researchers seeking to understand whether they have an adaptive benefit. Here we examine the costliness of initiation rituals across a large group of hunter-gather societies in Pama-Nyungan Australia and compare these with a range of possible adaptive benefits, including warfare, food sharing, demography, and mate competition. We find that in Australia, desert habitat was mostly strongly associated with these rites. Such rites may support the collective action, such as food sharing, necessary for survival in such a precarious environment.

1. Introduction

Evolutionary researchers have frequently explored the adaptive significance of religious and ritual practices, particularly those that entail significant costs to the participant. Some authors, using the logic of sexual selection and signalling theory (Zahavi, 1975, Grafen, 1990), have examined whether costly initiation rites could be a form of mating competition in which participants demonstrate their ability to survive the rites and thereby signal their overall genetic quality (Low, 1979; Ludvico & Kurland, 1995; Singh & Bronstad, 1997). The logic of costly signalling has been extended further to explore whether such signals support the establishment of co-operative groups thereby securing the benefits of their collective action. Ritual participation may be acting as a costly signal that conveys genuine commitment to the community and its moral and social codes (Brusse, 2020; Bulbulia & Sosis, 2011; Shaver & Bulbulia, 2016; Sosis, 2003). Costliness may be a particularly important feature of ritual practice because it increases the reliability of a signal by making its display hard to fake, discouraging dishonest commitment displays (Irons, 2001; Sosis, 2003). For costly signalling to be effective, high quality signallers should not just be able to bear higher costs but have a greater benefit compared to cost than low quality signallers (Johnstone, Rands, & Evans, 2009; Lang, Chvaja, Purzycki, Václavík, & Staněk, 2022; Lang, Chvaja, & Purzycki, 2024). Such a differential is often present in ritual; individuals able to incur high costs are willing to do so because this enables them to enter the group and participate in its successful collective actions, thus achieving a greater net benefit overall than non-participants. Participation in costly rituals has been positively associated with various prosocial outcomes such as reputation for trustworthiness (Hall, Cohen, Meyer, Varley, & Brewer, 2015; Purzycki & Arakchaa, 2013; Ruffle & Sosis, 2007; Shaver et al., 2018; Tan & Vogel, 2008), social network size (Power, 2017), longevity of communes (Sosis & Bressler, 2003) and participation in warfare (Henrich, Bauer, Cassar, Chytilová, & Purzycki, 2019; Sosis, Kress, & Boster, 2007). Warfare represents a particularly extreme form of group commitment as individuals may owe their lives to the sacrifice of other group members and they in turn may be required to give their lives for others. In a comparative study of 60 societies using data from the Human Relations Area Files, Sosis et al. (2007) found that males in societies that engage in high rates of inter-group warfare endure the costliest rites, but that there was no association between these rites and other collective actions including food sharing. They suggest that reciprocity can be employed in this activity which prevents free-riders from accruing long term benefits. In warfare, however, men cannot solely rely on expectations of future cooperation since they may not be alive to reciprocate.

In this study we test for a range of possible adaptive benefits of costly rituals across a large group of societies in Pama-Nyungan Australia. These communities have a number of characteristics that make them a relevant choice for examining the adaptive significance of costly ritual practice. Firstly, ritual, and in particular adolescent initiation for males, plays a central role in Australian life and is frequently costly to the individual. Rites include sub-incision (a deep cut along the underside of the penis), scarification, tooth extraction and fire ordeals (Berndt &

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Berndt, 1996; Maddock, 1974; Meggitt, 1974). Secondly, there is abundant ethno-historic evidence of conflict between groups in Australian aboriginal societies (reviewed by Allen, 2014), suggesting it is a relevant collective action problem. Thirdly, both the costliness of initiation and the intensity of conflict vary between societies, allowing meaningful comparisons to be made. Fourthly, all these societies are hunter-gatherers. Sosis et al. found that costly rites tended to be more associated with hunter-gatherer societies and they suggest this is because larger societies are able to coerce participation in warfare through punishment (*e.g.* imprisonment), so are less dependent on ritual signs of commitment. The finding suggests a detailed analysis of costly male rituals across a large group of hunter-gathers might yield additional insight into the evolution of these rites. Australian communities did not adopt agricultural methods to any great extent, despite proximity to New Guinea horticulturalists in the north (Lourandos, 1997, Barker, 2009: 70). The material is an important dataset for evolutionary studies because it is one of the largest hunter-gatherer groups in the world for which we have both comprehensive ethnography and a well-attested language phylogeny (Bouckaert, Bowern, & Atkinson, 2018).

1.1. Hypotheses & predictions

We examine whether costly ritual practices serve to signal group commitment by testing whether they are associated with two variables associated with group collective action: warfare and beyond-household food sharing, and two further variables: group size and kinship. We also examine whether male rites serve to signal mate quality by testing whether they are associated with more polygynous societies. To control for the possibility that trait similarities might be the result of common ancestry not adaptation, we test associations with a comparative phylogenetic approach using the Pama-Nyungan language phylogeny (Bouckaert et al., 2018) as the control for non-independence (Mace & Holden, 2005).

1.1.1. Warfare

Whilst ethnographic accounts of inter-group conflict in Australia may relate to pressures brought about by colonial expansion, and may suffer from ethnocentric bias, they demonstrate some consistency in their descriptions of two main types of combat (Allen, 2014; Basedow, 1925; Warner, 1937; Wheeler, 1910). Firstly, regulated settling of disputes that normally involves the exchange of spears and sometimes individual hand to hand fighting. This only rarely led to serious injuries or fatalities (as the combat was structured in a way to avoid them). Secondly, active raiding of other groups that involved expeditions to other residential camps for the purposes of killing one or more of their party. Reasons for these raids included revenge for murders or unexplained deaths and disputes over women or territory. Such attacks nearly always resulted in fatal encounters and regularly escalated into repeated cycles of violence. Based on these descriptions, we consider that it is the presence of active raiding (not regulated settling of disputes) that equates closest to the presence of 'warfare' as commonly defined *i.e.* as armed combat between two political communities (Otterbein, 1994). We would therefore expect that the presence of costly rites would be expected to be associated with the presence of active raiding if the costly signalling hypothesis is supported.

