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Sibling competition and dispersal drive sex differences in religious celibacy

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ABSTRACT

Religious practices vary greatly worldwide. Lifelong celibacy is present in many world religions, but it remains unclear why the frequency of monks and nuns (male and female celibates) varies at different times and places. Here, we develop a two-sex inclusive fitness model of lifelong celibacy. We find that the sex that competes more over parental resources is favoured to have more celibates, that is more monks than nuns are expected when brother-brother competition is higher than sister-sister competition. Moreover, the extent to which brothers and sisters compete over the same parental resources influences these patterns: intermediate sibling competition leads to more extreme differences in the proportion of monks and nuns. The sex that disperses less is also favoured to have more celibates. We show how our model can explain variation in the frequency of monks and nuns in three populations that differ in post-marital residence, marriage systems and inheritance rules.

1. Introduction

Humans display a staggering cultural variation in religious practices. In recent years, explanations for this variation have focused on the potential role of religions as devices for the enforcement of group-level cooperation through fear of divine punishment, often against believers' immediate self-interest (Henrich, 2009; Norenzayan & Shariff, 2008; Purzycki, Bendixen, Lightner, & Sosis, 2022; Purzycki & Sosis, 2022). Several scholars have suggested that cross-cultural variation in supernatural beliefs, gods' concerns and religious practices results from differences in socioecological conditions, because these determine the coordination problems that different populations face (Bendixen & Purzycki, 2020; Purzycki & McNamara, 2016; Purzycki & Sosis, 2022). Empirical and phylogenetic studies support this explanation for some behaviours (Bendixen et al., 2023; Botero et al., 2014; Singh, Kaptchuk, & Henrich, 2021), but evidence for a positive effect of religion on prosociality is mixed (Galen, 2012; Ge, Chen, Wu, & Mace, 2019; Hoffmann, 2013; Oviedo, 2016).

However, religious practices are not necessarily solutions to cooperation dilemmas at the group level. A recent inclusive fitness model has shown that male lifelong celibacy – the renunciation of marriage, reproduction and sexual activity – cannot be favoured by selection if it benefits only the social group as a whole (Micheletti, Ge, Zhou et al., 2022). Instead, male celibacy can only be favoured when the decision is under parental control and when having a celibate brother makes men more competitive for reproductive opportunities (Micheletti, Ge, Zhou,

et al., 2022). These conditions are met in an Amdo Tibetan Buddhist population where parents sent a son to the local monastery until recently: men with a monk brother have more children, because they do not have to share parental resources with their brothers, suggesting that this an adaptive strategy used by their parents to reduce sibling conflict (Micheletti, Ge, Zhou, et al., 2022; Zhou, Ge, et al., 2022). Male religious celibacy – however it may have originally arisen – is maintained by individual families who decide to adopt it only when it serves their inclusive fitness interests, not through enforcement by monastic institutions.

Religious celibacy varies considerably across space and time. While the practice is open to men in all religious traditions that encourage it, female celibates can be exceedingly rare or more numerous than their male counterparts. Nuns play a significant role in Catholicism and Orthodox Christianity, though their abundance relative to male celibates varies considerably (Kaczynski, 2020). For example, female celibates formed a significant minority of the clerical population in medieval and early modern England (Knowles & Hadcock, 1953), whereas they outnumbered male celibates in Renaissance Venice (Davidson, 1978). Nuns are few and enjoy little recognition in Tibetan Buddhism (Micheletti, Ge, Zhou, et al., 2022; Zhou, Ge, et al., 2022) and also in Theravada Buddhism, the dominant form of the religion in Sri Lanka, Myanmar, Thailand, Laos and Cambodia; they are instead more common and respected in Vietnam, China, Korea and Japan (Jerryson, 2016; Kieschnick, 2007; Powers, 2007). While both male and female celibates are present in Hinduism, the former are far more numerous (Bevilacqua,

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2017; Clementin-Ojha, 1988; Powers, 2007). Lastly, only men are allowed to become celibate dervishes in Sufi sects that feature this practice (Bahir, 2007; Qirko, 2004).

The drivers of this variation remain unclear. If celibacy is adaptive – as it is for the renunciants’ parents in the case of Tibetan monks (Micheletti, Ge, Zhou, et al., 2022) – differences in socioecological conditions could drive asymmetries in the inclusive fitness returns accrued through celibate sons and celibate daughters and these could, in turn, result in variation in their frequency. Competition over the inheritance of land or cattle has been shown to drive sibling rivalry and parental discrimination in pastoralists and agriculturalists (Gibson & Gurmu, 2011; Ji et al., 2013; Mace, 1996). In the male celibacy model discussed above (Micheletti, Ge, Zhou, et al., 2022), higher levels of male celibacy are favoured when monks provide a greater benefit to their brothers, as is the case if competition between them for parental resources is more intense and monk brothers are instrumental in securing reproduction. The intensity of competition may differ between brothers and between sisters; and siblings of opposite sexes may also be in competition over the benefits provided by their celibate siblings. Moreover, sex-specific demographies, including sex biases in dispersal, have been shown to drive sex differences in incentives to perform altruistic behaviours, as they alter the extent to which individuals compete against kin versus non-kin for reproductive opportunities (Micheletti, Ruxton, & Gardner, 2018, 2020).

Here, we develop an inclusive fitness model of the coevolution of male and female celibacy, considering that this decision is made by parents, as is the case in most religions where the practice is encouraged and occurs on a reasonably large scale (Qirko, 2002). We assess the potential for sex differences in competition between same-sex siblings and the extent of competition between brothers and sisters to drive sex differences in incentives for celibacy for males and females. We also study the effect of sex differences in demography, namely dispersal at marriage. We then explore how biases in these different ecological parameters can together explain the variation in the frequencies of male and female celibates in different societies worldwide, drawing on three well-described examples from the literature: contemporary Tibetan populations, medieval and early modern England, and Renaissance Venice. Moreover, we assess the potential for parent-offspring conflict (Trivers, 1974) over the decision to become celibate and sexual conflict (Trivers, 1972) between mothers and fathers over the decision to commit a son or daughter to lifelong celibacy.

