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Author for correspondence:

Jeremy Koster

e-mail: jeremy.koster@uc.edu

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Kinship ties across the lifespan in human communities

Jeremy Koster^{1,2}, Dieter Lukas², David Nolin³, Eleanor Power⁴, Alexandra Alvergne⁵, Ruth Mace^{6,7}, Cody T. Ross², Karen Kramer⁸, Russell Greaves⁸, Mark Caudell⁹, Shane MacFarlan⁸, Eric Schniter¹⁰, Robert Quinlan¹¹, Siobhan Mattison¹², Adam Reynolds¹², Chun Yi-Sum^{12,13} and Eric Massengill¹²

¹Department of Anthropology, University of Cincinnati, Cincinnati, OH 45221-0380, USA

²Department of Human Behavior, Ecology, and Culture, Max Planck Institute of Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

³Department of Anthropology and Population Research Institute, Penn State University, University Park, PA 16802, USA

⁴Department of Methodology, The London School of Economics and Political Science, Houghton Street, London WC2A 2AE, UK

⁵School of Anthropology and Museum Ethnography, University of Oxford, 51 Banbury Road, Oxford OX2 6PE, UK

⁶Department of Anthropology, University College London, 14 Taviton St, London WC1H 0BW, UK

⁷School of Life Sciences, Lanzhou University, 222 Tianshui NanLu, Lanzhou, Gansu 73000, People's Republic of China

⁸Department of Anthropology, University of Utah, Salt Lake City, UT 84112, USA

⁹Paul G. Allen School for Global Animal Health, Washington State University, Pullman, WA 99164, USA

¹⁰Economic Sciences Institute, Chapman University, Orange, CA 92866, USA

¹¹Department of Anthropology, Washington State University, Pullman, WA 99164, USA

¹²Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA

¹³Harvard-Yenching Institute, Vanserg Hall, Suite 20, 25 Francis Avenue, Cambridge, MA 02138, USA

JK, 0000-0002-7291-6478; DL, 0000-0002-7141-3545; EP, 0000-0002-3064-2050; AA, 0000-0002-3151-9919; RM, 0000-0002-6137-7739; CTR, 0000-0002-0067-4799; KK, 0000-0002-9157-7758; MC, 0000-0003-4456-3318; SM, 0000-0002-6332-9829; SM, 0000-0002-9537-5459

A hypothesis for the evolution of long post-reproductive lifespans in the human lineage involves asymmetries in relatedness between young immigrant females and the older females in their new groups. In these circumstances, inter-generational reproductive conflicts between younger and older females are predicted to resolve in favour of the younger females, who realize fewer inclusive fitness benefits from ceding reproduction to others. This conceptual model anticipates that immigrants to a community initially have few kin ties to others in the group, gradually showing greater relatedness to group members as they have descendants who remain with them in the group. We examine this prediction in a cross-cultural sample of communities, which vary in their sex-biased dispersal patterns and other aspects of social organization. Drawing on genealogical and demographic data, the analysis provides general but not comprehensive support for the prediction that average relatedness of immigrants to other group members increases as they age. In rare cases, natal members of the community also exhibit age-related increases in relatedness. We also find large variation in the proportion of female group members who are immigrants, beyond simple traditional considerations of patrilocality or matrilocality, which raises questions about the circumstances under which this hypothesis of female competition are met. We consider possible explanations for these heterogeneous results, and we address methodological considerations that merit increased attention for research on kinship and reproductive conflict in human societies.

This article is part of the theme issue ‘The evolution of female-biased kinship in humans and other mammals’.

1. Introduction

Humans are among the minority of mammalian species in which females exhibit prolonged post-reproductive lifespans [1]. Among anthropologists, adaptive explanations for this life-history strategy have focused on the inclusive fitness benefits of parental and grandparental investment [2,3]. Expanding on these perspectives, Cant & Johnstone [4] observe that in addition to the fitness effects of altruism, conceptual models also need to account for the inclusive fitness consequences of reproductive conflicts. That is, reproductive conflict occurs in social groups, including cooperative groups, when there are limited resources to support reproduction by females in the group. In humans, for instance, increased offspring mortality has been documented when a woman reproduces concurrently with her mother-in-law [5]. Females who are surrounded by fewer genetic kin are predictably more indifferent to the reproductive costs that competition inflicts than females living among many kin [4]. For example, whereas women are typically unrelated to their mother-in-law's offspring, their own offspring will be the genetic grandoffspring of the mother-in-law, who therefore has less to lose by ceding reproductive opportunities. To understand whether the resolution of reproductive conflicts might have shaped the evolution of life-history strategies, we need a better understanding of the kinship structure among interacting females and how this is influenced by demography.

