Headhunting and Warfare: Evidence from Austronesia*

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Abstract

Headhunting is the practice of acquiring human heads for ritual purposes that was historically widespread around the world. We hypothesize that headhunting emerged as a cultural response to frequent inter-tribal warfare and served as a mechanism to train warriors ready to defend their community. The practice was effective since, first, it allowed to verify warrior quality based on performance in headhunting raids and, second, it offered a system of rewards for men to develop and refine warfare skills. We use phylogenetic comparative methods and ethnographic data to empirically investigate this hypothesis in a sample of preindustrial Austronesian societies. Headhunting turns out to be substantially more prevalent in societies exposed to frequent warfare, accounting for shared cultural ancestry and a host of potentially confounding characteristics. Furthermore, Bayesian estimation of correlated evolution models suggests that, consistent with our hypothesis, the adoption of headhunting was driven by increased warfare frequency and the decline of this practice followed a reduction in intergroup conflict.

Keywords: Austronesia, Conflict, Correlated evolution, Culture, Headhunting, Phylogenetic comparative methods, Supernatural beliefs, Warfare

JEL Classification Numbers: D74, Z12, Z13

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1 Introduction

The view of cultural beliefs and practices as environmental adaptations performing important functions, such as enforcement of cooperation, resource management, and community defense, has a long tradition in anthropology. More recently, economists also began to study the origins and historical determinants of culture by focusing on its social benefits, particularly in societies lacking modern technologies and formal institutions.[1] We add to this burgeoning research agenda by investigating headhunting, a practice of acquiring human heads for ritual purposes. This paper hypothesizes that headhunting represented a cultural response to frequent warfare and provides supporting empirical evidence from a sample of preindustrial Austronesian societies.

Although no longer in existence, headhunting was historically practiced around the world (Heron, 2020). We focus on Austronesia, a vast region in the Indo-Pacific where headhunting was fairly widespread prior to early twentieth century, as documented in a rich ethnographic literature. Local practitioners believed that provision of human heads and their use in public ceremonies ensured plentiful harvests, prevented sickness, and generally secured material and spiritual well-being of their communities. For men, participation in successful headhunting raids was an important avenue for gaining social status, political power, and advantage in the marriage market.

Based on ethnographic evidence and theories of human trophy taking, we argue that headhunting represented an effective mechanism for training warriors providing community defense. The practice and surrounding beliefs offered substantial rewards to young men for developing warfare skills and engaging in risky missions. Their performance could be reliably verified by community members observing acquired heads, an ultimate proof of personal valor and success of the raid. Thus, headhunting addressed the notorious collective action problem in warfare by providing appropriate participation incentives and accurately rewarding skilled fighters. Since such a social arrangement is most valuable in communities facing severe external threats, we hypothesize that headhunting was more likely to be present in societies exposed to frequent inter-tribal warfare.

We use *Pulotu*, an ethnographic database describing over a hundred preindustrial Austronesian societies (Watts et al., 2015a), and apply phylogenetic comparative methods to empirically investigate this hypothesis. Although not commonly used by economists, this set of techniques allows to account for cultural non-independence between societies due to shared ancestry and directly explore the coevolution of various cultural traits (Mace

[1] See Gershman (2017), Leeson (2017), and Lowes (2023) for an overview.

and Pagel, 1994; Nunn, 2011). Our first set of results, based on phylogenetic logistic regression model, shows that there is a strong positive association between frequent warfare and the presence of headhunting, which holds after accounting for potentially confounding factors such as geographic and cultural isolation, social complexity, and subsistence production mode. In order to examine causal directions in this relationship, we next estimate joint cultural dynamics of headhunting and frequent warfare within the correlated evolution framework (Pagel, 1994). Our results suggest that the adoption and decline of headhunting were driven by, respectively, the increase and reduction in warfare frequency. In contrast, changes in warfare frequency were not significantly affected by the presence or absence of headhunting. These findings support the hypothesis that headhunting was a cultural adaptation to recurrent warfare.

This paper contributes primarily to two strands of literature. First, we expand the research agenda on the origins of culture within economics, particularly the study of traditional practices and beliefs that may at first seem unusual, harmful, or lacking a clear purpose or social benefit (Posner, 1980; Leeson, 2017). Some examples include reliance on ordeals in establishing guilt or innocence (Leeson, 2012; Leeson and Coyne, 2012; Maltsev, 2020), use of oracles in resolving interpersonal disputes (Leeson, 2014b), beliefs in the evil eye and witchcraft (Gershman, 2015; 2022). A common theme in these studies is that seemingly peculiar customs and supernatural beliefs serve important functions (e.g., administering justice, protecting property, and maintaining social order) in societies lacking alternative means of achieving those goals, such as effective government institutions or advanced technologies. Similarly, in our context, headhunting secures community protection in the absence of modern army structures and military equipment.

Within this literature, studies relating cultural arrangements to the challenges of collective defense and warfare are especially relevant to our work. Leeson (2014a) argues that the practice of human sacrifice protected communities from external predation. According to his theory, exchanging valuable property for humans that are subsequently sacrificed makes a community poorer and thus less attractive for outside plunderers. Nunn and Sanchez de la Sierra (2017) argue that a bulletproofing ritual, still performed in parts of the Democratic Republic of the Congo, mobilized community combatants to successfully repel external aggression. This ritual, ostensibly providing immunity against enemy bullets, caused individual combatants to underestimate the risk of fighting and induced greater combat effort on their part, which ultimately resulted in a higher level of community protection. Maltsev (2021) proposes that martyrdom, the idea that people gain spiritual benefits and status, often posthumously, for suffering as a result of fighting for their religious beliefs, fostered rebellious collective action by lowering the private costs of participants in case of failure. In an argument closely related to our conceptual framework, Piano and Carson (2020) suggest that the practice of scalp-taking among Native Americans solved the problem of monitoring the performance of warriors on the battlefield. Importantly, these studies linking culture to warfare largely rely on qualitative evidence to support their respective theories. In contrast, we conduct a comprehensive empirical investigation directly addressing the issues of confounding factors and likely directions of causality in the relationship between headhunting and frequent warfare.

There is, of course, a vast literature on the social functions of cultural practices and beliefs outside economics. The most directly relevant part of this research explores the role of religion in fostering collective action and participation in warfare (Glowacki and Wrangham, 2013; Alcorta and Sosis, 2022). In a seminal paper, Sosis et al. (2007) show that, in a sample of 60 preindustrial societies around the world, the harshest male initiation rituals are observed in communities frequently engaging in intergroup warfare. The authors rely on costly signaling theory to argue that violent rites of passage promoted cohesion among men and created a standing class of warriors for protection. Johnson (2008) reviews various channels through which religious beliefs and practices support group cohesion and improve combat performance in intergroup conflict.

The second research agenda to which we contribute is the study of cultural evolution using phylogenetic comparative methods. Since the application of this approach relies on linguistic trees, assumed to represent historical relationships between ethnic groups, most studies focus on ethnolinguistic clusters for which reliable phylogenies are available, such as the Austronesian, Bantu, and Indo-European families. Examples of cultural traits examined in this literature include kinship systems, marriage patterns, social hierarchies, and religious beliefs (Mace and Zhang, 2023). More narrowly, we contribute to the research on Austronesian cultures which so far explored such features as political complexity (Currie et al., 2010), marital residence patterns (Fortunato and Jordan, 2010), supernatural punishment (Watts et al., 2015b), human sacrifice (Watts et al., 2016), kinship terminology (Passmore and Jordan, 2020), games (Leisterer-Peoples et al., 2021), and gender-specific initiation rites (Bentley et al., 2021).

The rest of this paper is organized as follows. Next section provides a primer on the practice of headhunting in Austronesia. Section 3 lays out a conceptual framework viewing headhunting as a cultural adaptation to frequent warfare. Section 4 introduces the data used in the analysis and describes preliminary patterns. Section 5 presents the main empirical results. Section 6 concludes.

2 Headhunting in Austronesia: A primer

No! The custom is not horrible. It is an ancient custom, a good, beneficent custom, bequeathed to us by our fathers and our fathers' fathers; it brings us blessings, plentiful harvests, and keeps off sickness, and pains.

Aban Avit, a Kayan chief, as quoted in Furness (1902)

The practice of taking human heads for ritual use was historically widespread across numerous islands of Southeast Asia and Oceania populated by Austronesian societies. Linguistic and phylogenetic comparative analyses suggest that headhunting was likely practiced by the ancestors of all contemporary Austronesian peoples that inhabited the island of Taiwan over 5,000 years ago (Blust, 1995; Watts et al., 2015a). The first written records of headhunting among the Taiwanese aboriginal populations are found in Chinese sources dating back at least to the early 17th century (Baldick, 2013), but most of the ethnographic evidence was produced in the late 19th and early 20th centuries following active European contact with Austronesians. Throughout the past century, the practice was consistently suppressed by colonial administrations and centralized states across the region and it is now extinct, although some societies preserved headhunting-inspired rituals featuring coconuts, dolls, and other substitutes for human heads (George, 1996; Simon, 2012). Despite some differences in the ways headhunting was performed in the region, cross-cultural comparisons reveal important similarities which provide a foundation for theorizing about the common purpose, or social function, of this practice. In what follows, we focus on these typical features of headhunting and also note some of the variations.