2. Methods

We adapt and expand a model of the evolution of lifelong celibacy by Micheletti, Ge, Zhou, et al. (2022) to consider the coevolution of male celibates and females celibates. We consider a large population structured into a large number of groups, each with a limited number N_i of adults of sex $i \in \{m, f\}$ and, for mathematical tractability, we assume that each produces large numbers K_i of sons and daughters (we adopt the assumptions of Micheletti, Ge, Zhou, et al., 2022; see Servedio et al., 2014 for the role of simplifying assumptions in mathematical models). Before reaching sexual maturity, boys become celibates (“monks”) with probability x_m and girls become celibates (“nuns”) with probability x_f , with the decision being made by their mother and father jointly (we explore individual, mother and father control, together with parent-offspring and sexual conflict in the Supporting Information [SI] §1–3.5, 9). Children grow to become young adults, and then non-celibates disperse from their natal group to a randomly chosen group with sex-specific probability d_i . Non-celibate sex- i individuals then compete to obtain one of the limited number N_i of adult spots in the group; those who do reach adulthood and reproduce, starting a new cycle. Monks and nuns abstain from participating in this competition, but may boost their siblings’ competitiveness, increasing their reproductive success.

As only non-celibate individuals compete for reproduction, the

probability that a focal sex- i individual participates in this competition is formally given by $s_i(x_i) = 1 - x_i$ and the marginal cost of celibacy is given by $c_i(\bar{x}_i) = -(\partial s_i(x_i)/\partial x_i)/s_i(\bar{x}_i) = 1/(1 - \bar{x}_i)$, where x_i and \bar{x}_i are the probability that the focal individual commits to lifelong celibacy and the population average probability, respectively. We consider that, in this competition for reproduction, a non-celibate individual’s chances of securing a reproductive spot increase as a function of the fractions of their siblings who are celibate. We model this by assigning to each individual a ‘competitiveness’ coefficient $t_i(x_{i,\text{sib}}, x_{j,\text{sib}})$, where $x_{i,\text{sib}}$ and $x_{j,\text{sib}}$ are the fractions of the focal individual’s celibate sex- i and sex- j siblings, respectively. Thus the marginal benefit provided by sex- i celibates to their same-sex siblings is given by $b_{ii}(\bar{x}_i, \bar{x}_j) = (\partial t_i(x_{i,\text{sib}}, x_{j,\text{sib}})/\partial x_{i,\text{sib}})/t(\bar{x}_i, \bar{x}_j)$, whereas the marginal benefit to opposite-sex siblings is given by $b_{ij}(\bar{x}_j, \bar{x}_i) = (\partial t_i(x_{i,\text{sib}}, x_{j,\text{sib}})/\partial x_{j,\text{sib}})/t(\bar{x}_i, \bar{x}_j)$, where \bar{x}_i and \bar{x}_j are the population average fractions of sex- i and sex- j celibates, respectively. We consider that, all else being equal, an individual’s competitiveness is either boosted equally by same and opposite sex siblings or more by same sex than opposite sex celibate siblings ($b_{ii} = b_{ij}$ or $b_{ii} > b_{ij}$, respectively, when evaluating at $\bar{x}_i = \bar{x}_j = \bar{x}$). That is, men benefit more from celibate brothers (“monks”) and women from celibate sisters (“nuns”), or both sexes benefit equally from monks and nuns.

We perform a kin selection analysis (Frank, 1998; Hamilton, 1964; Rousset, 2004) to assess what proportions of monks and nuns are favoured by natural selection and explore the potential role of sex asymmetries in dispersal and sibling competition over parental resources in shaping these differences (see SI §1–3, for full model derivation). In the main text, we focus on differences in b_{ii} and b_{ij} to identify general results; in figures, for the purposes of illustration, we make the marginal benefit functions b_{ii} , b_{ij} and the competitiveness functions t_i explicit (introducing intensity of competition parameters; see SI §9.1).

3. Results

3.1. Inclusive fitness model of celibacy

We initially consider a case in which celibates benefit only siblings of the same sex. Analysing the model, including both direct and indirect – i. e. kin-selection – effects, we find that a parent favours a child of sex i (with $i \in \{m, f\}$) to become a celibate when:

$$-c_i(\bar{x}_i) + b_{ii}(\bar{x}_i) > 0, \quad (1)$$

where $c_i(\bar{x}_i)$ is the marginal cost paid by the focal sex- i individual who commits to lifelong celibacy by virtue of their renouncing to compete for reproduction, and $b_{ii}(\bar{x}_i)$ is the marginal increase in the competitiveness of their same-sex siblings, owing to them being celibate. Specifically, by sending a sex- i child to the monastery, a parent incurs an inclusive fitness cost $-c_i(\bar{x}_i)$ because that offspring does not reproduce. At the same time, they receive an inclusive fitness benefit $b_{ii}(\bar{x}_i)$ because the competitiveness of their other sex- i children is increased as a result (notice that (1) captures two conditions, that for sons to become monks and that for daughters to become nuns; they can be obtained by replacing i - j with m - f as appropriate). This means that a parent is favoured to make a sex- i child a celibate simply when the benefit to non-celibate children of the same sex outweighs the costs to celibate ones, as parents are equally related to both (see SI §9.3). This was shown for monks by Micheletti, Ge, Zhou, et al. (2022); here, we find that the same condition holds for nuns.

We find that differences in within-sex competition generate differences in the frequency of monks and nuns. Selection favours more celibates of the sex whose reproductive success is more dependent on obtaining parental resources and thus competes more intensely over them with same-sex siblings. If competition between brothers is higher than competition between sisters (in which case $b_{mm} > b_{ff}$), more monks

than nuns are favoured; instead, if sisters compete more (in which case $b_{mm} < b_{ff}$) more nuns than monks are favoured (see Fig. 1). As competition between brothers and between sisters increases, the fraction of celibates in the population also increases, whereas the fraction of non-celibates decreases (see Fig. 1, pie sizes).