The main factor that influences whether adult females are interacting with close kin is whether and where they move relative to their parents' location [6,7]. In most populations of mammals and birds, there appears to be a strong sex bias in dispersal [8]. Accordingly, populations are generally classified into those where females are philopatric and remain with their kin and those where females disperse and join other, unrelated females. Empirical studies of kinship generally support that in a given population females either remain with kin or not, but also highlight important fluidity in these patterns where only subsets of females remain philopatric [9] or dispersing females end up with kin [10]. Such fluidity in settlement patterns appears to characterize many human populations [11], leading to potential differences between females in their relatedness to other group members depending on their movement history, with corresponding implications for the resolution of reproductive conflicts.

Arguments related to kinship structure among females are further complicated since it is not a static aspect of a female's environment, but changes dynamically across the lifespan [12]. For instance, in human societies that are characterized by male philopatry and female-biased dispersal, younger females are predicted to be surrounded by fewer genetic kin than older females. In this scenario, females leave their kin and join a new group, where they mate with males who are typically related to the older females in the group. Therefore, usually the resulting offspring of these young females exhibit high genetic similarity to the older females (with allowances for paternity uncertainty) such that older females are related to the majority of individuals in their local group. This asymmetry favours younger females in reproductive conflicts with older females because the latter have relatively more to gain via alloparental investment. According to theory, these could be the conditions favouring the evolution of post-reproductive lifespans in females [4].

The conceptual arguments linking kinship structure to residence patterns and age were formalized quantitatively by Johnstone & Cant [1], who derive individuals' relatedness to group members as a function of mating patterns and the dispersal and demography of males and females, respectively. The model provides confirmatory evidence that when females disperse and mating occurs within the local group, the relatedness of females to other group members increases with age as they have sons who remain as breeding members of the group. Given the extent to which female-biased dispersal characterizes hominoid species, this pattern is dubbed the 'ape case' [1]. The model is also flexible enough to accommodate the kinship dynamics of cetaceans, another species with prolonged post-reproductive lifespans. Among killer whales, neither males nor females disperse from their natal group, but because mating occurs with individuals outside the group, females exhibit relatively low relatedness to males other than their sons [13]. As they age and have more sons in the group, female killer whales, therefore, display overall increases in average relatedness to other group members that parallel the aforementioned increases in the ape case [13].

When applied to the evolution of human life-history traits, the female-biased dispersal that typifies African apes has often been assumed to characterize the social organization of human ancestors [4]. By dispersing, young adult females may reside primarily among their mates' female kin, not their own. In that hypothesized scenario, the resulting reproductive conflicts among the females potentially help to explain distinctive human traits, such as prolonged post-reproductive lifespans. However, it is currently difficult to make strong empirical inferences about the social organization of prehistoric hominins, particularly given the flexible residence and dispersal that distinguish contemporary human societies [11]. Heterogeneous residence rules across human societies include patrilocal and matrilocal, which purportedly correspond to the typical dispersal patterns of the ape case and the typical mammalian case, respectively. In addition to cross-cultural variability [14], adherence to normative residence rules within societies is likewise variable. Human couples maintain affiliative bonds with both the husband's and wife's kin, and the ability to move between these groups throughout an individual's life permits flexible residence arrangements that can confound even seasoned ethnographers [15].

Given this diversity and flexibility, empirical research on kinship in human societies is needed to inform our understanding of the potential for reproductive conflict and cooperation among women. In this study, our aim is to investigate the extent to which movement influences kinship patterns across human communities and whether this is associated with predictable variation in individual levels of kinship across female lifespans. Given the expected flexibility in human settlement patterns, and the extent to which individuals adhere to these rules, we consider variation in group kinship across the lifespan for immigrants (of both sexes) in each community, drawing contrasts to natal residents to contextualize these changes. To assess these patterns, we compile genealogical and demographic data from 19 communities to examine age-related variation in relatedness to group members. The study communities vary in terms of settlement history, subsistence strategies,

Table 1. Descriptive statistics for the study sites. Descent rules are reported when known. Sample size corresponds to the number of residents in the communities. Natality status was calculated only among adults (males older than 21 and females older than 18). For each respective sex, the percentages in the table reflect the proportion of adults who are natal members of the study community. For the data on average women per household, the household is considered to be the most relevant resource-sharing units at that locale. For the Gambian study sites, these correspond to multi-family compounds. Blank cells for the descent rules indicate a lack of information.