The practice of headhunting involved both the act of obtaining human heads and surrounding rituals and beliefs. Hoskins (1996), among other scholars, emphasizes the ritual meaning of headhunting to distinguish it from simple trophy taking and directly incorporates this notion in her widely-used definition of the practice as "an organized, coherent form of violence in which the severed head is given a specific ritual meaning and the act of headtaking is consecrated and commemorated in some form." Similarly, Baldick (2013) stresses the importance of related beliefs and rituals when placing headhunting among the fundamental pillars of traditional Austronesian religions, and Simon (2012) argues that "without ritual, it is not headhunting, but rather merely a gruesome form of homicide." We first briefly consider these two main aspects of the practice, raid mechanics and rituals involved, and then turn to the key motives behind these seemingly puzzling behaviors.

Heads were usually taken during special headhunting raids, but also as part of fighting motivated by other reasons (Downs, 1955). Some headhunting expeditions involved just a few men ambushing one or two victims, while others were performed by large groups attacking entire settlements, as observed among the Iban of Borneo and the Roviana of the Solomon Islands (Aswani, 2000). While the number of heads was not essential for the ability to perform rituals, it did affect the status earned by individual headhunters and reflected the general success of the raid (Aswani, 2000; Watson Andaya, 2004). The attacks were typically aimed at out-groups, often neighboring tribes, although longer-distance travel could also be undertaken (McKinley, 1976; Schefold, 2007; Simon, 2012). More rarely, heads were collected from rival groups within the same larger society, like among the Ilongot of the northern Philippines (Rosaldo, 1980). The identity of victims varied from high-status individuals to anyone caught in an ambush, including women, children, and the elderly. Interestingly, the latter categories were sometimes considered a special prize demonstrating the headhunter's ability to penetrate deep into foreign territory and capture "those very individuals whom men should protect" (Watson Andaya, 2004).

Headhunting raids, big or small, were not arbitrary and followed a well-defined protocol. Although the details of this protocol varied across societies, and sometimes were very intricate, there is commonality to its basic structure involving the raid itself and activities preceding and following it (Baldick, 2013). Each headhunting party typically had a leader, sometimes the tribal chief himself, who was responsible for organizing the raid and conducting preliminary rituals and investigations. Common pre-raid activities included consulting bird oracles and generally looking for good and bad omens in nature and dreams, asking gods for success in expedition and offering them animal sacrifices, selecting men suitable for the raid. Once the required rituals were completed, the raid was conducted on a day deemed favorable. An expedition was typically considered a failure if a group member was killed, regardless of heads taken, in which case post-raid celebrations were limited or canceled. If, however, a raid was carried out without losses, a choreographed community-wide celebration followed that could last for several days.

Upon their return, headhunters were greeted by other villagers, particularly women, who offered them congratulations, along with food and drink.[2] Further community activities included singing, dancing, feasting, recitation of myths, speeches praising the courage of headhunters, rites of passage for the young men, sacrifices to the spirits of ancestors and local deities. Heads captured in the raid were usually placed on a pole and played an integral part in festivities. They were also "prepared" in advance by boiling, smoking, or temporary burying in the ground to remove flesh from the skull. In the process, bits of flesh and brain were sometimes eaten by headhunters ostensibly to acquire the vital force

[2] In some cases, like among the Toraja of Sulawesi, while headhunters were away, women engaged in a series of rituals and adhered to a variety of restrictions to ensure a successful raid (Downs, 1955).

of their victims (Baldick, 2013). The skulls were then preserved within community and served as a sign of accumulated status (Aswani, 2000). Overall, although men obviously had the crucial role of procuring heads, headhunting was a "collective act with a divine nature" and engaged the entire community (Hung, 2020).

So, why did some Austronesian societies practice headhunting? A reasonable starting point is a list of reasons provided by the practitioners themselves. Numerous items on that list may be grouped into individual-level (man the headhunter) and collective-level motivations. Baldick (2013) summarizes both categories by stating that headhunting was performed to "obtain general prosperity and give the community strength and the head-taker prestige."

Bringing heads was a universally accepted way for young men to display their fighting prowess, courage, and masculinity, qualities that made them desirable marriage partners (McWilliam, 1994; Simon, 2012). In some cases, headhunting success, marked by a special tattoo or dress, was actually required for marriage eligibility (Hoskins, 1996). Headhunters acquired great status within their communities and could earn claims to political leadership based on successful management of raids and the number of heads collected (McWilliam, 1996; Watson Andaya, 2004; Simon, 2012). Other, less frequently mentioned personal motivations vary from prosaic, such as getting released from debt, atoning for adultery, seeking revenge, or even simply venting emotions (Hoskins, 1996; Simon, 2012), to highly spiritual, such as earning a safe passage to afterlife (Hung, 2020).

In addition to these personal benefits earned by successful headhunters, the practice was widely believed to be essential for collective well-being, which commonly included such rewards as better agricultural crops, prevention of sickness and other misfortunes, and promotion of fertility among women (Hoskins, 1996; Schefold, 2007; Baldick, 2013). In some cases, these outcomes were presumably secured through gratification of deities to whom the captured heads were sacrificed. Besides these broad community-level benefits, severed heads were sometimes required to end periods of mourning and for mortuary rituals (Baldick, 2013). Occasionally they were also needed for inauguration of communal property such as longhouses and canoes (Dureau, 2000). Finally, pointing more directly to our hypothesis, some cultures underscored the role of headhunting in defending their territory and resources against enemies (Watson Andaya, 2004; Simon, 2012).

The following basic patterns emerge from ethnographic accounts. First, both at the individual and collective levels, strong incentives were in place to motivate headhunting. Although participation was typically voluntary, young able men avoiding headhunting expeditions risked not getting married and effectively gave up their community status and prospects for political power. Second, communal-level benefits and rituals tied to headhunting clearly reflected the perceived crucial role of the practice for social welfare and the collective-good nature of successful raids. This was also manifested in the broad participation of community members in headhunting rituals and celebrations.

Interestingly, many features of Austronesian headhunting were also observed in societies far outside the region. For example, the reasons behind the practices of scalping and headhunting among Amerindian tribes, as summarized in Chacon and Dye (2007), are strikingly similar to the ones listed above. At the individual level, these included desire for status, demonstration of fighting prowess, and securing a marriage. At the community level, like in Austronesia, human trophies were believed to enhance fertility among women, promote agricultural crops, appease local deities, and were sometimes required to end periods of mourning. High fertility and general prosperity were also the main motives behind headhunting among the Jivaro of South America, known for their "shrunken head" trophies, and the Naga of northeastern India (Baldick, 2013; Hoskins, 1996). Heron (2020) pinpoints some commonalities among twelve headhunting societies from around the world including status-seeking as a key factor driving participation in raids and the importance of community-wide ceremonies. The common features of headhunting and its presence in highly distinct cultures suggest that the practice may have evolved independently multiple times and performed vital functions across communities.

3 Conceptual framework

Given the ethnographic evidence summarized above, we suggest that exposure to frequent inter-tribal warfare, and the concomitant need for protection, were the fundamental factors in the adoption and persistence of headhunting. The building blocks of this hypothesis were discussed in earlier studies on warfare and human trophy taking in small-scale preindustrial societies including, most recently, Johnson (2017), Heron (2020), and Piano and Carson (2020). Here, we bring these ideas together in Austronesian context and formulate the main hypothesis for our empirical analysis.

The survival of any society engaged in repeated intergroup conflict depends on its ability to maintain an effective class of warriors willing to tolerate risky and potentially deadly fighting. In the absence of centralized state, organized army, and modern technologies, creating proper incentives for taking such risk, even with the goal of providing an essential public good (community safety) is inherently complicated (Glowacki et al., 2020). The practice of headhunting represented a surprisingly comprehensive solution to this fundamental problem by addressing the two key issues: 1) verification of warrior quality via accurate measurement of their performance in foreign territory and 2) provision of strong incentives for men to develop and practice required warfare skills.

The role of human trophies, heads in particular, as ultimate evidence of success in dominating the enemy has been universally accepted across societies, from Iron Age Europe and medieval Japan to pre-colonial Americas and Austronesia (Keeley, 1996; Aswani, 2000; Chacon and Dye, 2007; Heron, 2020). Unlike other trophies, such as limbs or personal belongings, a head is an incontrovertible proof of a single individual's death. No person can remain alive without a head, and warriors cannot free ride by collecting multiple trophies from a single individual. Furthermore, a head sometimes makes it possible to verify the foreignness and status of the victim, providing further useful evidence to the community.[3] Taking a head is undoubtedly a costly signal of individual physical ability, skill, and courage since it requires not only killing the victim but also spending extra effort and incurring additional risk to sever the head and bring it back home (Johnson, 2017).[4] Thus, the practice of headhunting provided a unique mechanism for credibly measuring warrior quality and success in environments where such evidence was difficult to obtain through other means.