Having analysed a case where celibates only benefit siblings of the same sex, we now consider that they may also benefit opposite sex siblings to some extent or even equally. Analysing this more general version of the model, we find that parents favour a sex- i child to become a celibate when:

$$(-c_i(\bar{x}_i) + b_{ii}(\bar{x}_i, \bar{x}_j))(r_{\text{off}} - (1 - d_i)^2 r_{\text{grp}}) + b_{ij}(\bar{x}_i, \bar{x}_j)(r_{\text{off}} - (1 - d_j)^2 r_{\text{grp}}) > 0. \tag{2}$$

where d_i and d_j are the probabilities that non-celibate sex- i and sex- j young adults, respectively, disperse from the natal group to a randomly chosen group; r_{off} is the relatedness between a parent and their offspring; r_{grp} is the relatedness between a parent and their offspring's groupmates of either sex, including their offspring; and $b_{ii}(\bar{x}_i, \bar{x}_j)$ and $b_{ij}(\bar{x}_i, \bar{x}_j)$ are the marginal increases in the competitiveness of the same-sex and opposite-sex siblings of the focal sex- i individual,

respectively, owing to them being celibate.

The condition for committing a sex- i child to lifelong celibacy can be interpreted in terms of inclusive fitness effects for the parent who makes the decision. By doing so this parent incurs: a fitness cost $-c_i(\bar{x}_i)$ owing to a complete loss of reproductive opportunities for the monk son and a benefit $b_{ii}(\bar{x}_i, \bar{x}_j)$ owing to an increase in competitiveness for his non celibate sons to whom the parent is related by r_{off} ; a benefit $c_i(\bar{x}_i)$ and a cost $-b_{ii}(\bar{x}_i, \bar{x}_j)$ due to corresponding decreases and increases in competition, proportional to the scale of competition $(1 - d_i)^2$, for all sex- i young adults in the group who are related to the parent by r_{grp} (first term in condition (3)); a benefit $b_{ij}(\bar{x}_i, \bar{x}_j)r_{\text{off}}$ owing to an increase in competitiveness for their non celibate sex- j children thanks to them having a celibate sex- i sibling; and a cost $-b_{ij}(\bar{x}_i, \bar{x}_j)(1 - d_j)^2 r_{\text{grp}}$ owing to a corresponding increase in competition among young adult females in the group (second term).

We consider that celibates benefit siblings of their same sex more than those of the opposite sex. As in the special case explored above, we find that selection favours parents to have more celibate children of the sex that competes more with same-sex siblings over parental resources: more monks are expected when brother-brother competition is higher (in which case $b_{mm} > b_{ff}$), whereas higher sister-sister competition results in more nuns (in which case $b_{mm} < b_{ff}$). The extent of the difference in the benefit provided to same-sex vs opposite-sex siblings varies depending on the extent to which brothers and sisters compete over the same resources. We find that, as brother-sister competition increases (that is when $b_{mm} - b_{fm}$ and $b_{ff} - b_{mf}$ get closer to zero), differences in the frequencies of monks and nuns favoured under parental control become more extreme up to an intermediate level and then decrease again (see Fig. 2a-c). This is because, when the overlap in resources is small, the sex with the lower competition can benefit from celibates of the higher-competition sex, without the need for parents to recruit many celibates of the lower-competition sex; on the other hand, when the overlap in resources is considerable, the incentive to recruit celibates of the lower competition sex increases (see SI §9.7). Equal fractions of male and female celibates are expected to evolve when brothers and sisters all compete for the same pool of parental resources and thus the competitiveness of men and women is boosted equally by monk brothers and nun sisters (in this case, $b_{mm} = b_{fm}$ and $b_{ff} = b_{mf}$; see Fig. 2d).

We also find that sex differences in dispersal may drive biases in the relative proportion of monks and nuns, when brothers and sisters compete, at least to some extent, over parental resources. Specifically, individuals of the sex that disperses less are favoured by parents to commit to lifelong celibacy with a higher probability. That is, we predict that more boys will become monks than girls nuns when dispersal is female-biased ($d_m < d_f$), whereas more girls are expected to become nuns than boys monks when dispersal is male biased ($d_m > d_f$) (see Fig. 2b; see also SI §9.8). This is because the sex that disperses less experiences more competition with their kin and thus parents are more incentivised to make them celibate, forgoing the opportunity to attempt to reproduce, and thus decreasing kin competition. Moreover, we find that higher brother-sister competition leads to more extreme biases in the relative proportion of monks and nuns that are favoured (see Fig. 2c, d). This is because, as brother-sister competition increases, the inclusive fitness cost associated with a child making their siblings more competitive falls less on siblings of the same sex and more on siblings of the opposite sex (see SI §9.9).

Moreover, we uncover scope for parent-offspring conflict (Trivers, 1974). Celibacy can still evolve if it is under the control of the focal individual but, in this case, expected proportions of monks and nuns in the population are considerably lower than under parental control. Parents always favour their children to become celibates more than the children themselves would, because they are equally related to their celibate and non-celibate children, whereas the individual is always more related to themselves than to their siblings. Therefore, the parent-offspring conflict identified for monks by Micheletti, Ge, Zhou, et al.