site number	group	country	descent rule	average relatedness	community size	women per household	per cent natal female adults	per cent natal male adults
1	Savannah Pumé	Venezuela	bilateral	0.085	76	0.90	57.89	14.29
2	Miskito	Nicaragua	bilateral	0.100	92	1.07	53.33	21.43
3	Mayangna	Nicaragua	bilateral	0.044	322	1.88	80.65	38.89
4	Coastal Afro-Colombians	Colombia		0.012	188	1.22	48.15	45.83
5	Inland Afro-Colombians	Colombia		0.006	306	1.11	46.59	47.54
6	Dominica	Dominica		0.017	422	1.33	94.63	96.60
7	Inland Emberá	Colombia		0.048	91	1.00	60.00	61.54
8	Choyeros	Mexico	bilateral	0.054	113	1.19	73.68	81.40
9	The Gambia, 2	The Gambia	patrilineal	0.011	573	1.56	80.50	89.39
10	Mosuo	China	matrilineal	0.014	218	2.13	82.14	91.36
11	Maya	Mexico	bilateral	0.035	544	1.20	84.15	94.74
12	Lamalera	Indonesia	patrilineal	0.005	1216	1.48	83.76	95.43
13	Coastal Emberá	Colombia		0.087	86	1.13	11.76	13.33
14	Maasai	Kenya	patrilineal	0.013	296	1.29	25.93	31.25
15	The Gambia, 1	The Gambia	patrilineal	0.005	1387	5.65	70.23	86.42
16	Mosuo	China	patrilineal	0.024	163	2.27	62.69	88.14
17	Alakāpuram	India	patrilineal	0.004	613	1.33	37.05	85.33
18	Tēnpattī	India	patrilineal	0.004	487	1.27	30.57	91.84
19	Tanna	Vanuatu	patrilineal	0.030	183	2.31	27.03	86.67

population, fertility rates, descent rules and sex biases in dispersal. Given that we also observe flexibility in the dispersal data of the communities in our sample, we are not classifying these along traditional binary lines of matrilineal versus patrilineal. Instead, we explicitly consider the ratio of immigrants in each sex.

Our analysis is framed around the predictions of Johnstone & Cant [1], specifically that individuals who disperse to new communities initially have few kinship ties but progressively exhibit greater relatedness as they have offspring who become members of the group. In this analysis, the outcome variable is the individuals' average relatedness to other community members [13]. Arguably, because sharing and competition over resources may be particularly acute within residential clusters of close kin (i.e. sub-units of the larger community), the measure of community relatedness in this study could be too broad [16]. However, the present compilation of datasets do not permit the identification of relevant subclusters within the communities, a methodological consideration that we address in the discussion. Nevertheless, the numerator in the calculations of average relatedness for a given individual largely reflects the number of close, co-resident kin in the population. Therefore, in larger communities, although most individuals may be distantly related to the individual, variability in average relatedness frequently reflects the presence of close kin and the concomitant opportunities for reproductive conflict and cooperation.¹

2. Methods

The data for this study were obtained by the authors via censuses and genealogical interviews at their respective field sites (table 1). As noted, the sites exhibit diverse social organization, demography and subsistence strategies (see the electronic supplementary material for brief descriptions of each site). For all living residents in the respective study communities, the authors compiled data on age, sex and whether or not individuals are natal members of the community (figure 1). This latter variable is subject to interpretation, given the diversity of movement patterns in human communities. When groupings are geographically and temporally ephemeral, for example, then it can be challenging to distinguish between natal and non-natal members of the community. In this sample of sites, the Savannah Pumé of Venezuela exhibit such fluidity, and few older residents are therefore considered natal members of the community. Analogously, the Maasai community in this sample is a relatively new settlement that attracted a diverse set of immigrants, resulting in few older residents who are considered natal members of the community. More generally, the co-authors had to categorize individuals such as temporary migrants, children who had relocated with their parents, and foster children. The co-authors attempted to standardize norms about the categorization of such individuals, generally tending toward conservatism in the categorization of natal residents. For instance, children of divorced women who subsequently marry into a new community are generally not considered natal members of the new community. Therefore, relative to immigrants, the comparability of predictions for natal residents is less impacted by the fluidity of residence that characterizes several of the study sites.