In order for men to willingly participate in risky headhunting raids, they had to be properly rewarded. Hence, the second crucial element of the practice is a system of incentives and benefits available to headhunters. As discussed in the previous section, at the personal level, these came in the form of high social status and preferential treatment that comes with it, including best marriage opportunities and claims to political power. Even when enemy heads were not strictly required for marriage or formal transition to adulthood, men were also eager to participate in headhunting raids also due to their perceived importance for the community as a whole. Since heads were believed to secure material and spiritual prosperity of the entire community, there was a clear understanding that warriors provided an essential public good and had to be rewarded for it.[5] Furthermore, the ritual use of heads for systematically occurring events such as periods of mourning and consecration

[3]McKinley (1976) argued that a head was the preferred trophy in Borneo partly because the face signified the "social personhood" of the enemy. The Amaya people of the Damer island also explained that, unlike bodies, heads were portable and clearly encoded "the identity of otherness" (Pannell, 1992).

[4]While the heads brought to camp sent this useful signal to in-group members, headless bodies in the foreign territory also demonstrated military prowess and ferocity to the out-group.

[5]Both individual benefits reaped by headhunters and their perceived contribution to collective welfare may be seen as a special case of "cultural rewards" argued to be an important motivator for participation in warfare in small-scale societies (Glowacki and Wrangham, 2013).

of new communal structures, and the expectation from men reaching adulthood to bring heads, ensured that raids were conducted regularly. This contributed to both training new warriors and maintaining the fighting skills of others.

In sum, the practice of headhunting provided an effective mechanism for securing combat-readiness in the face of intergroup conflict. We hypothesize that headhunting was more socially valuable, and thus more prevalent, in communities exposed to frequent warfare. Furthermore, we argue that the adoption and demise of headhunting were dynamic cultural responses to changes in conflict frequency. Existing evidence of such patterns is very limited. Heron (2020) explores twelve headhunting societies around the world, including several from Austronesia, and notes that all of them were characterized by a high level of intergroup violence. Similarly, in the context of scalping, Piano and Carson (2020) show that, across twelve North American cultural areas, the practice was largely present in regions with medium or high frequency of warfare. In the remainder of this paper, we use phylogenetic comparative methods to systematically investigate the relationship between the presence of headhunting and warfare frequency in a large sample of Austronesian societies.

4 Data and preliminary patterns

4.1 *Pulotu* database and main variables

Our empirical analysis relies on *Pulotu*, an ethnographic database documenting historical and contemporary features of 137 Austronesian societies (Watts et al., 2015a; 2022). We focus on a subset of 129 societies for which data on headhunting and warfare are available. Both of these variables, along with other characteristics used in later analysis, belong to the "traditional state" section of the dataset capturing information prior to large scale modernization. The majority of societies in our sample were pinpointed before the start of the 20th century, with 90% observed prior to 1935. Overall, *Pulotu* is comparable in nature to the *Ethnographic Atlas* and the *Standard Cross-Cultural Sample* datasets documenting preindustrial societies around the world and commonly used in quantitative social sciences (Lowes, 2021).

Headhunting, defined in *Pulotu* as a practice of killing people for the sole or primary purpose of obtaining their heads, is a binary variable (present or absent). Headhunting is found in 31% of cultures in our sample and its distribution is mapped in figure 1. Warfare refers to lethal conflict with other societies and its frequency is coded on the following ordinal scale: frequent (18% of the sample), common (19%), occasional (26%), and rare

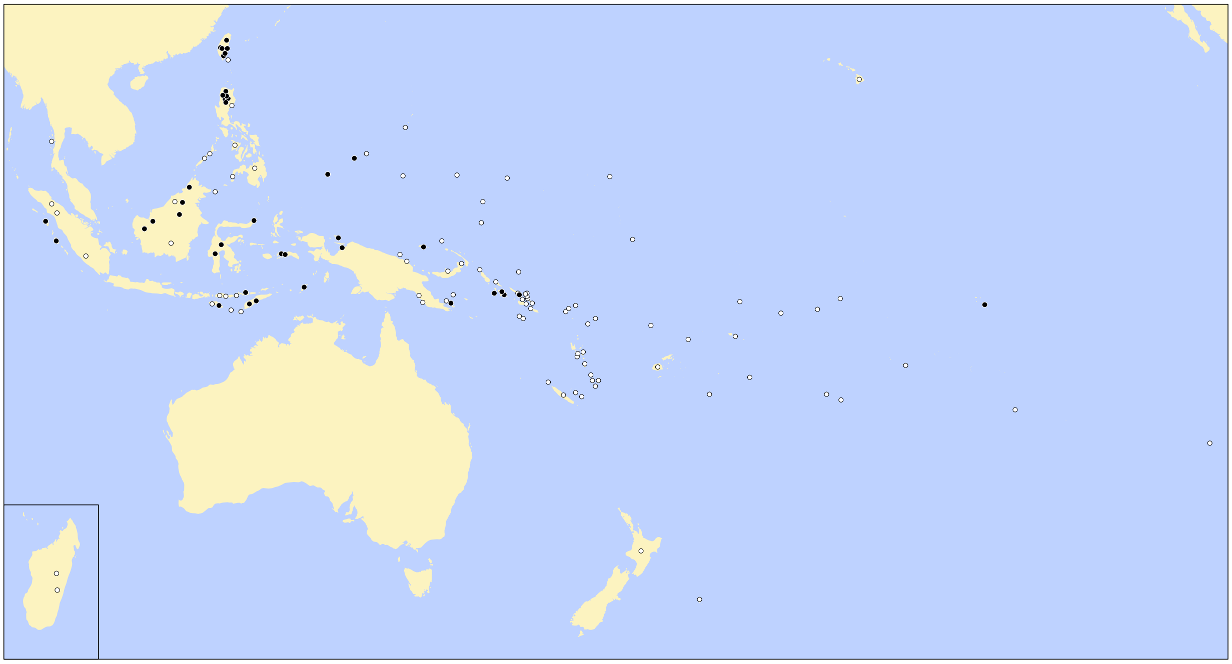


Figure 1: Spatial distribution of headhunting across Austronesian societies.

Notes: Black (white) circles indicate the presence (absence) of headhunting. The inset map in the bottom-left corner shows the island of Madagascar.

or never (37%). The rough frequency cutoffs separating these categories are one year, five years, and one generation. For a subset of our analyses requiring binary variables, we create an indicator for frequent vs. infrequent warfare by grouping the first two and the last two categories of the original classification.

Figure 2 shows the basic correlation between our variables of interest. Headhunting was only present in about 8% of societies that never or rarely engaged in lethal intergroup conflict. Its incidence rises sharply in societies with more frequent warfare, exceeding 50% in cases when it happens at least on a yearly basis. In terms of our binary warfare variable, headhunting was present in 50% (20%) of societies with frequent (infrequent) warfare.

This positive bivariate association is consistent with our main hypothesis viewing headhunting as a cultural adaptation to frequent warfare. However, it does not necessarily imply the presence of a causal relationship of this kind for three reasons. First, this may be a spurious correlation driven by some omitted factors. Second, causality may also run in the opposite direction. Indeed, it is possible that headhunting raids generated response attacks triggering vicious cycles of revenge warfare and increasing its frequency.[6] Finally, a third

[6]The extent to which this mechanism is operational has been debated in the literature. For example, Heron (2020) argues that headhunting and warfare likely reinforced each other, while Johnson (2017) suggests that, by signaling their ability to inflict extra-lethal violence on their victims, headhunting societies could avoid a conflict spiral through deterrence.

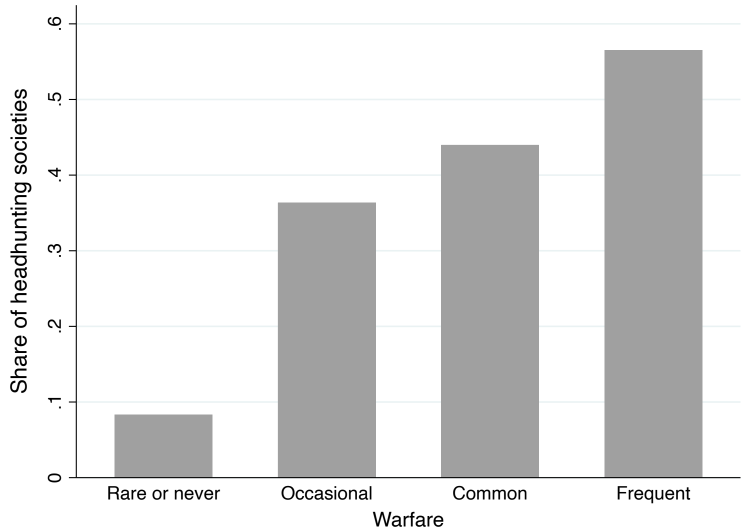


Figure 2: Correlation between warfare frequency and headhunting.

problem for causal inference, pointed out by Galton over a century ago but still commonly ignored in cross-cultural research, is the non-independence of observations in our sample due to shared ancestry. In other words, the observed correlation between headhunting and frequent warfare may simply reflect the process of cultural inheritance. Before addressing these three challenges through phylogenetic comparative methods, we set the stage for this analysis by matching *Pulotu* societies to respective Austronesian languages and formally show that the problem of cultural non-independence is indeed present in our sample.