1.1.2. Food sharing

The practice of sharing food within hunter gatherer groups is widespread and well documented, however there are few quantitative comparisons and none, to our knowledge, which relate specifically to Australia. In cross cultural studies, the presence of resource stress, including chronic food scarcity, low plant and animal richness and low and unpredictable precipitation, was predictive of more customary beyond-household sharing of resources (Ember, Skoggard, Ringen, & Farrer, 2018; Skoggard, Ember, Pitek, Jackson, & Carolus, 2020). In this study we have therefore used environmental ecology, specifically desert location, as a proxy for a high level of beyond-household food sharing. Australian deserts are one of the world's most hostile inhabited places (Gould, 1980: 61). Rainfall is both low and highly variable and they contain a much lower range of edible species than, for example, the African Kalahari desert (Gould, 1969). As well as the cross-cultural data, there is strong theoretical support to suggest that food sharing intensity is associated with high daily variances in food acquisition (Kaplan et al., 1985) and diet composition (Gurven, 2004). Ethnographies report the use of extensive food sharing in the Australian desert. Even small game is redistributed such that 'everyone gets a share'… with people compelled to share food 'in order to assure that, when an emergency arises… the relationships that require sharing between kin are strong' (Gould, 1981: 432–5 quoted in Gurven, 2004). As well as food, sharing access to water such as creeks and waterholes is an important characteristic of Australian desert societies (Meggitt, 1974: 67), where rainfall is not only low but localised and highly variable (Gould, 1969). Furthermore, authors specifically examining ritual variation have suggested costly rites may be particular important in marginal habitats such as deserts, with the strong bonds forged through these rites enabling groups to be better adapted to compete for limited resources (Hayden, 1993; Whitehouse, 2004; Whitehouse, 2022).

1.1.3. Demography & Kinship

If male rites signal group commitment we should also expect that larger groups, which are likely to face greater free-rider problems (Olson, 1965; Sosis et al., 2007), will experience selective pressures favouring the development of high cost rites that deter these free-riders. Independently, we should also expect societies composed of unrelated males to have higher cost rites than those that are patrilineal since the latter will have expectations of solidarity based on their kin ties, leading to less reliance on costly signals of commitment (Sosis et al., 2007). In Australia, societies with patrimoieties are composed of patrilineal clans each connected to a clan estate (Dousset, Koch, & McConvell, 2015). Related males are more likely to live together in these societies and therefore would be expected to have less costly rites.

1.1.4. Mate quality

If male rites signal mate quality we would expect the costliness of these rites to increase as competition for mates increases. Polygynous societies offer males greater potential reproductive success than monogamous societies and consequently there is greater competition for female parental investment. In stratified polygynous societies, this competition may be manifested in resource displays with wealthy males likely to out-compete poorer males (Irons, 1979). In non-stratified polygynous societies, such as Australian hunter-gatherers, ritual signalling is likely to be a more important mechanism to communicate mate quality. If the hypothesis is valid, we would expect the most extensively polygynous societies to have the costliest male rites.

2. Dataset

The characteristics of male initiation in Australia make it a relevant choice for the analytical study of costly rites. It is, firstly, a highly significant ceremony in Australian life frequently involving complex settings, multiple age-stages and painful ordeals and mutilations (Berndt & Berndt, 1996; Maddock, 1974). Secondly, it has been the subject of extensive ethnography. Ceremonies begin around puberty and may take place multiple times for one individual at subsequent ages. Initiation has a similar general pattern across the country: the novice is removed from the main camp and segregated, transition rites (including painful mutilations) are performed and secret knowledge revealed, and the boy returns to camp as an adult. Despite the large volume of ethnography available, no dataset of Australian initiation currently exists and a key requirement of this study was the preparation of data suitable for comparative analysis. Systematic recording of information relating to Indigenous Australian life began around 1850 (Arthur & Morphy, 2005:

249) and this study uses material predominantly from then until around 1910. Authors such as Howitt (working between 1846 and 1904) and Mathews (1870–1912) in the south east, Taplin (1859–1873) in the south, Roth (1894–1906) in the north east and Spencer & Gillen (1896–1901) in the centre and north, travelled extensively over a number of years recording different aspects of Indigenous Australian life. They also corresponded with informants in more remote locations. The focus of the study is on this early work because of the greater number of Indigenous Australian communities for which material is available and because there was less impact from European contact. Later authors also made detailed accounts but by this time many communities had suffered such severe disruption, including forced relocation to Aboriginal stations away from their homelands, that interpretation of this material is difficult. In particular, it becomes challenging to allocate practices to specific linguistic groups which is a key requirement of this study. In total, 92 publications from 21 different authors were used and material from most areas of Pama-Nyungan Australia is included, with the exception of Western Australia. It is important to engage with this ethnography sensitively, particularly within the historical context of the European invasion of Australia and its disastrous impact on Indigenous people and their culture. Whilst all the material included in the dataset has been previously published, in most cases this took place over 100 years ago in very different historical circumstances. In this context, it is important to acknowledge Indigenous Australian ownership of traditional cultural knowledge and, in particular, to respect secrecy over certain elements. In this study, only generalised ritual traits have been re-published that have been extensively characterised in the public domain, for example in widely read publications such as Berndt & Berndt's *The World of the First Australians* (1996). Two of the 28 selected costly traits (see below) did not meet these generalised conditions and were anonymised, naming them ordeal1 and ordeal2 in place of a fuller description.

Ritual material was allocated to the relevant linguistic group consistent with information contained in the original ethnography. Language and location were cross-checked for accuracy using the comprehensive language database *Austlang* (https://collection.aiatsis.gov.au/austlang). Allocation of each society, traced from publication reference to linguistic group, is listed in SI (1).

2.1. Ritual costliness

Sosis et al., 2007 assessed the costliness of male rites using graduate student scoring of ethnographic descriptions on a 1–4 scale. In this study we took a similar approach, but used trained physicians rather than students so that ratings for the likely pain and longer-term health risks of ritual procedures were informed by an expert understanding of human physiology. The final dataset includes 28 costly procedures across 109 societies (Fig. 1). Each procedure was independently assessed by two experienced UK medical specialists (both orthopaedic consultants). Reviewers ranked separately, on a scale of 0–10, the likely painfulness of each procedure and its longer-term health risks (see SI (1)). Scores for the ten costliest procedures are shown in Table 1.