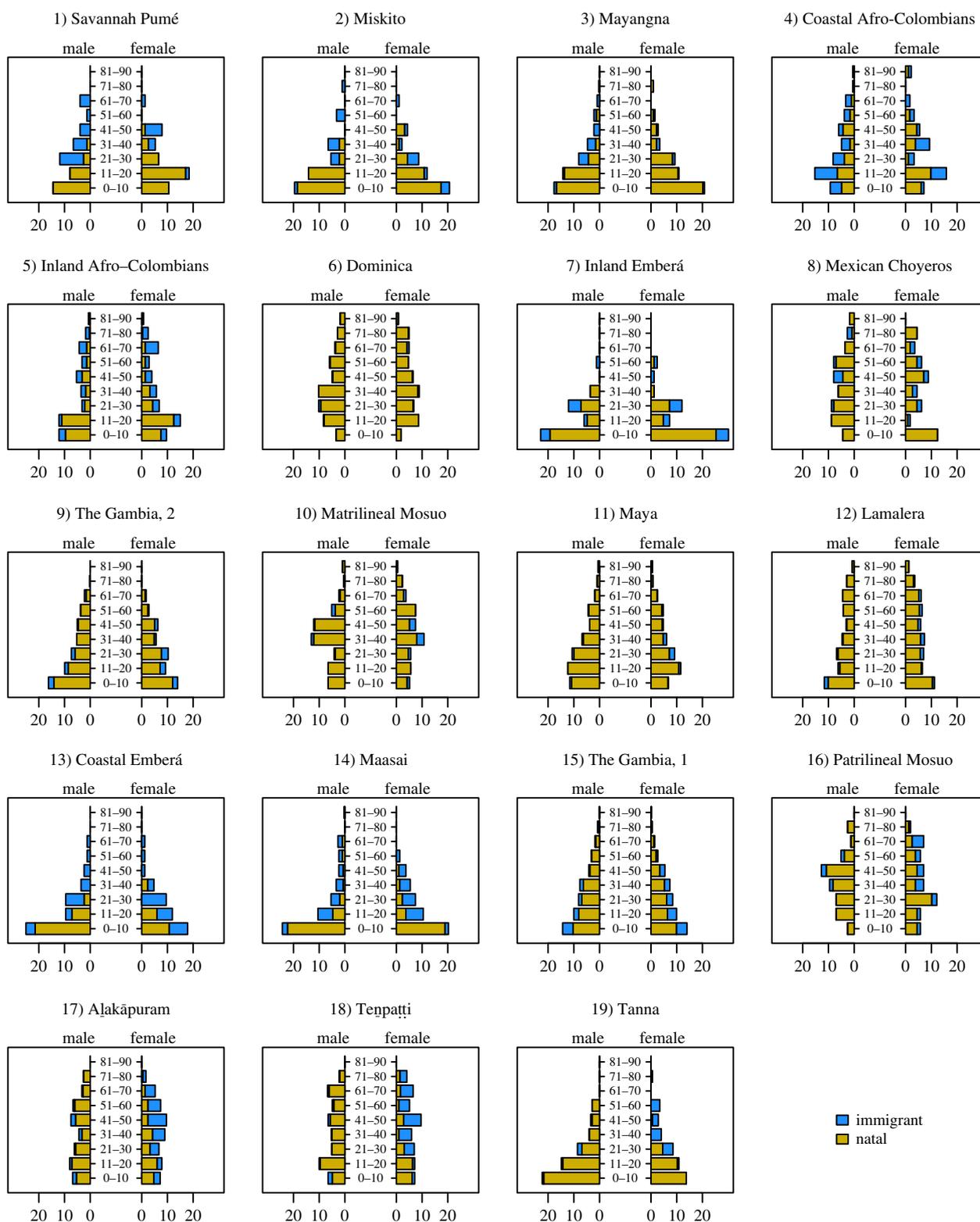


Figure 1. Population pyramids for the study communities. In the plot, sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in table 1). The numbers on the horizontal axes represent the percentage of the total represented by the respective age-sex categories.

For each site, the data also includes genealogical relationships that were elicited via interviews with informants. These genealogies permit the calculation of relatedness among individual residents of the communities. These calculations employ standard methods for estimating the coefficient of relatedness from genealogies [17]. For any given dyad, the coefficient is therefore constrained to lie between 0 and 1, which we anticipate to provide a useful approximation of genetic similarity. The genealogies from our study sites include

at least three generations of depth for residents, typically permitting us to distinguish cousins and closer genealogical relationships. As shown by Pemberton [18], pedigrees of three generations capture much of the variation in genetic relatedness among individuals. Some datasets provide even greater depth, and this varying thoroughness introduces between-site variation into the sample. In some communities, most notably the matrilineal Mosuo community, women were often unable to reliably indicate the father of their children. The data are

cross-sectional and represent the composition of the community at a single point in time.

In our primary analysis, we examine the average relatedness of adults to other adult residents in the community. A focus on adults has parallels to the ethological literature and its attention to inbreeding avoidance among reproductively mature individuals [19]. Accordingly, we consider females to be adults when they are 18 years or older and males to be adults when they are 21 years or older. These ages align with evidence that Aché women typically give birth the first time at 19 years old and that men in natural fertility populations are commonly 3 years older than women when their first child is born [20,21].

The analysis is oriented primarily toward illuminating demographic patterns within the respective study sites. We therefore model average relatedness at each site separately using regression models with the main effects and interaction terms of the three predictor variables: age, sex and natality. In some datasets, there were missing values for individuals' age and natality. Typically, these individuals were not permanent residents of the respective communities, so although their genealogical connections were included in the calculations of dyadic relatedness, the average relatedness of these individuals were not included in the statistical models. Because the outcome variable, average relatedness, is bounded to lie between 0 and 1, we use beta regression models [22]. Since average relatedness for some individuals is zero, we add a constant (0.0001) to all values for identifiability of model parameters.² We interpret the models graphically, plotting their predictions as a function of age interacted with the categorical predictors, sex and natality. As a supplemental analysis, we model average relatedness among all individuals in the study communities, including children. We also consider a multilevel analysis of the aggregated cross-cultural dataset, and we evaluate simpler site-specific models that omit sex as a predictor.