4.2 Accounting for shared ancestry

In order to account for relatedness between species in statistical analyses of their traits, evolutionary biologists rely on phylogenetic trees inferred from molecular data. Drawing on parallels between biological and cultural evolution, anthropologists suggested that relatedness between societies, particularly ethnic groups, for the purpose of cross-cultural analyses can be approximated using linguistic trees inferred from language characteristics (Mace and Holden, 2005; Nunn, 2011). Once each society is linked to its language, phylogenetic comparative methods can subsequently be applied.

We follow this approach and match societies in our sample to Austronesian languages arrayed on time-calibrated linguistic trees by Gray et al. (2009). More specifically, the authors provide a sample of 4,200 trees from the posterior distribution of a Bayesian analysis of terms from the Austronesian Basic Vocabulary Database (Greenhill et al., 2008). This variety of likely linguistic trees reflects the problem of phylogenetic uncertainty, with each tree representing just one estimate of historical relationships between languages. As shown below, phylogenetic uncertainty can sometimes be directly incorporated in statistical analyses, while in other cases, we can test for robustness across the entire sample of trees or rely on a single "representative" tree. Due to data limitations, we were only able to match 107 of 129 societies to Austronesian languages covered by Gray et al. (2009). We then pruned the trees accordingly, that is, eliminated languages outside of our sample while preserving the tree structure.

The joint distribution of binary headhunting and warfare variables across societies placed at the tips of a linguistic tree is shown in figure 3. Here, for the purpose of illustration, we use the so-called maximum clade credibility tree, a summary tree representing a "point estimate" based on the entire sample of 4,200 candidates (Heled and Bouckaert, 2013). The horizontal axis reflects time and the length of tree branches is measured in years. The root of the tree is placed at about 5,200 years ago, when the ancestors of all Austronesian populations began spreading from Taiwan throughout the Pacific region and beyond in a "pulse-pause" type of movement (Gray et al., 2009). Societies at the bottom of the figure are the aboriginal settlers of Taiwan, whereas the large, relatively recent clade at the top corresponds to Polynesian societies. A simple visual inspection of trait bundles at the tips of the tree suggests that their distributions are phylogenetically structured: societies that are more closely related to each other tend to have similar trait values. For example, both headhunting and frequent warfare are typically present among aboriginal societies of Taiwan, whereas Polynesian cultures tend to lack both.

To formally confirm this visual pattern, we tested both variables for the presence of phylogenetic signal using the D statistic, specifically designed for the case of binary traits (Fritz and Purvis, 2010). A D statistic of 1 indicates that the trait is distributed independently of the tree structure (there is no phylogenetic signal), and a value of 0 corresponds to phylogenetic patterning implied by the Brownian motion threshold model of evolution. Negative values of D indicate that a trait is more phylogenetically conserved compared to the Brownian motion baseline. We computed the D statistic for each of the 4,200 trees, allowing 1,000 permutations per tree, and then derived its mean and standard deviation. We then tested hypotheses corresponding to the reference cases of $D = 0$ and $D = 1$. The average D statistic of -0.39 (with a standard deviation of 0.09) and formal tests imply that the headhunting trait contains a genetic signal (p-value less than 0.001) and its observed distribution is not significantly different from what is expected under the Brownian motion model ($p = 0.81$). We get similar results for warfare frequency, with the average D statistic of -0.18 (standard deviation of 0.08). Like headhunting, this trait has a strong

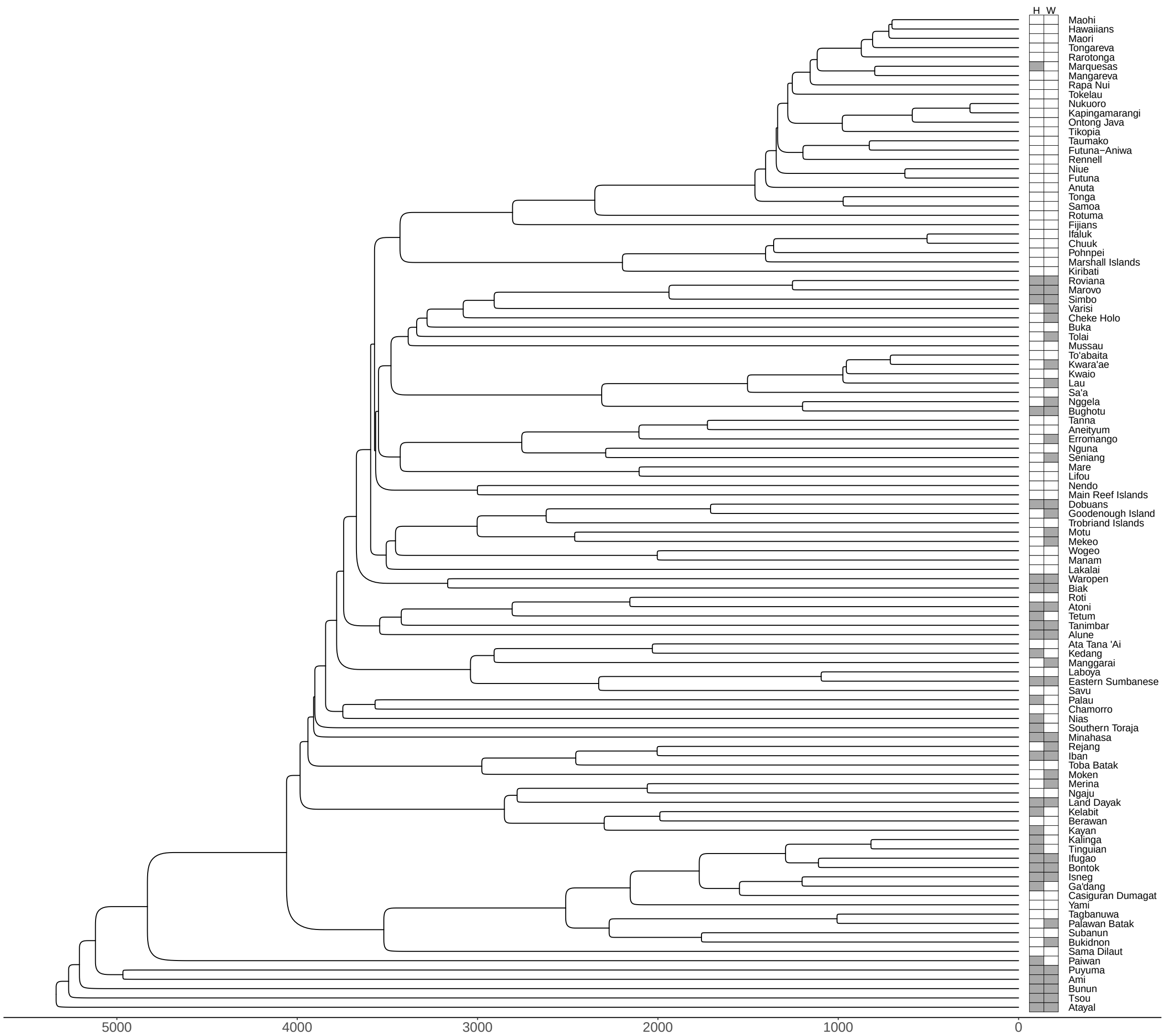


Figure 3: Headhunting and warfare at the tips of the linguistic tree.

Notes: Names of societies from our sample are listed at the tips of the maximum clade credibility tree of Austronesian languages. Shaded cells indicate the presence of headhunting (H) and frequent warfare (W) in respective societies. Horizontal axis represents time measured in years before present.

phylogenetic signal ($p < 0.001$) and its patterning is consistent with the Brownian motion baseline ($p = 0.67$).

In sum, both traits at the center of our investigation are phylogenetically structured, likely reflecting cultural non-independence of Austronesian societies. This motivates our reliance on phylogenetic comparative methods in the empirical analysis.

5 Phylogenetic comparative analysis

5.1 Phylogenetic regression approach

As mentioned earlier, a positive relationship between warfare frequency and the presence of headhunting is consistent with our main hypothesis, but it may also be driven by confounding factors. In this section, we employ a phylogenetic regression setting to examine this possibility, while accounting for cultural relatedness between observations in our sample.