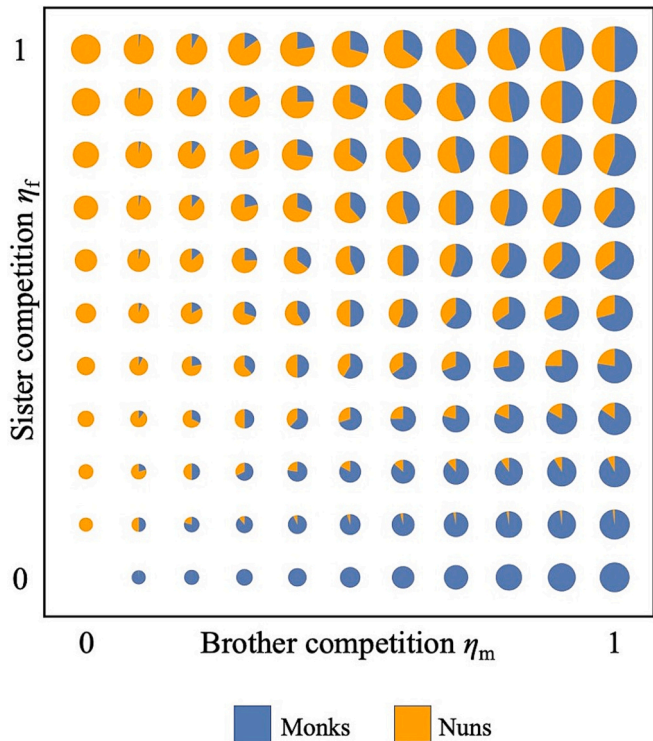
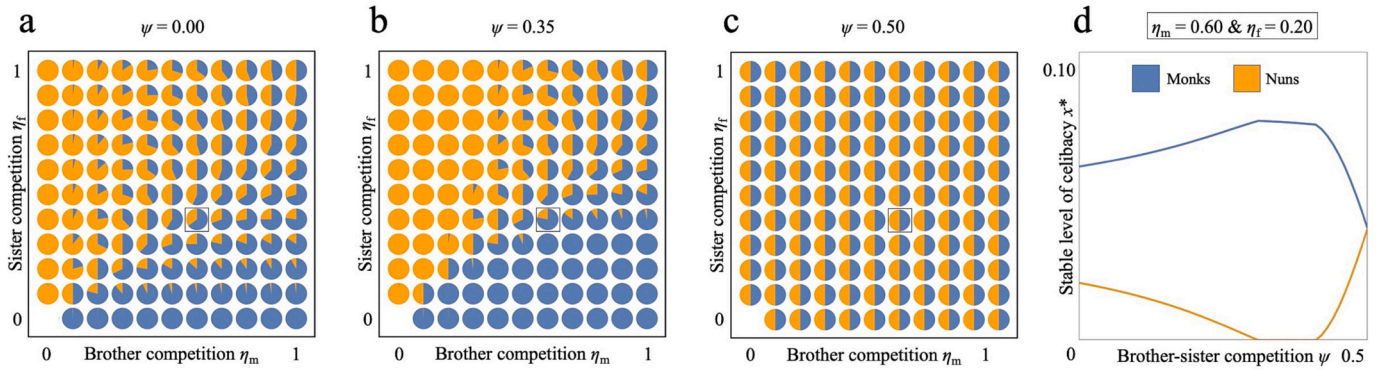


Fig. 1. Convergence-stable proportions of monks and nuns, under parental control, as a function of brother competition and sister competition. Intermediate convergence-stable levels of male and female celibacy obtain when condition (1) for both is equal to zero (see Supplementary Material, §5). Each pie chart shows the proportion of male celibates (blue) and female celibates (orange). For illustration we assume functional form $t_i(x_{i,\text{sib}}) = 1 + \eta_i \sqrt{x_{i,\text{sib}}}$ for non-celibate competitiveness, where η_i modulates the intensity of competition between siblings of sex i and $x_{i,\text{sib}}$ is the fraction of his sex- i siblings who are (notice that b_{ii} is a function of t_i , see Methods). Other parameters are: $d_m = d_f = 0.5$, $N_m = N_f = 10$. Pie chart size represents the total fraction of celibates in the population, standardised by the case with the highest proportion of celibates ($\eta_m = \eta_f = 1$). Parameter values are chosen simply to best illustrate the results of the model (see Supplementary Material, §6). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Brother competition and sister competition