Models are fit with Markov chain Monte Carlo estimation using functions from the *Rstan* package [23] and auxiliary functions from the *rethinking* package [24]. Weak regularizing priors are implemented for all model parameters. We do not adopt any particular threshold for statistical significance, but we make sure to note the effects for which the models consistently predict age-related increases or decreases in the posterior samples. Data and coding scripts are available as supplemental files on the Open Science Framework (<https://osf.io/h8cqr/>).

3. Results

Our models examine the average relatedness of individual adults to all other adults in the community. Model predictions for each site are plotted in figure 2 (see also electronic supplementary material, table S1). Before interpreting predictions for specific sites, it is important to acknowledge that the confidence in predictions is a reflection of varying sample sizes, both across sites and across demographic subclasses within sites. In smaller communities, such as the Emberá sites, the predicted slopes may exhibit high heterogeneity, but there is little confidence that the slopes are conclusively positive or negative, nor are the slopes for demographic subclasses distinguishable from each other. The uncertainty relates in part to the small size of these communities, though another consideration is the high mobility and dispersal rates that characterize these sites. That is to say that age-related variation in relatedness cannot be discerned in small communities. The Savannah Pumé community is also small, but for immigrant females, the model confidently predicts an increase in relatedness with age. Similarly, low sample sizes within demographic subclasses can also

reduce confidence in the corresponding model predictions. At the patrilineal Mosuo site, for example, the predicted effects of age are roughly comparable for male and female immigrants. However, there are substantially more female immigrants than male immigrants. Consequently, there is relatively more confidence in predictions for the average female immigrant.

In larger communities, individuals exhibit minimal relatedness to most of the other residents. This lowers the average relatedness among residents, and slopes in these communities typically seem relatively flat. Because of the larger sample size in communities, however, there is higher confidence in the predicted means (e.g. the downward trends in Lamalera). On the other hand, a comparison of the predicted values to the empirical data shows that age and the moderating effects of sex and natality typically explain only a modicum of the variation in average relatedness in large communities.

With those caveats in mind, we assess model predictions. Initially, we focus on age-related increases in average relatedness given the importance of such increases in recent theorizing of reproductive conflict [1]. For natal residents, increases with age are rare and evident primarily among males and females in the Mayangna community (site 3) and the female residents of the Coastal Afro-Colombian community (site 4) and the Mexican *choyer* community (site 8). For immigrants, increases are relatively more common and apparent among female immigrants in the patrilineal communities of Lamalera (site 12), the patrilineal Mosuo (site 16), Ałakāpuram (site 17), Tenpañi (site 18) and Tanna (site 19). Similar age-related increases for female immigrants are evident in two communities characterized by bilateral descent and female philopatry, the Savannah Pumé (site 1) and Mayangna (site 3). For male immigrants, conclusive age-related increases are evident primarily in the Mayangna community.³ Collectively, these results accord with expectations from Johnstone & Cant [1] that adult immigrants initially have few kin in the community, but then their relatedness increases over time as they have descendants who join them as residents in the group.

Although prevailing theories focus on age-related increases in relatedness over time, declines are also interesting because they imply a different set of tradeoffs that merit theoretical attention. In this sample, declines in average relatedness are evident in several communities. For instance, the statistical models predict decreases for both natal females and males in Lamalera (site 12) and Ałakāpuram (site 17). There is a decrease with age for natal males in Tenpañi and a decrease for natal females in the smaller Gambian community (site 9). There is also moderate evidence for a decline in relatedness with age among natal residents of both sexes in the larger Gambian community (site 15). For natal females in Dominica (site 6), the predicted relationship with age also trends negative. Among immigrants, however, there is little evidence for decreases in relatedness with age at any of the sites.

(a) Supplemental analyses

For a supplementary analysis of age-related variation in relatedness, we also calculated and modelled average relatedness among all individuals in the community, including both adults and children (electronic supplementary material,