Since our outcome variable, the presence of headhunting, is binary, we use the phylogenetic logistic regression model developed by Ives and Garland (2010). This is a generalization of the standard logit model, in which observations are phylogenetically structured. As in regular logit, the probability of an outcome variable taking the value of 1 is linked to a vector of regressors $\boldsymbol{x}$ via a logistic function

$$\mathbf{P}(Y = 1|\boldsymbol{x}) = \mu(\boldsymbol{x\beta}) = \frac{e^{\boldsymbol{x\beta}}}{1 + e^{\boldsymbol{x\beta}}},$$

but the variance-covariance matrix of Y has a more complicated structure relative to the case of independent observations. Specifically, the covariance elements of this matrix depend both on the strength of phylogenetic signal in the outcome variable, capturing the shared cultural evolutionary history of societies, and on the model's regressors. The functional form of this covariance matrix reflects a two-step process assumed for the evolution of the binary trait Y. In the first step, Y evolves along the branches of a given phylogenetic tree according to a two-state continuous-time Markov process, with constant instantaneous probabilities of switching between 0 and 1 (Pagel, 1994). The sum of these probabilities, or the overall transition rate α, measures the strength of phylogenetic signal in trait Y, with greater values (higher switching rates) corresponding to weaker signal. This process gives rise to a probability distribution for trait values at the tips of the phylogenetic tree. In the second step, following the evolution of Y along the tree branches, its values are further affected by regressors in a way that no longer depends on phylogeny. Thus, the first step of the evolutionary process determines the correlation of trait values between societies, whereas its second step sets the mean trait values in response to independent variables.[7] Note that the estimated value of α in this setting only reflects "residual" phylogenetic signal in Y unexplained by regressors.

In the absence of phylogenetic signal, that is, when α approaches infinity, this model collapses to the standard logit framework. However, when the signal is present, standard

[7] See Ives and Garland (2010) and Ho and Ané (2014) for technical details of the model and the exact structure of the covariance matrix for Y.

logit estimates are biased and subject to inflated type-I errors (Ives and Garland, 2010). We estimate the phylogenetic logistic regression model using the algorithm proposed by Ho and Ané (2014) and implemented in the `phylolm` package for R software. This algorithm is linear in the number of tips of the phylogenetic tree and allows fast estimation of regression coefficients and phylogenetic signal based on a quasi-maximum-likelihood approach. We use the maximum clade credibility tree (shown in figure 3) in the baseline analysis and show in appendix C that our results are robust across the entire sample of phylogenetic trees from Gray et al. (2009).

We control for a range of characteristics that could confound the relationship of interest by affecting the presence of headhunting, frequency of warfare, or both, as suggested by earlier work on culture and conflict.[8] Our first group of control variables includes the approximate year in which a society is observed and two measures of isolation. These are geographic remoteness, namely, the (log-transformed) distance to the closest landmass inhabited by a different society, and cultural assimilation, as captured by the presence of influence from major world religions (Christianity, Islam, Buddhism, or Hinduism) on local supernatural beliefs. Altogether, these variables to some extent account for spatial barriers to cultural diffusion of headhunting and its possible decline as a result of exposure to foreign religious traditions and prolonged contact with outside cultures and colonial administrations. The same measures, particularly geographic isolation, could simultaneously affect the incidence of warfare (Younger, 2008).

Second, we control for several metrics of social complexity: (log) population size, level of political authority, and social stratification. Population size has been argued to be an important determinant of general cultural complexity, warfare, and the pace of religious conversion in small-scale societies (Fogarty and Creanza, 2017; Younger, 2008; Watts et al., 2018). The presence and type of political authority and degree of social stratification have both been linked to headhunting in previous studies. Simon (2012) argues that headhunting was in part an attempt by ambitious men to augment their political power, which could in principle lead to the development of incipient chiefdoms. Similarly, Aswani (2000) views headhunting as a means to validate political and spiritual authority by the Roviana chiefs. Heron (2020) hypothesizes that headhunting was more likely to emerge in societies that were relatively egalitarian, but allowed for some degree of authority and leadership. Both interpersonal and intergroup violence have also been associated with the extent of social and political hierarchy in societies (Gat, 2008).

[8]Detailed definitions and summary statistics for all variables are reported in appendix A.

Table 1: Phylogenetic logistic regression estimates

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Warfare								
Occasional	1.898**	2.158**	1.807**	1.608**	2.276***	2.051***	1.813***	1.995***
	(0.871)	(0.879)	(0.778)	(0.765)	(0.742)	(0.746)	(0.696)	(0.748)
Common	2.122**	2.700***	2.284***	1.977**	2.102***	2.216***	1.688**	2.204***
	(0.888)	(0.936)	(0.818)	(0.792)	(0.780)	(0.772)	(0.770)	(0.851)
Frequent	3.406***	3.681***	3.286***	3.422***	2.713***	2.963***	2.548***	3.351***
	(1.080)	(1.072)	(0.996)	(1.050)	(0.900)	(0.957)	(0.913)	(1.094)
Year of observation		0.695	0.297	0.086	0.218	0.115	0.217	−0.002
		(0.620)	(0.539)	(0.551)	(0.626)	(0.644)	(0.631)	(0.648)
Geographic isolation			0.013	0.014	−0.285*	−0.446**	−0.209	−0.288
			(0.135)	(0.130)	(0.169)	(0.189)	(0.169)	(0.200)
Major religion				−0.716	−1.584**	−2.593***	−0.888	−2.475**
				(0.596)	(0.789)	(0.964)	(0.711)	(0.998)
Population size					0.451**	0.432**	0.267	0.346*
					(0.192)	(0.194)	(0.200)	(0.204)
Political authority								
Sublocal						0.087		0.839
						(1.288)		(1.385)
Local						1.483*		1.845*
						(0.886)		(1.035)
Supralocal						1.573*		1.889*
						(0.942)		(1.065)
Social stratification								
Moderate							0.182	
							(0.680)	
High							0.147	
							(0.832)	
Agriculture								1.001
								(0.720)
Group hunting								0.733
								(0.696)
Phylogenetic signal α	0.13	0.13	0.12	0.08	0.20	0.20	0.27	0.19
Observations	107	107	107	102	96	92	85	88

Notes. Dependent variable is the presence of headhunting. Omitted categories are: "none or rare" for warfare, "absent" for political authority and social stratification. ***, **, and * denote statistical significance at the 1, 5, and 10 percent level, respectively.

Finally, we account for differences in subsistence production mode through two binary variables. One captures agriculture or horticulture as predominant sources of food and the other indicates land-based group hunting as a non-negligible subsistence activity. As mentioned in section 2, headhunting was typically believed to be essential for securing good crops, providing a possible link to reliance on agriculture for subsistence. On the other

Table 2: Average marginal effects for warfare frequency

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Occasional	0.183	0.220	0.207	0.175	0.378	0.335	0.352	0.324
	(-0.12, 0.64)	(0.07, 0.49)	(0.01, 0.53)	(-0.01, 0.53)	(0.18, 0.54)	(0.10, 0.50)	(0.12, 0.53)	(0.08, 0.48)
Common	0.224	0.334	0.308	0.246	0.342	0.367	0.324	0.364
	(0.00, 0.64)	(0.17, 0.59)	(0.13, 0.59)	(0.04, 0.60)	(0.13, 0.54)	(0.13, 0.54)	(0.07, 0.54)	(0.09, 0.54)
Frequent	0.525	0.567	0.552	0.584	0.466	0.505	0.508	0.562
	(0.22, 0.78)	(0.38, 0.75)	(0.29, 0.75)	(0.29, 0.77)	(0.21, 0.66)	(0.21, 0.66)	(0.19, 0.69)	(0.24, 0.67)
Observations	107	107	107	102	96	92	85	88

Notes. Omitted category is "none or rare." For each estimate, 95% bootstrap confidence intervals are provided, based on 10,000 replications.

hand, some studies suggest that human trophy taking may have derived from group hunting of animals (Piano and Carson, 2020), which motivates the inclusion of our second variable. The type of subsistence production mode may also have indirect effects on the variables of interest through the degree of inequality and social complexity (Gershman, 2015).

Table 1 presents estimation results for different specifications, with data availability dictating respective sample sizes. The coefficients corresponding to warfare frequency are positive and statistically significant across the board, even in the most demanding specifications.[9] Table 2 reports the relevant average marginal effects, along with the 95% bootstrap confidence intervals. These estimates are large and imply that, other things equal, societies with occasional or common inter-tribal warfare are about 20-35 percentage points more likely to practice headhunting relative to those in which warfare is rare or non-existent. The average increase in that likelihood associated with frequent warfare exceeds 50 percentage points.

Among other covariates, the influence from major religions enters with a negative sign and is statistically significant in 3 out of 5 specifications, suggesting that contact with outside cultures is negatively associated with the practice of headhunting. In specifications of columns 5–8, geographic remoteness also enters with a negative sign and is statistically significant in two specifications, consistent with the absence of headhunting in more isolated cultures. Importantly, larger societies and those with political authority present at local or supralocal levels are more likely to practice headhunting, in line with the arguments mentioned earlier. On the other hand, social stratification and production mode indicators are not statistically significant.

[9]Following the recommendations of Ives and Garland (2010; 2014), we also calculated bootstrap confidence intervals for all coefficient estimates, without qualitative changes regarding statistical significance.

Regression results show that the positive relationship between warfare frequency and headhunting is not driven by other relevant characteristics and is robust to accounting for cultural non-independence between observations.[10] However, they do not rule out the possibility of reverse causality. In the following section, we exploit phylogenetic relationships between Austronesian societies to directly explore the coevolution of headhunting and warfare in a setting that suggests the likely causal directions in this relationship.