2.2. Warfare

Data on warfare and active raiding were collected directly from ethnographies. Material was reviewed from broadly the same time period as initiation rites (1850–1910). Reports of conflict were linked to a total of 63 groups (see SI (1)) and in 37 of these there were specific references to active raiding. Their geographic distribution further supports the accuracy of the categorisation because active raiding groups tend to be clustered together (see Fig. 2). This makes intuitive sense

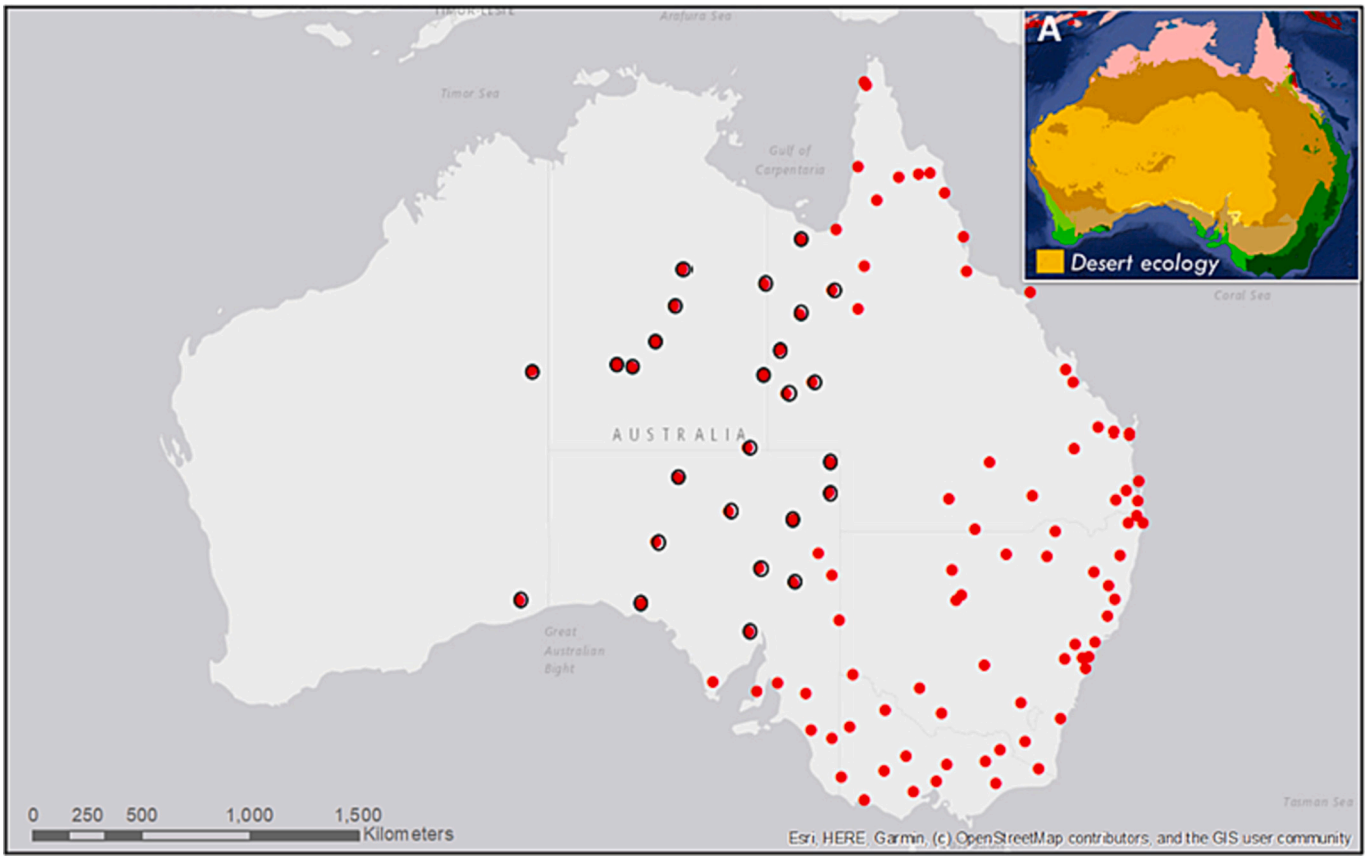

Fig. 1. Location of 109 Pama-Nyungan societies with initiation data. Societies with the high cost initiation rite sub-incision are circled in black. Map A illustrates the Köppen-Geiger climate classification for Australia (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006), indicating the central desert area (see Results).

Table 1
Ten highest cost initiation procedures (recorded in >10 societies) based on physician assessments of likely painfulness and longer term health risks. For full list of procedures see SI (1).

	# Societies	Cost Score
Sub-incision - extended cut	14	17.0
Sub-incision	29	16.5
Scarification on chest or stomach	46	12.5
Fire ordeals *e.g.* standing on hot coals	28	12.5
Tooth avulsion - front tooth	71	12.0
Tooth avulsion - 2nd tooth	15	12.0
Scarification on arms or legs	28	11.5
Scarification on back or shoulder	34	11.0
Circumcision	32	10.0
Binding around upper forearm	43	8.5

because they are likely to be caught up in cycles of violence with each other.

2.3. Other variables

2.3.1. Food sharing/ecology

Desert location was used as a proxy for a high level of beyond-household food sharing as discussed above. Societies were categorised as either desert or non-desert using the Köppen-Geiger classification (Kottek et al., 2006).

2.3.2. Group size

Data on Australian group sizes was taken from Binford's database which includes 38 Pama-Nyungan societies (Binford, 2001).

2.3.3. Kinship

Data was sourced from the *Austkin* database (Dousset et al., 2015) using a search for the social category patri-moieties, aligning communities to the language tree using *Austlang* (see above).

2.3.4. Mate quality

Two measures were used to categorise the extent of polygyny. Firstly, the percentage of males married to more than one female and, secondly, the average age difference between males and females on first marriage. A high age difference tends to be associated with high levels of polygynous marriage (Binford, 2001: 299). Data for the two selected measures was sourced from Binford's database as above. Comparative data was not available on the range of polygyny within a society, for example the difference between minimum and maximum number of wives per male, which would have provided further information on the intensity of mate competition.