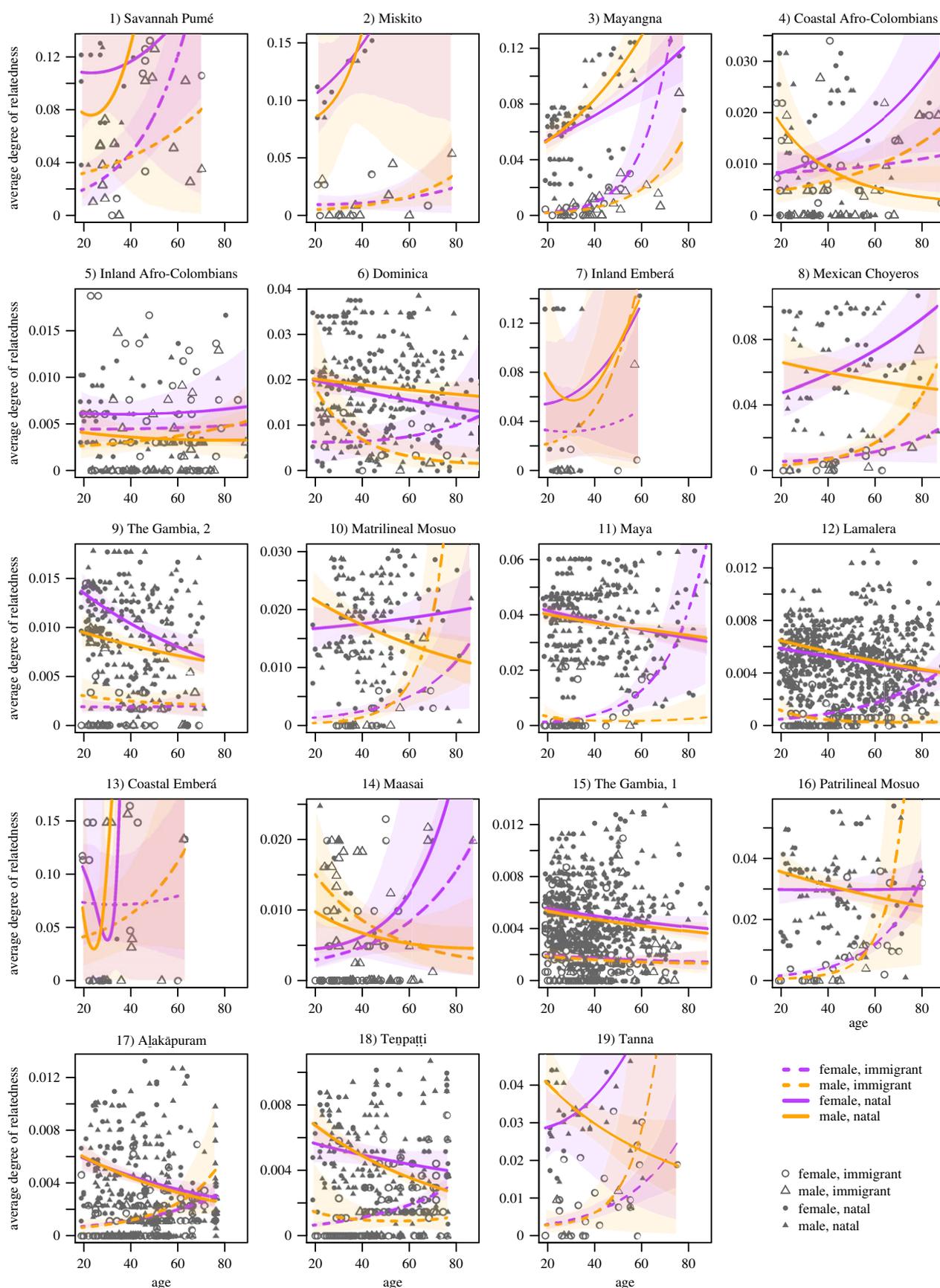


Figure 2. Model predictions for adults' relatedness to all other adults in the study communities, which is expected to vary as a function of individuals' age, sex and natality status. All predictions are based on beta regression models with three-way interaction terms (and the corresponding two-way interactions) between these variables. Shaded intervals depict 89% confidence intervals around model predictions. Note that the scale of the vertical axis changes for each community. Sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in table 1).

figure S1 and table S2). In general, the predictions from these models resemble the models for relatedness among adults. Noteworthy differences include the flattening of slopes for

female immigrants in Lamalera (site 12), the Maasai (site 14), Ałakāpuram (site 17) and Tenpaŋti (site 18). This preliminarily suggests that juvenile female immigrants to

these communities have more kin ties (potentially including siblings) than women who arrive as adults. There is also clearer evidence for age-related increases in relatedness among natal males and females in the Miskito community (site 2).

As an additional supplementary analysis, we aggregated and analysed the cross-cultural dataset using a multilevel beta regression model. For this analysis, we calculated the proportion of adult males and females in each community who are natal residents to reflect patrilocal or matrilocal biases (these quantities are reported in table 1). These 'contextual effects' are then separately interacted with the individual-level effects, *age*, *sex* and *nativity*. The purpose of these models is to assess whether matrilocal and patrilocal biases in the communities moderate the age-related variation that is evident among individuals. Perhaps because they are overparametrized, these statistical models largely recapitulate our prior findings, revealing few noteworthy differences that vary as a function of the residence biases that characterize the study communities (electronic supplementary material, figure S3). Overall, in these aggregated models, the most consistent difference is between the average relatedness of natal residents and immigrants. As in the model of Johnstone & Cant [1], the philopatric sex consistently exhibits higher relatedness to group members.

Finally, we view these analyses primarily as descriptive and exploratory, which initially led us to consider the full three-way interactions between *age*, *sex* and *nativity*. However, visual inspection of the predictions in figure 2 reveals that, conditional on *age* and *nativity*, there are few differences between males and females. In the supplemental file, we consider simpler models that omit *sex* as a predictor and moderator. These models often receive greater Watanabe–Akaike information criterion weight than the models presented here. In other words, in models that include *age* and *nativity* as predictors, *sex* typically explains little variation in average relatedness (electronic supplementary material, table S4).