5.2 Correlated evolution of headhunting and warfare

5.2.1 The model and estimation approach

We employ the model of correlated evolution of binary traits on phylogenies developed by Pagel (1994) and adapted in subsequent research to examine cultural dynamics. In our application, the traits are headhunting and frequent warfare, and their observed bundles across Austronesian societies are represented in figure 3. Since each trait can only take the values of 1 (present) and 0 (absent), there are four possible combinations of trait values, or states. The model fits an evolutionary process giving rise to the observed joint distribution of trait values.

Each trait is assumed to evolve along the phylogenetic tree according to a continuous-time Markov process.[11] The probability of change in trait value depends only on the initial state at the beginning of the relevant tree branch, but not on previous history. Instantaneous transition rates between values 0 and 1 are assumed to be constant, and the possibility of both traits changing their values in the same instant is ruled out (this, of course, can happen over a longer period of time).

Given these assumptions, there are eight transition rates, denoted as q_{ij}, connecting different states. The subscripts i and j identify the initial and final states of a particular transition, respectively, and their possible values 1, 2, 3, and 4 correspond to states $(0, 0)$, $(0, 1)$, $(1, 0)$, and $(1, 1)$, as illustrated in figure 4. For example, in our analysis, q_{24} captures the probability of acquiring the practice of headhunting over an infinitesimally short time interval from the state in which warfare is frequent, but headhunting is absent.

[10] Estimates of α at the bottom of table 1 show a rather strong phylogenetic signal (Ives and Garland, 2010), which validates our use of the phylogenetic logistic model. Note that these values are technically not comparable across specifications due to differences in samples, and thus, linguistic trees, employed in the estimation. Appendix B presents standard logit estimates for reference.

[11] Note that the phylogenetic logistic regression model from previous section relies on the same assumptions in the first stage of the evolutionary process for the binary outcome variable.

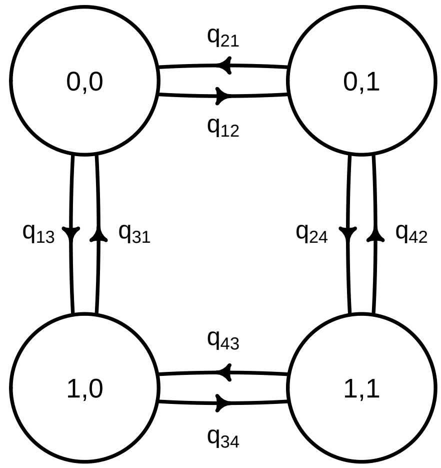


Figure 4: Transitions between states in the model of correlated evolution.
Notes: In our analysis, headhunting is the first trait and frequent warfare is the second trait in the pair.

If traits evolve independently, the rates of change in the values of one trait do not depend on the current value of the other trait. In such a model of independent evolution, $q_{12} = q_{34}$, $q_{13} = q_{24}$, $q_{21} = q_{43}$, and $q_{31} = q_{42}$, that is, there are at most 4 distinct parameters to estimate. By testing for the above constraints, one can distinguish between independent and dependent evolution of traits. In addition, as shown below, specific constraints on transition rates can be tested to examine the order of trait evolution.

In his original paper, Pagel (1994) showed how to find maximum likelihood (ML) point estimates of transitions rates and test constraints on them using standard likelihood ratio statistics. An alternative approach, more common in recent studies, is to employ Bayesian methods, which in particular allow to explicitly incorporate phylogenetic uncertainty in the analysis (Currie and Meade, 2014). Given the available sample of Austronesian language trees and following recent best practices, we rely on the reversible-jump Markov chain Monte Carlo (RJ MCMC) approach proposed by Pagel and Meade (2006). In this approach, MCMC methods are used to directly search among the numerous possible models of trait evolution, defined by the number of distinct transition rate parameters, and simultaneously estimate the posterior distributions of these rates while moving around the available sample of phylogenies. A particular advantage of this method is that it avoids overparameterization by settling on the most parsimonious models providing good fit for the data. At stationarity, a converged Markov chain samples from the posterior distribution of models of trait evolution and the parameters of these models.

As with any MCMC estimation, there are several parameters that need to be set to perform the analysis. In choosing these settings, we largely follow Watts et al. (2016)

who employ the RJ MCMC method to explore the correlated evolution of human sacrifice and social stratification across Austronesian societies. We use uniform prior for models of evolution and exponential hyperpriors for transition rate parameters, with the range informed by ML estimates. Thus, before running the RJ MCMC analysis, we found ML estimates of transition rates for both independent and dependent evolution models for each of the 4,200 linguistic trees and computed their averages. These varied roughly from 0 to 0.3, and we accordingly set the hyperprior ranges to $(0, 0.4)$ to cover this interval for all rates. Each analysis was run for one billion iterations, with half of them discarded as a burn-in period to ensure convergence. We sampled from the chain every 10,000 steps to avoid auto-correlation between iterations. All computations were performed using BayesTraits software (Meade and Pagel, 2021).

In a Bayesian setting, hypotheses regarding correlated evolution and its directionality can be tested using Bayes factor (BF) defined as twice the difference between the log marginal likelihoods of the posterior distributions for two competing models (for example, unconstrained correlated versus independent evolution). We used a stepping-stone sampler with a $\text{Beta}(0.4, 1)$ distribution to estimate the log marginal likelihood of each run, with 1,000 iterations across 100 stones (Meade and Pagel, 2021). We apply standard rules of thumb from Raftery (1996) when interpreting the magnitude of BF values: 0–2 as indicating no support for the first model (with a higher value of marginal likelihood) over the second one, 2–5 as positive evidence, 5–10 as strong support, and above 10 as very strong support.

5.2.2 Results

We start by running the RJ MCMC analysis for the unconstrained case allowing for any form of correlated evolution. The resulting posterior distributions of transition rates are shown in figure 5, along with the averages indicated by vertical lines. The distributions of q_{13} and q_{42} clearly stand out as these parameters are set to 0 in the vast majority of iterations. Other transitions rates have similar means and roughly bell-shaped distributions, with the exception of q_{43} which is set to 0 in 12% of sampled iterations. Indeed, the model of evolution visited most frequently (slightly more than 80% of the time) at the stationary distribution of the Markov chain is the one in which $q_{13} = q_{42} = 0$ and the remaining rates are set equal to each other. In the second most frequently visited model (only 8% of the time), $q_{43} = q_{42} = 0$, with other rates set equal to each other. Table D.1 in the appendix lists the top ten models (out of 452 visited in total) accounting for 96% of the posterior sample.

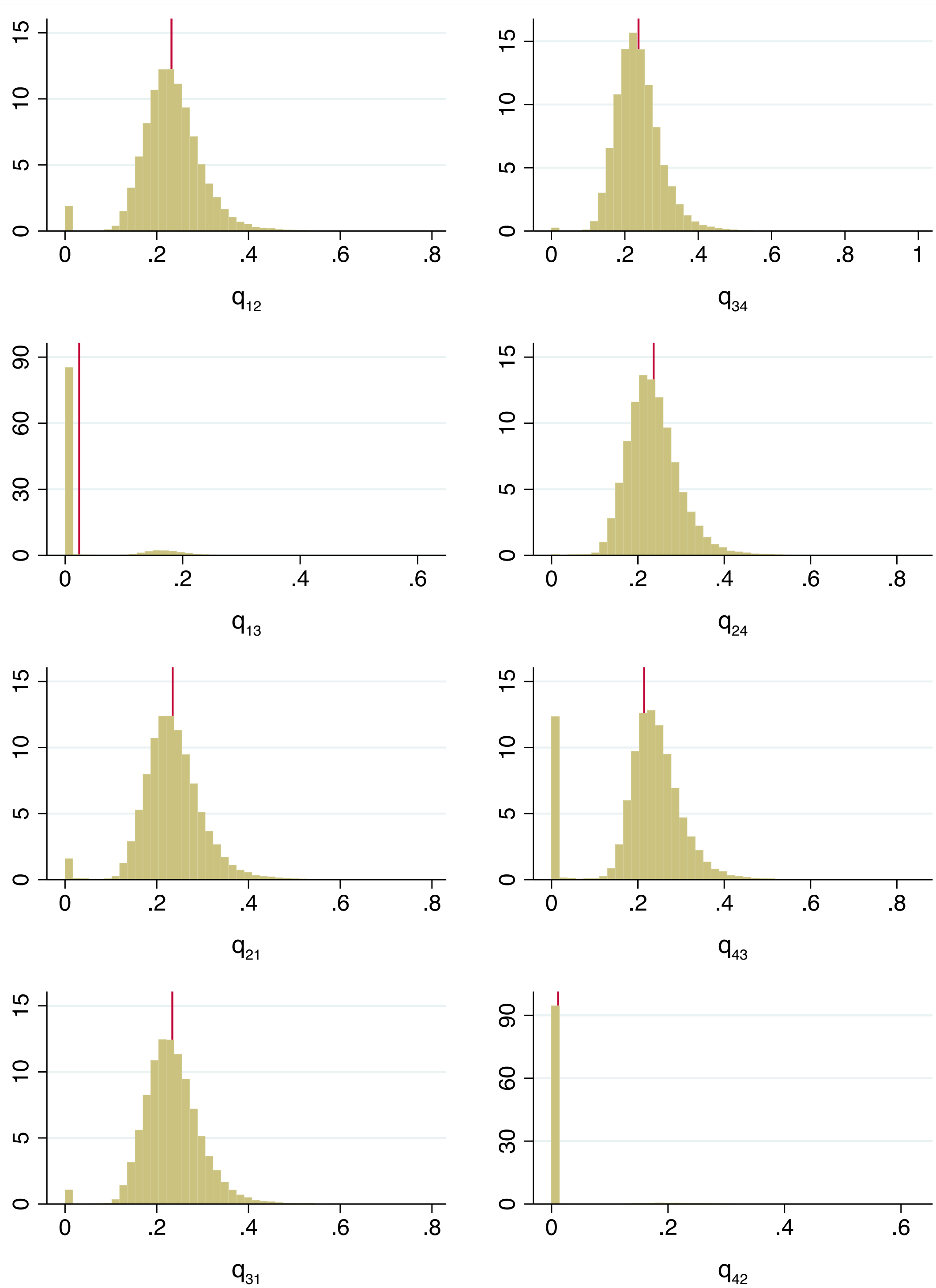


Figure 5: Posterior distributions of transition rates in the correlated evolution model.