2.4. Use of binary traits

One of the challenges with preparing the ritual dataset is reporting variation both within and between societies. Whilst data has been collected within a specific period (1850–1910), variation might still occur in this timeframe, especially since societies were heavily affected by colonial expansion during the period. Observed ritual differences might also be due to other factors, for example, seasonal variation or, perhaps, reduced or unusually plentiful resources. Variation could also be due to observer error or oversight. Such inconsistencies are likely to have resulted in missing data for some groups. Conversely, if societies have multiple ethnographic accounts it may lead to a greater variety of attributes being observed. To help address these problems, binary categories are used for the analysis. Whilst this approach has the disadvantage of flattening some of the variation, the major advantage is that differences in reporting will have much less impact. Whether a society is categorised as 0 ('low') or 1 ('high') is likely to be much less affected by

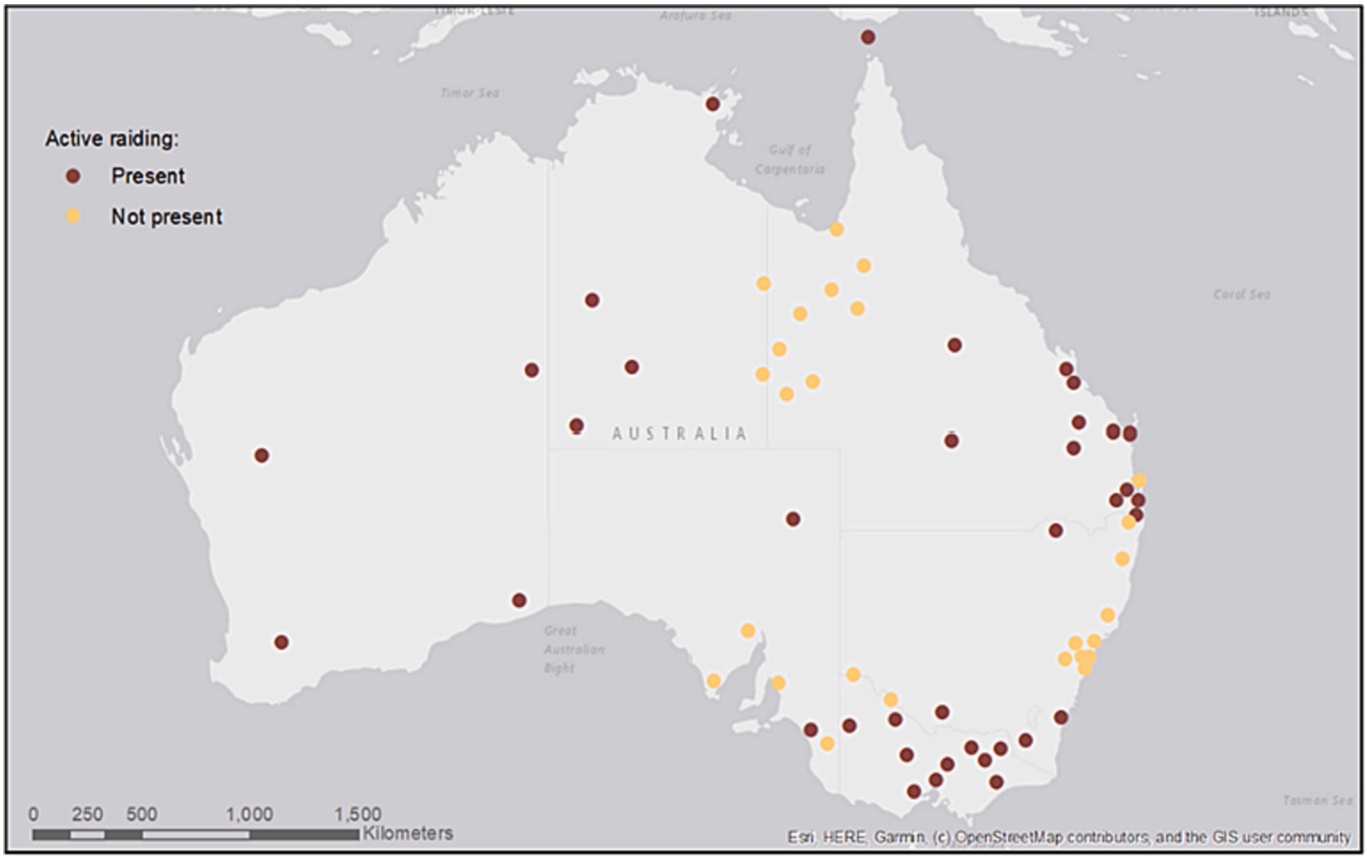

Fig. 2. Location of 63 Pama-Nyungan societies with warfare data indicating whether active raiding is present or not.

inconsistencies in reporting. Binary categories also allow use of the Pagel discrete method, discussed below, that enables mechanisms of causality to be tested. Methods to create binary categories include using the median as the split point or dividing the data into three categories and discarding the middle category (Rucker, McShane, & Preacher, 2015). Here the analysis has been conducted using both approaches but, where sufficient data is available, we have focused on the latter because it removes the more arbitrary classification of middle values, thereby preserving more of the statistical power of the continuous dataset (Gelman & Park, 2009). Binary categorisations and final datasets are included in SI (2).

3. Comparative phylogenetic method

In examining associations between traits it is important to understand whether they provide evidence of adaptation or could instead be the result of common ancestry. We can only be confident the trait is an adaption if it has evolved (or been lost) more than once in association with another trait or environmental condition. The problem of non-independence (or 'Galton's problem') is addressed in this study by using phylogenetic comparative methods. Failure to correct for shared ancestry can lead to high error rates, both in registering false associations but also failing to detect positive ones (Nunn, 2011: 144). To test associations between cultural traits, language phylogenies can control for non-independence on the basis that the language and cultural histories of a population tend to be closely related (Mace & Holden, 2005). In Australia, this assumption is supported by analyses indicating ritual traits have phylogenetic signal *i.e.* patterns of distribution closely related to language (Learmouth, 2016: 31, and paper in progress with current authors).

The method used is Pagel (1994) discrete test for binary traits, using a Pama-Nyungan language phylogeny tree distribution from Bouckaert et al. (2018), see SI (3). The presence (state 1) or absence (state 0) of the two traits being compared are mapped onto societies on the language phylogeny, and the model estimates the rate at which trait presence should be gained (0/1) and lost (1/0) to generate the observed distribution of states across the tree. In other words, the model solves for transition rate values that maximise the likelihood of the observed data distribution. The calculation takes place independently for both traits to produce a likelihood value for the independent model *i.e.* one in which the traits do not influence each other. The calculation is then repeated allowing transition rates to vary depending on whether the other trait is present or not. This dependent model solves for eight transition rates (compared to four, two for each trait, in the independent model). If allowing these rates to vary results in a significantly higher likelihood of generating the observed data than with the independent model, it suggests the traits are influencing each other and therefore may have co-evolved.

A further advantage of the discrete method is its operation within a Bayesian framework as part of the *Bayes Traits* software platform (Pagel & Meade, 2006). Language phylogenies, including Pama-Nyungan, contain uncertainties in relationships that can be accommodated using a sample distribution of trees, rather than one consensus tree. *Bayes Traits* uses the Markov Chain Monte Carlo (MCMC) algorithm to search and sample tree space, generating marginal likelihood estimates of model fit integrated over the tree sample.