4. Discussion

Our analyses show age-related increases in relatedness among immigrants in several of the study communities that conform to predictions [1]. That is, immigrants of the more commonly dispersing sex initially have low relatedness, but they accrue more kinship ties as they age and reproduce. These increases are evident both among immigrant females to societies in which most males remain in their natal locality (patrilocal communities) and among migrating males in societies in which most females do not move (matrilocal communities). Not all communities show this pattern, however, and exceptions occur especially among the Gambian communities and the small communities with fluid residence patterns and unstable settlement histories. This fluidity also suggests that traditional labels of matrilocality versus patrilocality do not fully capture the diversity of migration patterns across human communities. Nevertheless, our results provide partial support for the prediction that average relatedness of immigrants to other group members increases as they age. That is, in societies where immigrants exhibit changes in relatedness that vary as a function of age, the effects are positive, not negative. However, the predicted positive effects are not evident at all study sites. In the

following, we discuss additional factors that were not modelled in this analysis, but that potentially shape the observed variation in kinship ties across the lifespan.

In this analysis of community relatedness, age is seldom associated with increases in average relatedness among natal members of the community. A notable exception is the Mayangna site in Nicaragua. The increase for females in this community is noteworthy because there are biases toward matrilocality and dispersal by males. This result therefore departs from the conceptual model advanced by Johnstone & Cant [1], which anticipates that females in such circumstances would start to show gradual declines in average relatedness as they age. To explain this departure, a factor to consider is the high fertility rate and population growth in this indigenous Nicaraguan community. As a matriline expands, older women are increasingly surrounded by daughters ($r = 0.5$) and nieces ($r = 0.25$).⁴ By contrast, for younger females in an expanding population, a high proportion of their peers are cousins ($r = 0.125$). To some extent, therefore, the effects of age on relatedness at this site may be a by-product of the population growth rate, which is considerably higher than the long-term growth rates that characterized Paleolithic and Neolithic human populations [25].⁵ Conversely, decreases in age-related relatedness were observed for natal residents of several communities that have a lower ratio of younger to older individuals (e.g. Alakāpuram), which suggests a potential need to account for demographic non-stationarity in populations when conducting comparative research on kinship (see [26] for a similar argument).

To explain cross-cultural heterogeneity in relatedness across the lifespan, we argue that there are likely to be recursions between relatedness and demographic outcomes. In other words, the fertility, mortality and dispersal of individuals plausibly vary in response to the presence of kin in the group. Over time, variation in these outcomes can consequently amplify or reduce relatedness to other group members. For instance, high average relatedness among older individuals could indicate greater longevity or fertility due to support from kin, possibly augmented by the dispersal of individuals with few local kinship ties. Effects of kin on fertility and mortality have received substantial attention from human behavioural ecologists [27,28]. By comparison, dispersal in human populations has received less attention [29,30]. Studies of non-human mammals provide evidence of facultative dispersal strategies as a function of the presence and rank of local kin [31–34]. Comparable anthropological research is empirically challenging, but ethnographers who conduct longitudinal studies can potentially examine decisions about residence and dispersal as kin availability fluctuates. In addition, there is an opportunity for theoretical models and simulations that allow demographic outcomes to vary non-randomly and dynamically in response to local kinship ties. In particular, whereas the theoretical model of Johnstone & Cant [1] assumes that all individuals have equivalent probabilities for reproduction, dispersal and mortality, it is beneficial to consider models in which these probabilities depend in part on an individual's relatedness to others in the group.

Whereas adult immigrants frequently show increases over time in average relatedness, these effects were not apparent in the Gambian communities, which were previously analysed by Mace & Alvergne [16]. Polygyny is the norm in this

setting, and men and their wives live in extended family compounds. For females at this study site, although there were minimal changes in average relatedness with age when examining kinship among all members of the community, their relatedness to other adults in the compound increased as their offspring reached adulthood.⁶ In other words, whereas the predicted effects were not evident in our community-level analysis, age-related variation in relatedness to other compound members accords with expectations from the Johnstone & Cant [1] model.

The discrepancy from the Gambia between relatedness in compounds and communities provides a cautionary note regarding the interpretation of the results of this study. That is, reproductive conflict is expected to be acute when individuals are drawing on the same resources. For example, the killer whales studied by Croft *et al.* [13] live in pods composed of closely related individuals who share access to harvested food resources. Ethnographically, there are analogous examples of human communities that share food resources communally, including indigenous South Americans who collectively prepare and consume meals as a community [35]. More commonly, however, residents of human communities share preferentially with subsets of co-residents, including close kin [36–39]. Whereas our analysis helps to substantiate the asymmetries of relatedness that distinguish young immigrants from older affinal kin, this does not necessarily imply that these respective individuals are drawing on the same resources. In some settings, it is plausible that humans facultatively employ behavioural strategies to minimize such reproductive competition.