Notes: The figure shows posterior distributions of transition rates in the unconstrained correlated evolution model estimated by the RJ MCMC method, based on 50,000 sampled iterations. Vertical lines mark the mean values. Each row corresponds to the rates that must be equal in the independent evolution case.

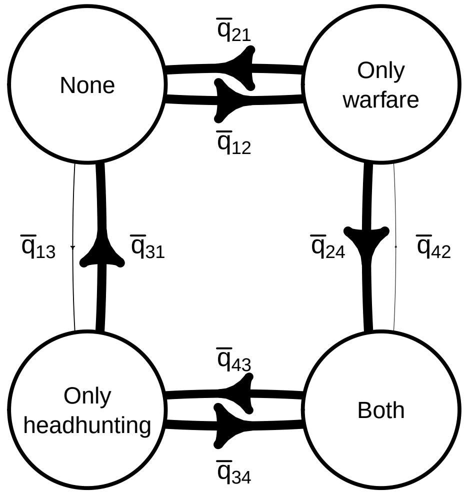


Figure 6: Average estimated transitions rates

Notes: The width of arrows reflects the relative magnitude of average transition rates. "Warfare" refers to frequent warfare.

Each row in figure 5 corresponds to the pairs of rates that must be identical in the independent evolution case. Striking differences between two pairs (q_{13} and q_{24}, q_{31} and q_{42}) suggest that models of correlated evolution dominate the posterior sample. A formal test confirms that there is strong support in favor of correlated evolution, with the value of BF exceeding 7. Thus, headhunting and frequent warfare coevolved.

Figure 6 graphically shows the estimation results using the flow diagram, in which the width of arrows reflects the relative magnitude of respective average transition rates. It illustrates several interesting findings. First, frequent warfare appears to be a prerequisite for gaining the practice of headhunting. The value of $q_{13} \approx 0$ suggests that it is virtually impossible to adopt headhunting from a state in which warfare is rare or nonexistent. Second, reducing the frequency of warfare or eliminating it appears to be a necessary condition for losing the practice of headhunting. The value of $q_{42} \approx 0$ suggests that it is virtually impossible to lose it from a state in which both headhunting and frequent warfare are present. Third, changes in warfare frequency appear to be independent of headhunting, as implied by the similarity of the relevant pairs of transition rates ($q_{12} \approx q_{34}$ and $q_{21} \approx q_{43}$).

We formally test these hypotheses by running the RJ MCMC analysis after imposing constraints on transitions rates and comparing the resulting fit to the baseline unconstrained correlated evolution case using BF. The types and results of these tests are summarized in table 3. The first four tests aim to establish that headhunting was an evolutionary response to frequent warfare. As shown in rows 1 and 2, the hypotheses that

Table 3: Testing hypotheses about the order of trait evolution

	Constraint(s)	Hypothesis	BF
(1)	$q_{13} = q_{24}$	H gain is independent of W	3.32
(2)	$q_{31} = q_{42}$	H loss is independent of W	4.39
(3)	$q_{13} = 0$	H gain impossible prior to W gain	–2.19
(4)	$q_{42} = 0$	H loss impossible prior to W loss	–2.32
(5)	$q_{12} = q_{34}$	W gain is independent of H	–1.00
(6)	$q_{21} = q_{43}$	W loss is independent of H	–0.63
(7)	$q_{13} = q_{42} = 0$, $q_{12} = q_{34}$, $q_{21} = q_{43}$	Joint	–6.88

Notes. H and W stand for headhunting and frequent warfare, respectively. Bayes factors (BF) are computed as twice the difference between log marginal likelihoods of the unconstrained and constrained models.

the practice is gained or lost independently of warfare frequency are both rejected (unconstrained model fits the data substantially better). Furthermore, formal tests in rows 3 and 4 favor the hypotheses that the gain (loss) of headhunting is impossible prior to the gain (loss) of frequent warfare (constrained models fit the data better). In rows 5 and 6, we test that the gain and the loss in warfare frequency, respectively, are independent of headhunting. These constrained models fit the data slightly better than the unconstrained model: although the BF are not large enough to strictly prefer the former, there is no evidence in favor of the unconstrained model. Finally, the model imposing joint constraints specified in rows 3–6 is strongly preferred over the baseline of unconstrained dependent evolution, as shown in row 7. Overall, these tests indicate that the practice of headhunting evolved in response to frequent warfare, consistent with the idea that it was a socially useful cultural adaptation to recurrent inter-tribal conflict.

We performed multiple sensitivity tests to confirm the robustness of our results. First, we ran each analysis three times to ensure that the results are consistent across runs, with standard Gelman and Rubin (1992) diagnostic indicating convergence. We doubled the number of iterations in the chain, half of it in burn-in phase, with results identical to the baseline. We experimented with different settings for the stepping-stone sampler and obtained very similar estimates of the relevant marginal likelihoods. Sampling every 1,000th iteration of the converged chain yields results that are very close to the reported baseline. Finally, we also examined sensitivity to assumptions on the prior distributions of parameters. We found very similar estimates for average transition rates when doubling the width of our baseline hyperprior interval and when assuming an alternative in which the mean and variance of the gamma prior are both seeded from a uniform hyperprior.

6 Concluding remarks

This paper examines the now-defunct practice of acquiring human heads for ritual use. Gruesome as headhunting was, we argue that it fulfilled an important social function. Specifically, the headhunting complex provided both a system of incentives for men to develop warfare skills by participating in risky raids and a way to verify the quality of their performance. In other words, it represented an effective mechanism for maintaining a regular class of trained men ready to protect their community from external threats. Such a mechanism should have been particularly useful in societies that were exposed to frequent warfare and, unlike most contemporary nations, lacked specialized military institutions and modern technologies to organize for warfare and monitor the performance of combatants.

We leverage phylogenetic comparative methods to empirically investigate this hypothesis in a sample of Austronesian societies. The evidence is consistent with our prediction: accounting for a range of confounding characteristics and cultural non-independence of observations, there is a strong positive relationship between the frequency of warfare and the presence of headhunting. Furthermore, Bayesian estimation of the correlated evolution models shows that, in line with our hypothesis, frequent warfare drove the adoption of headhunting, but not the other way round. The demise of headhunting, in turn, followed the reduction in warfare frequency once the practice ceased to be socially useful.

Appendices

A Definitions of variables and summary statistics

The source of all original variables is *Pulotu* database, version 1.2 (Watts et al., 2022), with the exception of social stratification (Watts et al., 2016).

Headhunting. A practice of killing people for the sole or primary purpose of obtaining their heads. Coded as present or absent.

Warfare frequency. Frequency of lethal conflict with other societies, coded on the following ordinal scale: frequent, common, occasional, rare or never. The cutoffs separating these categories are one year, five years, and one generation. A binary indicator (frequent vs. infrequent warfare) is created by grouping the first two and the last two categories of the ordinal classification.

Year of observation. Approximate year to which ethnographic data on a particular society refer.

Geographic isolation. Natural logarithm of (one plus) the distance to closest landmass inhabited by a different culture (i.e., any culture other than the one being coded). If there was a different culture present on the same island, the distance is set to 0.

Influence from a major religion. A binary variable equal to 1, if there is evidence of Christian, Muslim, Hindu, or Buddhist influence on local supernatural beliefs. Produced using three separate original variables.

Population size. Natural logarithm of the estimated population size.

Political authority. A right to manage interactions between living human beings, vested in a specific office and exercised over a specific group of people. Comprises the following categories: 1) absent, or restricted to a group no larger than the household; 2) sublocal (encompasses a group larger than the household but smaller than the local community); 3) local (encompasses the local community and/or multiple sublocal groups); 4) supralocal (encompasses multiple local groups).