Male dispersal and female dispersal

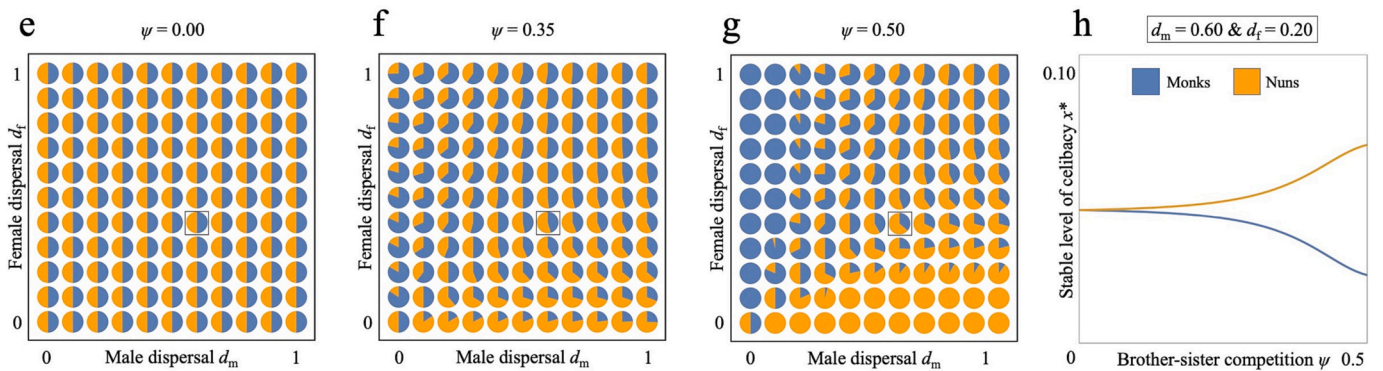


Fig. 2. Convergence-stable proportions of monks and nuns, under parental control, for different values of brother-brother competition η_m , sister-sister competition η_f , and brother-sister competition ψ . Each pie chart shows the proportion of male celibates (blue) and female celibates (orange). Intermediate convergence-stable levels of male and female celibacy obtain when condition (2) for both is equal to zero (see Supplementary Material, §5). For illustration we assume functional forms $s_i(\bar{x}_i) = 1 - \bar{x}_i$ and $t_i(\bar{x}_i, \bar{x}_j) = 1 + \eta_i \sqrt{(1 - \psi)\bar{x}_i + \psi \bar{x}_j}$ (notice that c_i is a function of s_i , and b_{ij} and b_{ji} are functions of t_i and t_j , see Methods). Other parameters are: $d_m = d_f = 0.5$ (in panels a-d), $\eta_m = \eta_f = 0.5$ (in panels e-h), $N_m = N_f = 10$. To facilitate reading and allowing focus on the effect of sex biases in ecology, pie sizes are not proportional to the total fraction of celibates in the population. Parameter values are chosen to best illustrate the results of the model (see Supplementary Material, §7). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(2022) holds for nuns too. Notice that the effects of sex biases in ecology (competition, dispersal) are qualitatively the same under individual control. We also find potential for sexual conflict (Trivers, 1972) between mothers and fathers. While mothers and fathers agree on the total proportion of their children who should be celibate, they may disagree on the abundance of monks relative to nuns. Whenever dispersal is sex-biased ($d_m \neq d_f$), a parent favours more celibates of their same sex; that is, fathers favour relatively more monks and mothers relatively more nuns. However, the entity of these differences is small compared to the effects of sex biases in ecological conditions explored above. Full details about parent-offspring conflict and sexual conflict, including conditions for celibacy to be favoured by natural selection in these cases, are provided in the SI (§9.3 and §9.4, respectively).

Moreover, we find that sex asymmetries in competition for parental resources between same-sex siblings, variation in brother-sister competition and sex biases in dispersal rates may act together to influence the relative frequency of monks and nuns. The sex that competes more with same-sex siblings is expected to have more celibates, with differences in the frequency of monks and nuns becoming more extreme as brother-sister competition increases up to an intermediate level. After that, the bias becomes less extreme and equal fractions of monks and nuns are favoured when brother-sister competition is at its maximum level (see Fig. 3a). Sex biases in dispersal alter these patterns, skewing

them towards more celibates of the sex that disperses less. Female-biased dispersal (patrilocality) results in a larger area of parameter space where more men are expected to become monks than women nuns. Specifically, a preponderance of monks is favoured when competition is more intense among brothers, even if brother-sister competition is very high (see Fig. 3b). An analogous result is obtained under male-biased dispersal: a preponderance of nuns is favoured when competition is more intense among sisters, even if brother-sister competition is very high.

3.2. Variation in male and female celibacy: three examples

We now consider to what extent our model predicts observed variation in the frequency of monks and nuns in current and past populations by exploring three well-described examples, that differ in space, time and religious tradition: contemporary and 20th century Tibetan populations in China, medieval and early modern England, and Renaissance Venice. This requires estimates of clerical populations, which are available for these cases. Moreover, measures of within-sex and between-sex sibling competition and dispersal rates are needed. The level of competition between brothers and between sisters will be influenced by which sex owns property and the kind of wealth transfers at marriage practiced by a society and their entity. The bride's family is

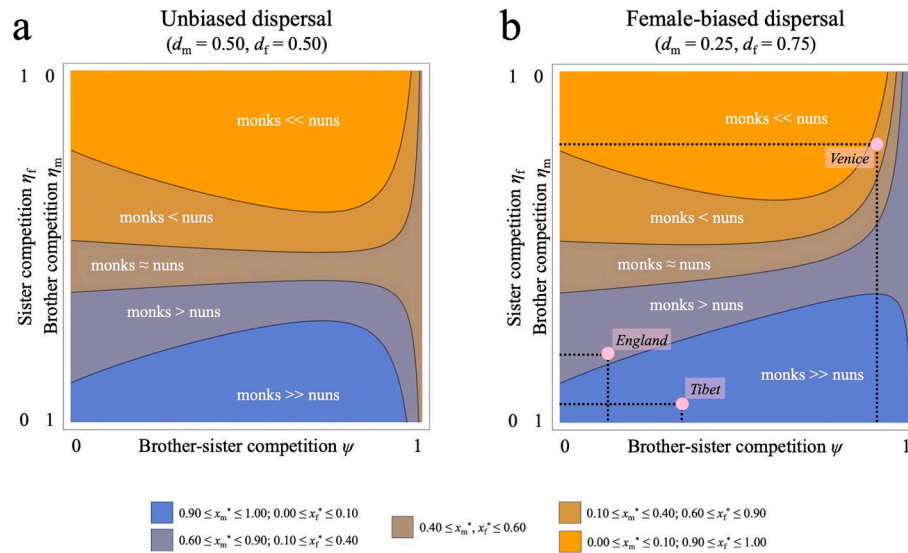


Fig. 3. Convergence-stable proportions of monks and nuns, under parental control, as a function of brother-brother competition η_m , sister-sister competition η_f , and brother-sister competition ψ , in an unbiased dispersal case (panel a, $d_m = d_f = 0.5$) and a biased dispersal case (panel b, $d_m = 0.25, d_f = 0.75$). Pink dots show the approximate location of contemporary Amdo Tibetans, medieval and early modern England and Renaissance Venice in the parameter space based on our review of the literature. Parameter values are chosen to best illustrate the results of the model (see Supplementary Material, §8). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

required to transfer wealth to their daughter or the groom's family (dowry), or the groom's family are expected to transfer wealth to the new couple or the bride's family (bridewealth), and in some societies both occur (Goody & Tambiah, 1973; Huber, Danaher, & Breedlove, 2011). Competition between men, as is generally under polygyny, tends to lead to bridewealth, whereas competition between females for the wealthiest husband, as is common under monogamy, tends to lead to dowry (Gaulin & Boster, 1990; Hartung et al., 1982; Mace, 2018). The scope for brothers and sisters to compete over the same resources will be influenced by their ecology. Immovable wealth (e.g., land) should be less conducive to division, whereas movable wealth (e.g. cash, cattle) should be easier to divide, leading to low and high brother-sister competition respectively (e.g., Mace, 1996). A mix of immovable and movable wealth should correspond to intermediate levels of brother-sister competition. Finally, in human societies dispersal mainly happens at marriage, with post-marital residence rules determining whether it is the wife that moves to the husband's household (patrilocal) or the opposite occurs (matrilocal) (Jordan, Gray, Greenhill, & Mace, 2009). We consider the three examples mentioned above in detail, and leave a more systematic cross-cultural analysis of determinants of religious celibacy for future work.