Bayes factors (Bfs) were used to test between independent and dependent models. These are calculated as twice the difference between the log marginal likelihoods of the posterior distributions of each model. Whilst interpretation is somewhat arbitrary, Raftery (1996) criteria are commonly applied: Bfs below 2 provide no support for the dependent model, 2–5 suggest positive support, 5–10 strong support, and Bfs over 10 indicate very strong support.

Analyses were performed in *Bayes Traits V3* following the procedures outlined in the *Bayes Traits* manual (November 2016). The analyses used a sample of 4058 Pama-Nyungan phylogenies supplied by Bowern (from Bouckaert et al., 2018), with branch lengths re-scaled by a factor of 0.001 to prevent rate estimates from becoming very small in the computation (see *Bayes Traits* manual). To ensure all available data was utilised, and to maintain consistency across all tests, full phylogenies were used in each case (306 taxa) with missing data coded as gaps (−). Increasing the amount of data available, even without comparator values, is likely to increase phylogenetic accuracy (Wiens, 2008; Wiens & Morrill, 2011) and the discrete model assumes missing values take either state 0 or 1 with equal probability (see *Bayes Traits* manual). The MCMC analysis requires transition rate priors to be set and, to reduce uncertainty and arbitrariness in this choice, a hyperprior was used. These priors are themselves drawn from prior distributions which is a less restrictive method for setting values (Bernardo & Smith, 2000; Currie & Meade, 2014). Hyperpriors were seeded from an exponential distribution based on a range informed using Maximum Likelihood (ML) estimates of transition rates for independent and dependent models. ML calculations used the maximum clade credibility consensus tree (Bouckaert et al., 2018) with number of optimisation attempts set to 100 to ensure stability of estimates. To avoid over-parameterizing the MCMC model, the reverse-jump method was applied which minimises the number of parameters by only adding additional ones if they improve model fit (Pagel & Meade, 2006). Each analysis was run for 1,010,000 iterations, with the first 10,000 removed as burn-in. At the end of each run, log marginal likelihoods (likelihoods integrated over all parameter values) were calculated using a stepping-stone sampler to ensure stable estimates (Xie, Lewis, Fan, Kuo, & Chen, 2011). This was run across the posterior distribution using 1000 stones with 10,000 iterations each. To ensure consistency, each analysis was run three times and the mean values reported. See SI (4) for the model parameters for each separate analysis and the *Bayes Traits* script used in each case.

While correlational research provides valuable insights it does not directly get at the processes leading to change and the evolution of new behaviours (Watts, 2022). Correlation between traits may not mean causation, traits might both be influenced by something else that leads them to vary together. An important further advantage of using the Pagel discrete method is that it provides a way of examining causation using analyses of transition rates to estimate the most likely pathway of trait evolution. To do this, constraint analyses were performed for hypotheses with BF support to assess why the dependent model was favoured and whether causality could be determined. For example, if desert location leads to the evolution of costly rites, these societies should gain those rites at a higher rate than non-desert groups. To test whether this is the case, the model is constrained to sample only models of co-evolution in which societies with desert and non-desert locations have an equal chance of gaining costly rites. If location does affect the rate of gain, the constrained model should have a substantially worse fit (as measured by BF support) than the unconstrained model. See SI (4) for further details of the constraint analyses including the B*ayes Traits* script used.

4. Results

Results are summarised in Table 2 below. There was very strong support for the co-evolution of high cost male initiation rites and desert location (Bf 13.6). There were no significant differences between using the three-category or median approach to binary classification of high/low cost rites (see SI (4) for detailed results).

To examine the association between costly rites and desert location in more detail, we also analysed the distribution of the highest cost rite, sub-incision. Comparison of likelihoods between dependent and independent models suggested very strong support for the co-evolution of sub-incision and desert habitat (Bf 22.5). To contextualise these results, both traits were mapped onto the consensus language tree (Bouckaert et al., 2018) and compared to the distribution of desert location (see Figs. 3 & 4).

There was a very close correspondence between desert location and both high cost rites and sub-incision, however some non-desert societies

Table 2
Bayes factors (comparisons of likelihoods) between independent and dependent models of evolution of high cost male rites with selected variables. Results suggest very strong support for the co-evolution of costly rites and desert location.

Evolution of high cost male rites with:	Independent *vs* Dependent model
	Bayes factor (Bf)
Warfare	
Presence of active raiding	−3.3
Ecology	
Desert location	13.6
Demography & kinship	
Large group size	−2.6
Absence of patrimoiety	−3.7
Mate quality	
High polygyny rate	1.6
High marriage age difference	1.5

also had high cost rites (17 out of 48). This result may be related to the use of a binary distribution. Binary categories were used to provide greater confidence over missing data but they inevitably flatten variation. Examining scores for all 32 societies classified as high cost indicates those with the highest values have predominantly desert locations (see Fig. 5).

To provide a visual indication of evolutionary trends, maximum likelihood reconstructions of ancestral nodes were plotted on the consensus tree for the independent evolution of both traits compared to desert location. The relatively high probability of costly rites being present in deeper nodes of the tree suggests these rites may have been lost later in some societies in correspondence with their non-desert habitats *e.g. Badjiri*, *Kurnu* and *Nukunu*. To explore these evolutionary trends in more detail we analysed the Bayesian posterior distributions of the dependent model. Mean probabilities at the root of the tree gave no clear indication of likely states, although there was marginal support (64%) for sub-incision absence. Mean transition rates were also analysed from the posterior distribution (Fig. 6).

These analyses suggest high cost rites and sub-incision are harder to lose if the society is in a desert location than if it is not. High cost rites were more stable (1.7× less likely to be lost) in societies with desert habitats (C = 0.09 *vs* D = 0.15) as was sub-incision (3.4× less likely to be lost; G = 0.07 *vs* H = 0.24). The acquisition of sub-incision was much more likely with desert location than without (E = 0.23 *vs* F = 0.00) however, there was no difference in the acquisition of high cost rites with and without desert location (A = 0.15 *vs* B = 0.15). Restriction analyses were performed to assess support for these rate differences (see SI (4)). Rates of both loss (C & D) and gain (A & B) of high cost rites, and loss (G & H) and gain (E & F) of sub-incision were held constant and new likelihood values were compared to the previous unrestricted models (where these rates had been allowed to vary). There was strong support for desert societies being more likely to acquire sub-incision than non-desert societies (Bf = 5.1), but not for non-desert societies being more likely to lose the trait (Bf = 0.6). There was no support for desert societies being more likely to acquire high cost rites in general (Bf = −0.2) or for non-desert societies being more likely to lose them (Bf = −1.3).