In communities that are characterized by discriminative sharing, research would ideally be directed at the dynamics of kinship within resource-sharing subgroups [40,41]. In most ethnographic settings, however, there are methodological challenges that hinder such analyses, particularly the task of distinguishing the boundaries of the subgroups. At most of our study sites, individuals are organized in small households, usually occupied by a single adult woman (table 1). As a result, there are minimal opportunities for reproductive competition within females in the same household. Yet, households often maintain strong cooperative ties to other households in the community. The pooling of resources among households produces the conditions in which reproduction competition could be pronounced [1]. A key challenge is that these inter-household ties are rarely evident when using standard demographic and census methods. As a possible alternative, a combination of social network surveys [17] and community detection algorithms [42,43] could potentially provide opportunities to identify the subgroups in which reproductive competition is especially relevant for life-history strategies.⁷

5. Conclusion

In this study, we have considered a cross-cultural sample of sites with heterogeneous patterns of residence and dispersal. The sample includes sites at which dispersal is biased toward females (e.g. Tenpaʼi) or males (e.g. Mayangna). At other sites, including several of the larger communities, the majority of residents of both sexes are natal members of the community. There are also sites, including those affected by political disruptions (e.g. Colombia), at which most adults of both sexes are immigrants. Amid this variability, several study sites feature increases in relatedness that support

prevailing conceptual models [1]. That is, immigrants of the more commonly dispersing sex tend to show increases in local relatedness as they get older. There are noteworthy exceptions to this generalization, and given the limitations of the sample, it is premature to assume that this pattern typifies the majority of human communities. Furthermore, the demographic variables in this analysis usually explain only a minority of the observed variation in relatedness, which implies opportunities for additional variables to explain heterogeneity in kin ties. Nevertheless, evidence of the predicted asymmetries in relatedness are apparent in multiple settings, reinforcing the potential value of additional empirical research on inter-generational reproductive conflict [5,46–48].

More generally, this cross-cultural study reveals surprisingly diverse relationships between age and kinship in human communities. These results reinforce perspectives on the flexible kinship that distinguishes humans from other hominoids [11]. There are pitfalls to reasoning from ethnographic analogy, but this flexibility motivates a reconsideration of human kinship and life-history strategies. Currently, research is directed toward discerning the social structure of prehistoric hominins with the assumption that distinctive life-history traits evolved partly as a consequence of this social organization [1]. From this perspective, the emergence of flexible kinship arrangements in human societies is largely an epilogue that postdates the evolution of more remarkable human traits. However, the malleability of human kinship enables diverse adaptive responses to socio-ecological challenges. It is worthwhile to consider scenarios in which life-history traits evolved concurrently with the ability to reside and cooperate with different classes of kin throughout one's lifetime.

In terms of female-biased kinship, the theme of this special issue of *Philosophical Transactions*, this cross-cultural study underscores the importance of dispersal as a determinant of kin availability. In most cases, young adult immigrants to new communities have fewer co-resident kin than their same-aged natal counterparts. Although female immigrants can maintain intermittent affiliative ties to family members from their natal communities [49], women who do not disperse can expect to be surrounded by kin more consistently during their reproductive years. Therefore, in combination with broader debates about descent rules and daughter-biased inheritance [50], heterogeneity in female philopatry has a key role to play in evolutionary accounts of human social organization. A contribution of this study is that dispersal tendencies vary not only across societies, but also within populations. Dispersal is seldom obligatory, and a mixture of natal male and female adults is observable in nearly all study communities (see also [51]). Decisions about dispersal impose trade-offs on individuals, and society-level variation in residence rules may be explained in part by unidentified individual-level predictors that capture heterogeneous effects both across and within the sexes.

Data accessibility. Data are available as supplemental files on the Open Science Framework (<https://osf.io/h8cqr/>).

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Endnotes

¹Whereas we follow Croft *et al.* [13] by focusing on average relatedness as our outcome variable, we include a supplemental analysis in which we model the number of close kin in the community as the outcome variable.

²Alternatively, fitting the models as zero-augmented (hurdle) beta regression models provides qualitatively similar predictions.

³There is also moderate evidence for a positive slope for male immigrants in several additional communities, including the Mexican *choyero* community (site 8), the two Mosuo communities (sites 10 and 16) and Alakapuram (site 17). However, the low number of male immigrants in these communities precludes strong conclusions about this demographic subgroup.

⁴These coefficients of relatedness assume monogamous mating.

⁵Bottom-heavy population pyramids are evident at other study sites (e.g. Maasai) without accompanying age-related increases in average relatedness, which suggests that other factors can potentially counteract the age-related accumulation of close kinship ties in expanding populations.

⁶The dataset for that paper is the same used for the Gambian sites in this paper. Unlike the 2012 paper, however, the present study depicts results separately for each community rather than modelling individuals in an aggregated dataset.

⁷In addition to the Social Relations Model that has been used by evolutionary anthropologists (e.g. [44]), there are related statistical models that permit the identification of block structures in social network data, including models that permit the inclusion of covariates (e.g. [45]).

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