3.2.1. Tibetan areas in China

Recent sociodemographic surveys in two contemporary Amdo Tibetan populations in western China identified 268 Buddhist monks and 5 nuns in one case (98.2% male) (Micheletti, Ge, Zhou, et al., 2022; Zhou, Ge, et al., 2022) and 182 monks and 15 nuns in the other (92.4% male) (Du & Mace, 2019). Until recently, many parents sent one of their sons to the monastery when around 10 years of age to become a celibate monk, whereas daughters were very rarely destined for nunneries. Amdo Tibetans are agropastoralists, relying on farming, together with yak and sheep husbandry for their subsistence. Marriages could formerly be monogamous or polygynous or polyandrous, although monogamy is now the only legal form of marriage. Land and livestock are inherited by men patrilineally and, in the first population, it is the first-born son who generally inherits the parental household, whereas later born sons are more likely to become monks (Zhou et al., 2022). In the same population, men with a monk brother are wealthier and have more children, suggesting that parents can decrease competition between brothers by

sending a son to the monastery (Micheletti, Ge, Zhou, et al., 2022; Zhou, Ge, et al., 2022). Both populations are normatively patrilocal, women work hard on farming and domestic chores and men who stay in the parental household at marriage and inherit it have lighter workloads than the small minority of men who move to their wife's household (Chen, Ge, Zhou, Du, & Mace, 2022). In the second Amdo population, which relies more heavily on pastoralism, both dowry and bridewealth payments are paid at marriage, mainly in the form of cattle (Du & Mace, 2019). Overall, this means that competition over parental resources exists both between brothers and between sisters, but the former is much higher because, while both men and women need cattle to marry, men are at a significant advantage if they inherit land, which is a limited resource, or the bulk of the yak herd. Moreover, wealth is a mix of immovable (land, inherited patrilineally) and movable wealth (cattle/yaks, transferred at marriage) and therefore brothers and sisters in principle compete over the same parental resources to a certain extent. However, there is little evidence that sisters benefitted from their brother becoming a monk, whereas brothers did (Micheletti, Ge, Zhou, et al., 2022); which suggests that dowries have a small impact on women's success and sister-sister competition is thus low, which is also in line with this being a society where polygyny and polyandry were previously allowed. With these ecological conditions, our model predicts that monks should be much more abundant than nuns (see Fig. 3b), as is observed in these societies. Central Tibetan populations experience similar ecological conditions and nuns are reported to be very rare there too (Goldstein, 2010; Goldstein & Tsarong, 1985).

3.2.2. Medieval and early modern England

In medieval and early modern England, the ratio of male celibates living in communal religious institutions (monks and friars) to female celibates (nuns) remained quite stable throughout the 1066–1540 period, with the average being 80.7% males (SD = 2.3%; calculated from a census in Knowles & Hadcock, 1953; see SI §7). These figures exclude priests and other clerics; however, as data are scarce and clerics often had wives and children despite the prohibition to do so (Barrow, 2015), we do not consider them here. Parents often donated their sons and daughters to monasteries and convents as children to become celibate monks and nuns; in the 12th century, the western Church formally outlawed this practice of "child oblation", but religious institutions

continued to accept children donated by noble and landed gentry families (de Jong, 1995; Harris, 1993). In England at that time, marriage was monogamous and post-marital residence was patrilocal and wealth mainly consisted of land, which was inherited by men through the male line (Bertocchi, 2006; Friedrichs, 2000; Harris, 1993). An economic model has shown that, when land is the main form of wealth, primogeniture inheritance rules can emerge to leave the estate undivided (Bertocchi, 2006), and religious careers offered a viable alternative for non-inheriting sons in medieval and early modern Europe (Goody, 1976). During the same period, parents needed to provide their daughters with a dowry in order to secure a marriage, suggesting some competition between women for husbands (Gaulin & Boster, 1990). In England, these payments did not have a significant impact on family balances, as dowries were generated over multiple years using income from land, not by transferring portions of land to daughters (Harris, 1993). These arrangements mean that brother-brother competition was high because of unigeniture, competition between sisters was low because dowries were not expensive, and competition between siblings of opposite sexes was also low as land was not divided between them. In this case, our model predicts a much higher proportion of male than female celibates, as observed in the data (see Fig. 3b).

3.2.3. Renaissance Venice

A 1541 census of the city of Venice counts about 1000 monks and friars and about 2500 nuns, meaning that men constituted 28.6% of the clerical population (Davidson, 1978). Moreover, there were also 595 priests, who were required to be celibate but, unusually in Europe, were elected by their communities rather than selected by the ecclesiastical authorities (if these are included, the proportion of male celibates is 38.9%, that is still a majority of women) (Davidson, 1978). Many monks, friars and nuns came instead from aristocratic and affluent Venetian families and were often induced or forced to join these institutions as children. The concentration of nuns from upper social strata suggests that hypergyny – with women from families that acquired patrician status recently marrying into ancient ones (Chojnacki, 1975) – was increasing competition among upper class women in particular. Numerous reports of sexual transgressions suggest that vows of celibacy were not always respected, but members of religious order could not form their own families (Chojnacki, 1975). In Venetian patrician families, marriage was monogamous and post-marital residence was patrilocal; at the death of the father, all sons inherited parental property jointly (the *fraterna*), whereas women were only entitled to receive a dowry at marriage (Chojnacki, 1975). During the late 15th and early 16th century, Venice witnessed rapid dowry inflation (Guzzetti, 2002) (as also occurred in Florence from the 13th to 15th century [Botticini & Siow, 2003] and in 16th century France [Dewald, 1980] and 17th century Spain [Amelang, 1986]). This weighed heavily on family finances because wealth consisted in cash and shares of public funds, so resources invested in a dowry were no longer available for a father's other children (Harris, 1993). Taken together, Venetian inheritance rules and economic system mean that brother competition was relatively low because of joint inheritance, competition between sisters was high because of severe dowry inflation, and brother-sister competition was high because wealth consisted of capital, not land. Given these conditions, our model predicts a higher proportion of nuns than monks, as observed in the data (see Fig. 3b).