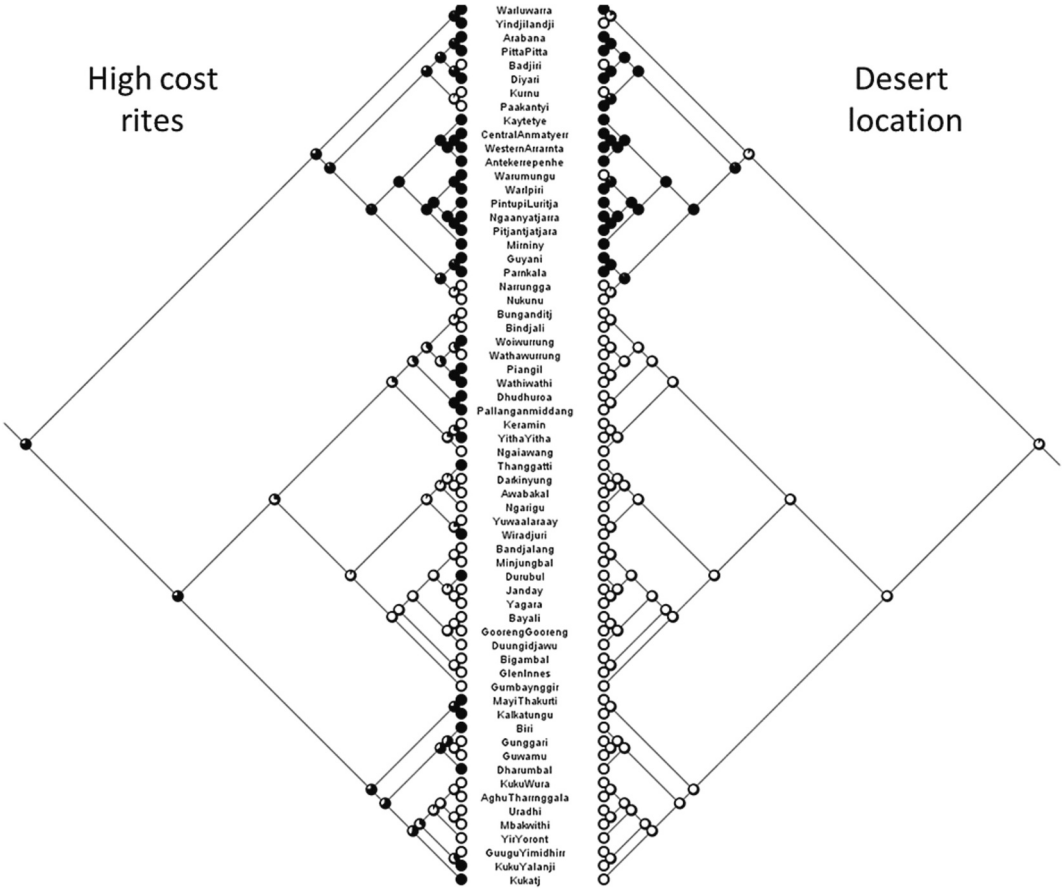

Fig. 3. Presence of high cost rites compared to desert location (both shaded black) by linguistic group (consensus tree, pruned to 64 groups with data). Relative shading of internal nodes is proportional to the probability that the character is present in the ancestral state, based on maximum likelihood values generated using the Mk1 model in Mesquite v3.40. High cost rites appear to have been lost in close phylogenetic neighbours in correspondence with their non-desert habitat *e.g.* Badjiri, Kurnu, Nukunu.

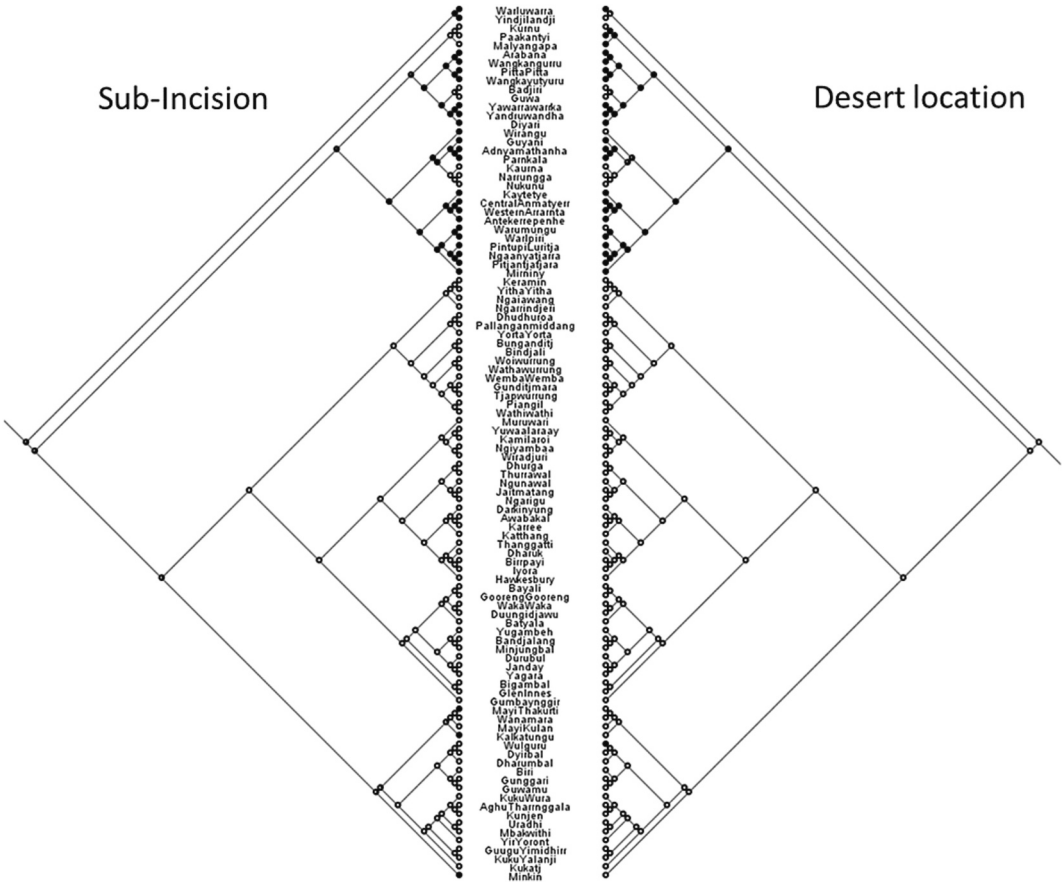

Fig. 4. Presence of sub-incision compared to desert location (both shaded black) by linguistic group (consensus tree, pruned to 100 groups with data). Relative shading of internal nodes is proportional to the probability that the character is present in the ancestral state, based on maximum likelihood values generated using the Mk1 model in Mesquite v3.40. In common with the general category of high cost rites, the sub-incision trait appears to have also been lost in close phylogenetic neighbours in correspondence with their non-desert habitat *e.g.* Kurnu, Guwa, Nukunu.