Social stratification. Comprises the following three categories: 1) egalitarian (minimal or no potential for wealth and/or status to be inherited between generations); 2) moderate (pronounced intergenerational differences in wealth and/or status existed between social groups, but one or more of the following conditions was met: (a) social mobility was not restricted at any level, (b) differences in status and/or wealth were not associated with pronounced differences in living standards, and/or (c) the social groups in question were not clearly delineated); 3) high (pronounced intergenerational differences in wealth and/or status, associated with pronounced differences in living standards, existed between clearly delineated social groups, and social mobility between two or more of the groups was restricted).

Reliance on agriculture for subsistence. A binary variable equal to 1, if agriculture or horticulture were the principal source of food.

Importance of land-based group hunting. A binary variable equal to 1, if land-based hunting performed by one or more groups represented a non-minor source of food.

Table A.1: Summary statistics

	Mean	St. dev.	Min	Max	Obs.
Presence of headhunting, binary	.318	.468	0	1	107
Influence from major religions, binary	.225	.42	0	1	102
Reliance on agriculture, binary	.74	.441	0	1	104
Importance of land-based group hunting, binary	.284	.453	0	1	102
Year of observation	1881	53.1	1668	1983	107
Geographic isolation	2.09	2.52	0	8.2	107
Population size	9.02	1.79	4.13	13.5	101
Warfare frequency, categories					107
Rare or never	.374	.486	0	1	
Occasional	.262	.442	0	1	
Common	.187	.392	0	1	
Frequent	.178	.384	0	1	
Political authority, categories					103
Absent	.136	.344	0	1	
Sublocal	.0583	.235	0	1	
Local	.32	.469	0	1	
Supralocal	.485	.502	0	1	
Social stratification, categories					91
Absent	.209	.409	0	1	
Moderate	.495	.503	0	1	
High	.297	.459	0	1	

B Standard logit estimates

Table B.1: Logit estimates

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Warfare								
Occasional	2.357***	2.288***	2.187***	2.275***	2.301**	2.061**	2.221**	1.991**
	(0.826)	(0.830)	(0.848)	(0.859)	(0.910)	(0.947)	(0.922)	(0.979)
Common	2.944***	2.971***	2.491***	2.378***	2.099**	2.282**	2.147**	2.241**
	(0.852)	(0.862)	(0.900)	(0.897)	(0.933)	(0.959)	(0.974)	(1.029)
Frequent	3.483***	3.530***	2.893***	2.817***	2.726***	3.011***	2.674**	3.367***
	(0.867)	(0.879)	(0.932)	(0.932)	(1.009)	(1.081)	(1.045)	(1.225)
Year of observation		0.007	0.003	0.001	0.002	0.000	0.001	−0.000
		(0.006)	(0.006)	(0.006)	(0.007)	(0.007)	(0.007)	(0.007)
Geographic isolation			−0.263*	−0.313**	−0.456**	−0.565***	−0.412**	−0.464**
			(0.141)	(0.152)	(0.185)	(0.203)	(0.190)	(0.216)
Major religion				−0.495	−1.586**	−2.646***	−1.363*	−2.497**
				(0.605)	(0.778)	(1.007)	(0.785)	(1.056)
Population size					0.452**	0.529**	0.421*	0.394
					(0.206)	(0.230)	(0.236)	(0.252)
Political authority								
Sublocal						0.125		0.845
						(1.349)		(1.555)
Local						1.498		1.866
						(0.949)		(1.169)
Supralocal						1.580		1.876
						(1.009)		(1.203)
Social stratification								
Moderate							−0.001	
							(0.782)	
High							−0.146	
							(0.953)	
Agriculture								1.018
								(0.942)
Group hunting								0.783
								(0.786)
Observations	107	107	107	102	96	92	85	88

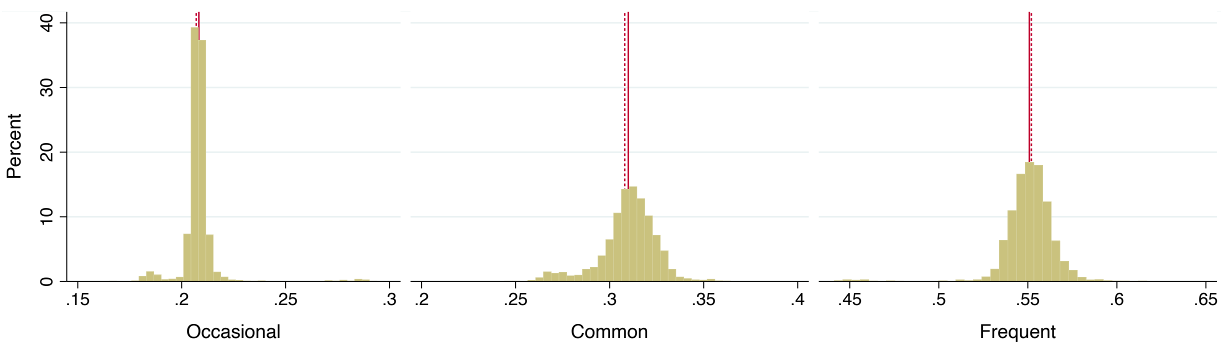
Notes. Dependent variable is the presence of headhunting. Omitted categories are: “none or rare” for warfare, “absent” for political authority and social stratification. ***, **, and * denote statistical significance at the 1, 5, and 10 percent level, respectively.

Table B.2: Average marginal effects for warfare frequency (standard logit)

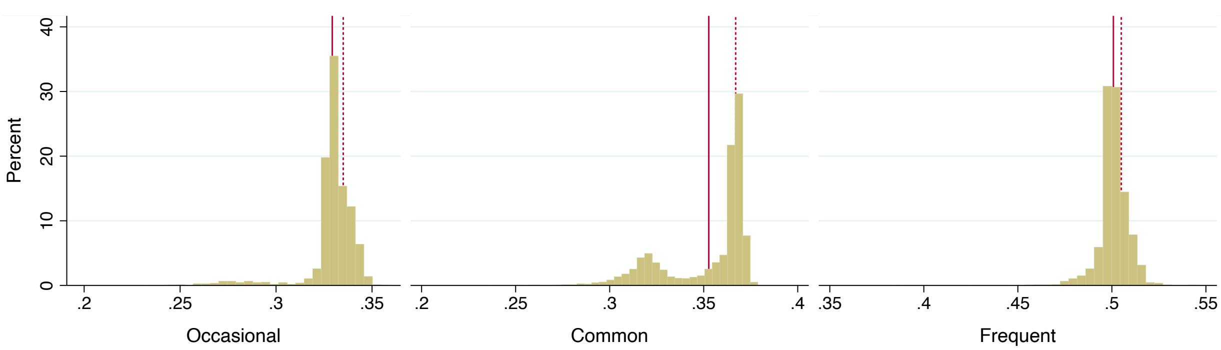
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Occasional	0.307***	0.289***	0.295***	0.326***	0.318***	0.262**	0.333***	0.244**
	(0.097)	(0.094)	(0.099)	(0.105)	(0.108)	(0.114)	(0.118)	(0.117)
Common	0.450***	0.448***	0.360***	0.348***	0.282**	0.300**	0.319**	0.286**
	(0.117)	(0.115)	(0.117)	(0.117)	(0.114)	(0.118)	(0.133)	(0.133)
Frequent	0.582***	0.580***	0.449***	0.444***	0.395***	0.429***	0.418***	0.483***
	(0.116)	(0.113)	(0.132)	(0.133)	(0.142)	(0.152)	(0.158)	(0.170)
Observations	107	107	107	102	96	92	85	88

Notes. Omitted category is "none or rare."

C Phylogenetic uncertainty in regression estimates



(a) Specification 3 from table 1



(b) Specification 6 from table 1

Figure C.1: Average marginal effects of warfare frequency in a sample of phylogenetic trees.

Notes. The figure shows the distributions of average marginal effects of warfare frequency, estimated via the phylogenetic logistic regression model from section 5.1 for 4164 Austronesian language trees from Gray et al. (2009). Of the original 4200 trees, 36 (less than 1%) were dropped due to non-convergence of the estimation algorithm. Solid vertical lines correspond to the mean values and dashed lines mark the estimates from table 2 corresponding to the default (maximum clade credibility) linguistic tree.

D Details of the correlated evolution analysis

Table D.1: Top ten models in the posterior sample

Model	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}	Frequency	Percent	Cumulative
1	×	0	×	×	×	×	0	×	40,264	80.53	80.53
2	×	×	×	×	×	×	0	0	4,126	8.25	88.78
3	×	0	×	×	×	×	×	×	1,535	3.07	91.85
4	×	×	0	×	×	×	0	0	559	1.12	92.97
5	×	×	×	×	×	×	×	0	350	0.70	93.67
6	×	×	×	×	×	×	0	×	350	0.70	94.37
7	×	0	×	×	0	×	0	×	244	0.49	94.86
8	0	×	×	×	×	×	0	×	226	0.45	95.31
9	0	×	×	×	×	×	×	0	174	0.35	95.66
10	0	×	×	×	×	×	×	×	159	0.32	95.98

Notes. RJ MCMC analysis of the unconstrained correlated evolution model. 0 indicates a transition rate set to zero and × indicates equal non-zero rates.

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