4. Discussion

We have developed a two-sex inclusive fitness model of lifelong religious celibacy under parental control and have shown that sex asymmetries in competition and demography can drive variation in the frequency of monks and nuns. Higher competition over parental resources between brothers than between sisters results in more monks being favoured by selection, as does higher female than male dispersal. Sex differences in the proportion of monks relative to nuns become more

extreme as the overlap between resources allocated by parents to sons and daughters increases, reaching a maximum for intermediate values. If brothers and sisters compete over exactly the same resources, equal numbers of monks and nuns are expected. Together these effects determine patterns of variation in the abundance of male celibates relative to female ones. Our model satisfactorily predicts the relative abundance of male and female celibates in three well-described cases: contemporary and 20th century Amdo Tibetan populations, medieval and early modern England, and Renaissance Venice.

Our model may help explain variation in other forms of parental favouritism, which are thought to have evolved in response to already established marriage transfer systems. It may also illuminate cases where religious celibates are not present or are not as numerous as expected. We consider two instructive cases. In the Mukogodo of Kenya, a formerly matrilineal foraging group, girls are breastfed for longer and are brought to the local clinic more often than boys, resulting in higher survival (Cronk, 1993). This is because, in this formerly foraging society that used to practice bridewealth through gifts of bee hives, women can now easily marry men from other, wealthier groups; so men struggled to accumulate enough cattle to obtain a bride when they came in competition with pastoralist groups in the area (Cronk, 1993). This means that competition between brothers became much higher than between sisters; in this case our model would predict that parents induce some sons to become religious celibates. However, this possibility is not available to Mukogodo parents, as religions that offer institutionalised celibacy, like Christianity, have only been introduced in the area very recently. For these reasons, parents can only invest differentially in sons and daughters, neglecting the former, to achieve the desired number of adult male and female offspring. A similar pattern of female-biased investment has been shown in an Amdo Tibetan population, where recent economic changes have resulted in greater workloads for women, meaning that daughters are now more valuable to their families (Du & Mace, 2018).

Strong male-biased investment is instead observed in contemporary South Asia. After sex-screening technologies became available in the mid-1980s, a stark increase in abortion of female fetuses was observed (Bhalotra & Cochrane, 2010) and, at the same time, higher under-five survival for those girls who were born (Anukriti, Bhalotra, & Tam, 2022). Later, the introduction of legislation banning sex-selective abortion resulted in a more balanced sex ratio, but also in lower female educational attainment (Rastogi & Sharma, 2022). These parental behaviours are driven by the economics of marriage in India; nowadays, women need very large dowries to secure a suitable husband and therefore parents either limit the number of births through sex-selective abortion (Bhalotra, Chakravarty, & Gulesci, 2020) or invest their resources in a smaller number of daughters (Anukriti et al., 2022). Patrician families in Renaissance Venice faced an analogous problem, but solved it by committing some of their daughters to a religious life at a young age (Chojnacki, 1975; Davidson, 1978; Guzzetti, 2002) (though differential parental investment or neglect cannot be excluded). This begs the question why Indian parents are not adopting the same strategy. We speculate that this is because this option is simply not available to them. In Hinduism, the major religion in India, female asceticism has always enjoyed little recognition and even now women form only about one tenth of the clerical population; moreover the decision to join a religious order was and still is made later in life, by the individual, not their parents (Bevilacqua, 2017; Clementin-Ojha, 1988). Why did oblation of young girls to a religious institution not evolve in India? It is possible that there was no selective pressure for it because dowry inflation occurred recently. Traditionally dowry was practiced only by the upper castes of north India, whereas bridewealth was dominant in the lower castes. Populations in the south engaged in reciprocal exchange of gifts of similar entity or bride exchange. It is only recently that dowry payments have become common, and increasingly expensive, in virtually all social strata (Anderson, 2004; Lankes, Shenk, Towner, & Alam, 2022; Srinivas, 1984; Srinivasan, 2005). It is likely that religious

institutions need a long time to evolve and so might not readily adapt to changed ecological conditions, generating a cultural adaptive lag. In this case, parents could only resort to differential investment, sex selective abortion, or both.

The model we have presented is functionally equivalent to an evolutionary model of infanticide if the benefit to siblings is only through relaxation of competition over parental resources. This is not true if celibates can bring other benefits like reputational advantage, control of the land where religious institutions are located or act as a reserve of heirs, should the family fortunes improve; this was the case for female claustration in Europe during the early and high Middle Ages (Hager, 1992) and in Portugal during the 15th and 16th centuries (Boone, 1986). It is unclear to what extent monks in Amdo Tibetan populations bring their families benefits beyond reduced competition between brothers. A sociodemographic study of Tibetan villages in Gansu province found that men with a monk brother have a similar reproductive success to men with no brothers (Micheletti, Ge, Zhou, et al., 2022), whereas a network analysis of another Tibetan village found that people who have a monk relative enjoy more social support (CaiRangDongZhi, Ge, Du, & Mace, 2023; Ge, CaiRangDongZhi, & Mace, 2024). Why is religious celibacy preferred by parents to inducing children to simply become helpers at the nest? It is possible that, in a context where religious institutions are pervasive, religious celibacy gives access to more advantages (e.g. prestigious social positions), religious institutions facilitate the enforcement of celibacy, or both.