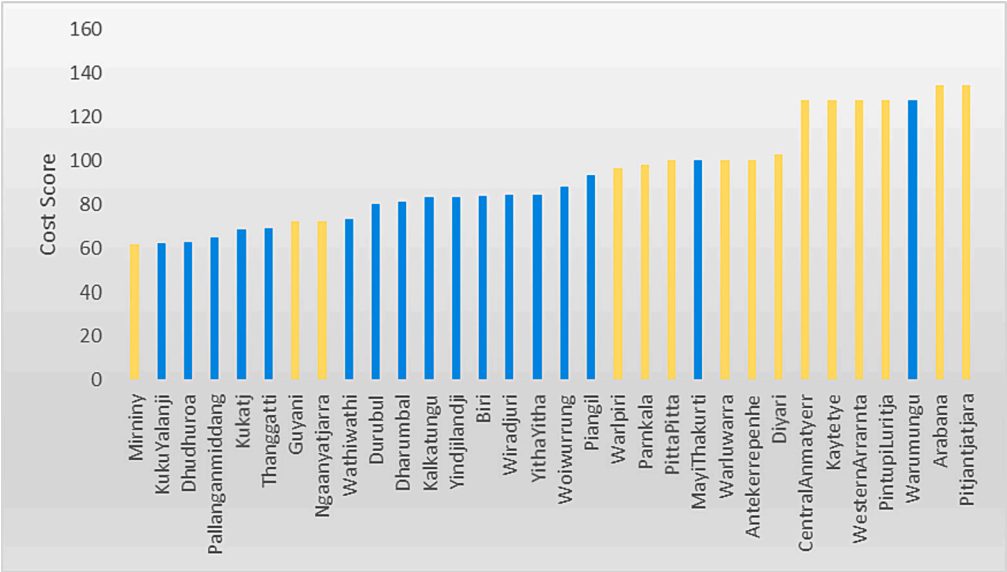

Fig. 5. Male initiation cost scores; desert societies in yellow, non-desert in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Discussion

In sum, our results suggest very strong support for the association between high cost rites and desert location but are inconclusive with regard to causation. Restriction rate analyses support the idea that societies moving into desert were likely to acquire sub-incision, but not

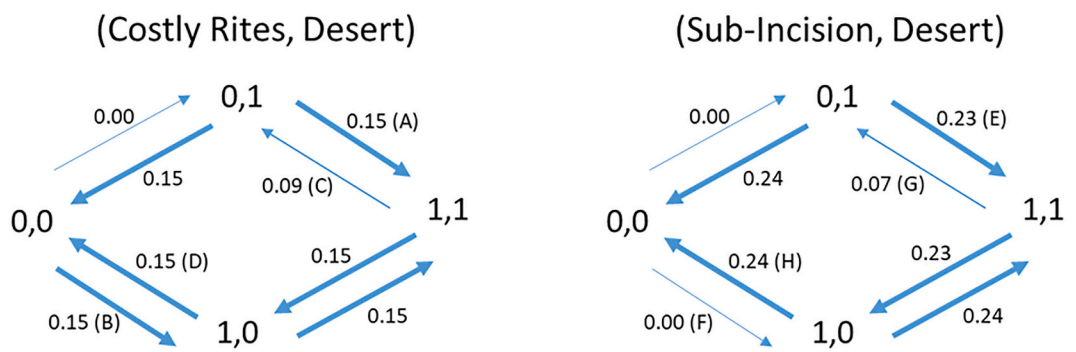

Fig. 6. Mean transition rates from the posterior distribution for dependent models of evolution of costly rites and sub-incision with desert location. Relatively more likely pathways are indicated by bolder lines. Sample sizes were sufficient to support reliability of rate estimates.

high cost rites in general. Mapping of traits onto the phylogeny suggested that societies moving out of desert environments may be likely to lose both high cost rites and sub-incision, however this supposition did not receive support in the restriction analysis.

These findings contrast with Sosis et al. (2007) study, which found that costly rituals were more correlated with rates of inter-group warfare than other collective action problems like food sharing. However, to put these contrasting findings into context, it is important to note several differences in the datasets used in our study and theirs. Sosis et al. used a dataset sub-divided between internal and external warfare, where internal was defined as within a cultural unit and external as between cultural units (Otterbein, 1994). Furthermore, they also sub-divided ritual costs between those involving permanent markings on the body (scarification *etc.*) and those involving non-permanent interventions (ordeals *etc.*). They hypothesized that external warfare would be associated with the costliest rites because it poses greater risks *e.g.* the elimination of one's entire kin group, and because it is more likely to be associated with permanent markings (which are generally more costly). They expected such markings would be more prevalent in the presence of external warfare because, firstly, they may help to unite unrelated males into a combat group and, secondly, such markings might hinder males from the movement between groups likely to be associated with internal warfare *e.g.* because of shifting alliances.

Our dataset does not divide easily into external/internal warfare as the ethnographic material does not always specify the cultural similarity, in terms of language spoken for example, of the group being attacked. Consequently we were not able to test whether external warfare was associated with higher costs (or whether permanent markings were more prevalent in external than internal warfare). Whilst our data lacks this granularity this shortcoming may not be too significant as Sosis et al. found that the costliness of rites was significantly higher in societies with *any type* of warfare (external or internal). They did find that the frequency of permanent markings was higher in external then internal warfare (in 3 out of 4 categories) but that overall costliness was not significantly higher in external *vs* internal warfare, although there was a trend in this direction.