Our inclusive fitness analysis could be interpreted as a model of the coevolution of male and female homosexual preference, under the assumption that this results in no direct descendants for the individual, while providing a reproductive benefit to their siblings (as in the “kin selection hypothesis” for homosexual preference; Pillard & Bailey, 1998; Trivers, 1974; Wilson, 1975). However, the applicability of our model to this case is limited by some of our assumptions. First, homosexual preference is not under the control of the parents, so the individual version of the model could apply, and this predicts very low levels of the behaviour. Second, individuals with a homosexual preference may still have descendants if heterosexual marriage is mandated and arranged by parents, as is the case in many societies (Apostolou, 2013). Third, some evidence for increased investment in sibling’s children by homosexual men has been found in Indonesia, Samoa and among the Istmo Zapotec of Mexico, but not in industrialised countries (see Gómez Jiménez & Vasey, 2022; Nila, Barthes, Crochet, Suryobroto, & Raymond, 2018 for recent reviews). Finally, our model would predict variation in the proportion of individuals exhibiting homosexual preference, in line with post-marital residence, an area with the potential to be investigated in future.

Our results could also help explain the origin, maintenance, and distribution of culturally-recognised “third genders”; cultural institutions where individuals of one biological sex assume at least some aspects of the social roles generally associated with the opposite gender, often in conjunction with a homosexual preference. Examples of men who reject traditional male roles are the Istmo Zapotec *muxes* in Mexico (Gómez Jiménez & Vasey, 2022), Samoan *fa’afine* (VanderLaan & Vasey, 2014) and other Polynesian third genders (Besnier, 1993). Both *fa’afine* and *muxes* do not marry, do not reproduce, and show higher investment in their nieces and nephews than other men and, in some cases, women (Gómez Jiménez & Vasey, 2022; VanderLaan & Vasey, 2014). They could thus be functionally equivalent to monks in our model, in terms of evolutionary consequences. Notice that both these cultures traditionally are patrilineal and practice bride price (Grant, 1995; Starkman, 2014), so the presence of non-reproducing men, rather than women is in line with our predictions. Cases of women assuming male roles have been described. In several sub-Saharan African cultures women may marry other women, but this generally happens exceptionally when the “woman husband” is widowed, infertile or has no sons and the practice seems to be driven by the desire to maintain the lineage and the economic advantages of having more children (Cadigan, 1998). In Albania,

until recently, a small minority of women lived as “sworn virgins”, assuming male roles in society but renouncing marriage and reproduction (Dickemann, 1997) and it is unclear to what extent they might be comparable to nuns. We leave a full exploration of the distribution of third genders and whether they conform to the predictions of our model to future work.

Our analysis highlights parallels between the evolution of religious celibacy in humans and instances of reproductive altruism (“helping”) in animal societies, where some individuals aid their parents in rearing more offspring either voluntarily or under manipulation, for a limited time or for their whole lives. Arthropods show a striking variation in the sex of helpers, with taxa characterised by female-only helping (e.g., ants, bees and wasps), male-only helping (webspinners), or mixed-sex helping (e.g., termites) (Davies, Ross, & Gardner, 2016). A recent mathematical model and phylogenetic analysis has shown that this variation is explained by sex differences in helping ability: helpers (who do not reproduce in the year they are helpers) tend to be of the sex that ancestrally was responsible for parental care and is thus preadapted for sib-rearing (Davies et al., 2016). The sex of helpers also varies in communal breeding birds and is explained by differences in competition for males and females. In temperate areas, where adult mortality is high, females can easily find a breeding vacancy, whereas males may still struggle to obtain mates, leading to male-only helping; on the other hand, in tropical areas mortality tends to be low and, as a consequence, females compete for limited breeding vacancies and males compete for mates, leading to both sexes helping (Zhang, Zhao, Møller, Komdeur, & Lu, 2017). These studies highlight that biases in the ecology of sex (Davies et al., 2016) can lead to sex differences in patterns of reproductive altruism. We have shown that the same is true in human societies for religious celibacy, a culturally-transmitted behaviour: parents are favoured to enforce celibacy more in children of the sex that competes more intensely for reproductive opportunities and that disperses less.

Recently, evolutionary research on religious behaviours has focused on the hypothesis that religions evolved to solve group-level cooperation problems, by offering coordination devices and through fear of divine punishment (Henrich, 2009; Norenzayan & Shariff, 2008; Purzycki et al., 2022; Purzycki & Sosis, 2022). Religious manifestations are expected to vary with the collective action problem faced by populations and these in turn vary with ecological conditions (Purzycki et al., 2022; Purzycki & Sosis, 2022). Here, we have explored sex differences in lifelong celibacy, a behaviour that does not solve a group-level cooperation problem (Micheletti, Ge, Zhou, et al., 2022), but that has a significant impact on an individual’s fitness and that of their relatives. We have shown that the social and ecological conditions expected to drive cross-cultural variation in religious practice are those that affect the balance of costs and benefits for the individual, not the group. This might be true of numerous other religious behaviours, which are adopted or rejected by individuals based on the inclusive fitness returns they entail – and this is why a behavioural ecology approach remains valuable in the study of cultural evolution (Micheletti, Brandl, & Mace, 2022; Micheletti, Brandl, Zhang, Peacey, & Mace, 2023). Nonetheless, the relationship between ecology, religious institutions and believers’ decision-making are likely to be complex. Religions may appear spontaneously or because they solve a cooperation problem; they may then be shaped by individual decisions, under the influence of ecology, and then become themselves part of the ecology. Institutions are not infinitely malleable and therefore they are likely to afford individuals new opportunities while precluding others: a tradition of religious celibacy gives parents a new way to decrease sibling competition, whereas the teaching that killing is sinful may increase the social costs of infanticide, helping to cement the first strategy. These feedbacks are likely to be complex. Modelling, coupled with rigorous cross-cultural research, will help us disentangle them.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used in this study.

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Appendix A. Supplementary data

Supporting materials for this paper: “Supporting information – model derivation and additional results” in pdf format, which contains the model derivation and includes an appendix with mathematical demonstrations, and “Supplementary material – model implementation and figures” in *Wolfram Mathematica*.nb format, which contains code to run the model and produce the figures. Supplementary materials to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2024.01.004>.

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