Another difference between the studies was the estimation of relative costliness (graduate student *vs* physician assessments) which may have contributed to different results. Comparison between the two datasets yields little insight into the effect of this. Only one Australian society (*Aranda*, here *Western Arrarnta*) was common to both, although it is worth noting that both high cost rites and warfare were assessed as present for this society in both datasets. A further difference is that Sosis et al.'s study used a broader frame of reference for capturing ritual costs whereas this study focused only on initiation (the most important costly ritual in Australian life). Another difference may be related to the nature of warfare in Indigenous Australia which tends to be associated with escalating cycles of revenge as opposed to capture of territory (or domestic animals). Raids take place by stealth in the early morning and, whilst enemy massacres are frequent, assailant casualties are often lower. Revenge raids by the enemy on the previous assailants then take place in a similar fashion. Thus, high-casualty open pitched battles are few, and this may lead to fewer circumstances when group members are required to make visible sacrifices on behalf of others. In turn, it may lessen the requirement for costly signals of commitment. However, we note this type of non-territorial warfare is common in hunter-gatherers (Allen & Jones, 2014), who also tend to have the costliest rites (Sosis et al., 2007). The implications of our results are therefore not just specific to Australia but raise a question around the connection between costly rites and warfare in other hunter-gatherer groups. We also note that Šaffa, Zrzavý, & Duda (2022) did not find an association between the presence of male genital mutilation and external warfare in their recent phylogenetically-controlled cross-cultural study.

In terms of food sharing, an important difference between the studies is that we used desert location as a proxy for greater food sharing because, unlike Sosis et al., we did not have quantitative data for this parameter. Furthermore, our choice of this proxy was based on connections observed cross-culturally rather than data collected specifically in Australia. Nevertheless, differences in our results can suggest areas of further discussion. Whilst we found a strong association between costly rites and desert habitat, Sosis et al. found no association between costly rites and food sharing (they did not test ecological parameters). They suggest reciprocity can be employed in food sharing which makes ritual signalling unnecessary. The reason for our positive result could be that ritual signalling is more advantageous in desert habitats because they are sparsely populated and therefore food sharing reciprocity is harder to monitor. In addition, it's possible that sharing access to water resources becomes more important in desert conditions.

If ritual performance is acting as a genuine signal of fitness for group membership, we would expect individuals failing the rite to suffer fitness consequences. However, the majority of novices seem to pass through successfully and ceremonies do not purposefully distinguish one individual from another (Berndt & Berndt, 1996: 166). Our data does not include other factors that might be relevant differentiators such as the frequency of performances and the manner or intensity of participation *e.g.* whether the novice cries out or is stoically silent during the rite. One example of group exclusion is noted in Hayden (2003: 104) however we note that such examples are rare in the ethnography. The lack of clear evidence for differentiated fitness consequences between novices lessens support for the costly signalling mechanism in Australia and suggests alternative adaptive theories may have some merit. We consider two possibilities below.

Firstly, might certain costly rites, such as sub-incision and circumcision, provide a physical or health benefit in desert habitats? There is some persistence to the idea that circumcision is associated with sandy conditions because it reduces infection under the foreskin (*balanitis*). However, a review of the evidence by Darby (2005) suggests this is unlikely and the practice may even lead to more complications. Wilson

(2008), combining signalling and sexual selection theory, hypothesized that because genital mutilation impairs the capacity for male fertilization it represents a hard to fake signal of reduced reproductive capacity. He predicted, and found cross-culturally, that genital mutilation was more prevalent in societies with higher rates of polygyny and those where wives lived at greater distances apart, suggesting this was because suspicion and conflict due to paternity uncertainty are higher in these circumstances. Šaffa, Zrzavý, & Duda (2022) also found an association between male circumcision and separate residences for co-wives (polygyny was not tested). In this study we did not find any association between polygyny and societies with high cost rites (that almost universally involve genital mutilation). It is however plausible that wives may live a greater distance apart in desert societies, although we did not have data to specifically test this. The sub-incision procedure has also been linked to medical benefits such as resistance from infection, due to the hardening of mucosa following the procedure, and other theories, such as increasing sensitivity during sexual intercourse (Basedow, 1927; Lobdell, 1975). However, neither of these ideas has empirical support or a clear rationale for why they would only apply in arid, desert conditions.

Secondly, Whitehouse's imagistic theory of ritual might provide an alternative explanation for costly desert rites. He suggests that recalling painful, traumatic events triggers enduring searches for meaning or 'trains of exegetical thinking' that, when combined with a stock of memories generated in rituals, leads to the development of highly elaborate bodies of knowledge (2004: 81). Effectively, the rite acts as a way of attaching high meaning to the information that, when combined with its frequent reinforcement, enables the effective in the knowledge transmission. The combination is important because, in isolation, traumatic rites may actually create false or unreliable memories (Xygalatas et al., 2013).

The acquisition of extensive ritual knowledge is a particular characteristic of central Australian rites which focus on the 'mythical geography of landscape' (Eliade, 1973: 56). Features such as water holes and rock formations represent concrete traces of sacred ancestral journeys (also known as Dreaming tracks) that are re-enacted with songs, performances and (often painful) rites at multiple ritual stages over many months and sometimes years as novices reach later age-stages (Elkin, 1934; Meggitt, 1966). The rites themselves take place during adolescence but the various ancestral songs are repeated and reinforced many times during adulthood (at the ceremonies of others). In precarious desert conditions, such ancestral tracks can provide vital practical information on routes between water sources and productive foraging grounds (Elkin, 1934: 171, Layton, 1992: 55, 72). Lewis (1976), observing route finding among initiated Aboriginal men in arid, central Australia over a three year period, noted that the spiritual world, manifested in sacred sites and Dreaming tracks, was their primary source of geographical knowledge. Potentially then, painful, costly rites may have been developed as a way of 'hard-wiring' detailed, and critically important knowledge, for Aboriginal people living in desert environments.

Instead of, or in addition to, adaptive reasons, the distribution of ritual traits such as sub-incision may be a result of diffusion (horizontal transmission) from the centre, perhaps influenced by novelty, the prestige of groups possessing them or other benefits discussed above. Such a process may have coincidently led to a distribution pattern skewed towards the central, arid area (Dixon, 2002: 15). However, the similarity between the east-west boundary of sub-incision and the east-west boundary of the desert (Fig. 1) suggests a strong influence from desert ecology. Furthermore, analyses discussed in the Methods section (and Figs. 3 & 4 here) suggest ritual trait distribution is closely associated with language, thereby demonstrating influence from vertical transmission. Whilst diffusion may have played a role in trait distribution, it seems likely that phylogeny and ecology have been more important drivers.

To conclude, our results suggest a very strong association between high cost rites and desert conditions, based on a comparative method which takes account of the phylogenetic relationships between societies. Transition rate comparisons were directionally supportive of desert conditions being the cause of high cost rites development (or lack of these conditions resulting in its loss), however we were only able to demonstrate this statistically with sub-incision. Mechanistically, our results lend some support to the hypothesis of costly ritual signalling supporting effective collective action, in this case in relation to life in desert conditions. However, we note that Whitehouse's imagistic theory may also provide a persuasive explanation for the development of high cost rites in Australian desert societies.

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Declaration of competing interest

None.

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