

# High consanguinity promotes intergenerational wealth concentration in socioeconomically privileged Krummhörn families of the 18th and 19th centuries

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## ABSTRACT

Previous research has demonstrated that consanguineous marriage is a vector for socioeconomic inheritance and for the maintenance of family structure and property. On the basis of reconstituted families from the Krummhörn, Ostfriesland in the 18th and 19th centuries, we examine statistical correlations between ascertained inbreeding coefficients ( $F$ ) based on family trees and socioeconomic status as well as the intergenerational transmission of landholdings. Semiparametric copula/bivariate regression models with non-random sample selection were applied to estimate  $F$  and the proportion of medium ( $0.0625 > F \geq 0.0156$ ) or high consanguineous unions ( $F \geq 0.0625$ ), respectively. Our estimates for  $F$  as well as for the proportion of medium ( $0.0625 > F \geq 0.0156$ ) or high consanguineous unions ( $F \geq 0.0625$ ) are significantly higher among socioeconomically privileged large farmer families than among the landless portion of the population. At the same time, our analyses show that a high level of consanguinity is associated with an increased intergenerational transmission of landholdings through the patriline (but not the matriline). We discuss the reproductive consequences of consanguinity among large farmers in connection with local resource competition, intensive kinship, and potential in-law conflicts.

## 1. Introduction: evolution, consanguinity, and wealth

Consanguinity or a “blood relationship” in a couple indicates that the genealogical distance between the spouses is relatively small. Most consanguineous marriages are between male and female first or second cousins. Romeo and Bittles (2014) have made the conservative estimate that more than one billion people in North Africa, the Middle East, and parts of Asia live in populations among whom  $> 20\%$  of unions are consanguineous. At the same time, numerous studies have shown that consanguineous unions can have a negative impact on the development and survival of the offspring (overview in Bittles & Black, 2010b; Bittles & Black, 2010a).

The phenomenon of so-called inbreeding depression explains the constitutional disadvantages that have been observed among the descendants of consanguineous unions. In homozygote form, recessive alleles often have negative consequences for the organism, as they are carried in the population, usually in heterozygote form, in the so-called “shadow of selection” of the dominant alleles, and can stockpile

harmful mutations (reviewed in Charlesworth & Willis, 2009). This association is especially visible in the case of incest, or mating between two members of the same nuclear family; i.e., reproduction between first-degree relatives (see Bischof, 1975b, although this is not a universal definition). In addition to having increased levels of pre- and perinatal mortality, the descendants of consanguineous unions suffer from fatal syndromes and severe disabilities at rates higher than descendants of non-consanguineous unions. Thus, sexually reproducing organisms usually avoid incest, and among human beings there is a transcultural taboo against mating between close relatives (Bischof, 1975b; Fox, 1983).

On the other hand, no degree of kinship outside of the nuclear family universally falls under the taboo against incest. On the contrary, Bischof (1975a) has described the phenomenon of assortative mating as the most widespread pattern of partner selection across cultures. The goal in assortative mating is for the partners to be “as similar as possible” phenotypically and “as dissimilar as necessary” genetically, thereby guaranteeing the highest possible compatibility with respect to

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various mutually relevant traits, while minimizing the reproductive costs associated with inbreeding depression. Helgason, Pálsson, Guðbjartsson, and Stefánsson (2008) showed that in the socio-economically relatively homogeneous population of Iceland between 1800 and 1965, reproductive unions between male and female cousins of the third and fourth degree had the highest number of live-born grandchildren. The authors attributed this pattern to the optimal genetic kinship between the parents with respect to fitness maximization. However, the degree of kinship that maximizes reproductive success may vary between populations or specific subpopulations under different ecological or genetic conditions. For example, the reproductive costs of consanguineous marriages at the genetic level may depend in part on the prevalence of rare hereditary diseases within the population. Moreover, the possible benefits of consanguinity may vary depending on local ecological, economic, and social conditions, such as the ability to monopolize inheritable resources or political claims to power.

Another potential reproductive cost of consanguinity is the limit it imposes on the maximum number of offspring. For example, in the case of a first-cousin marriage, the grandparents the two spouses have in common will have fewer great-grandchildren than they would if each of their grandchildren had reproduced exogamously. On the other hand, the great-grandchildren produced by the first cousins have a higher degree of relatedness. Thus, there is a trade-off between an exogamous strategy with increased dilution of relatedness over future generations and an endogamous strategy that leads to fewer (although genetically more closely related) descendants. We believe that an adaptive (in terms of fitness maximization) solution to this trade-off might also depend on ecological factors, such as the distribution and accessibility of resources or the level of extrinsic mortality.

Walker and Bailey (2014) found evidence of an association between consanguinity and socioecology. Their comparison of data from 46 small-scale societies showed that among populations who established settlements to engage in agriculture and livestock breeding, levels of consanguinity are noticeably higher than they are among hunter-gatherers and nomadic societies. The authors traced this pattern to differences between these societies in the role played by inheritable resources and the related levels of social inequality.

Bailey, Hill, and Walker (2014) examined the fitness consequences of consanguineous marriages in the same 46 small-scale societies, and ascertained that reproductive advantages tend to be more associated with consanguinity in horticultural societies than in societies of hunters and gatherers. The authors argued that an endogamous marriage preference in which reproductive success and inheritable prosperity are closely linked represents an adaptive reproduction strategy that largely prevents non-kin from accessing limited resources. Depending on the prevailing ecological conditions, kinship relationships can assume specific characteristics; and a basic distinction can be made between two extremes. In societies in which there are resources that can be monopolized, and the access to these resources is subject to relatively high competitive pressure (so-called contest competition), intensive kinship networks (Bugos, 1985; Shenk, Towner, Voss, & Alam, 2016) are more likely to develop. In such societies, the social relationships between individuals are heavily influenced by their degree of genetic kinship and consanguinity. On the other hand, if the access to resources is uncontrolled or there are fewer restrictions on accessing resources due to competition or the competition is of a more individual kind, more extensive kinship networks tend to develop (Shenk et al., 2016). In societies with higher levels of individual autonomy, the significance of the family network decreases, and genetic kinship becomes less relevant for social relationships. In such societies, consanguineous marriages are, as a rule, avoided. Our study population is the farming society of the Krummhörn (Ostfriesland, Germany). Because of its geophysical limitations, competition for access to fertile ground was fierce in the Krummhörn, and the distribution of land ownership was highly unequal (Knottnerus, 2004). During our study period, the habitat

was saturated, and the population had not been able to expand since the Middle Ages. As a consequence, the rate of growth in the population was practically zero. For the male and female landholders, the competition for local resources had varying reproductive ecology consequences (Volland & Dunbar, 1995): As a rule, the youngest son took over the parental farm (ultimogeniture, cf. Beise & Volland, 2008).

These agro-sociological conditions contributed to the widespread assumption that consanguineous marriage could improve a family's ability to compete in the contest for limited resources, as a marriage between kin could counteract the distribution of inheritable property and facilitate the bundling of familial resources into a single genealogical lineage. It thus appears that the endogamous marriage preferences among families in the region were the adaptive result of a trade-off between the costs of inbreeding depression and the benefits of wealth preservation.

While consanguinity is a reflection of resource constraints, it can also have a regulatory impact on intrafamilial social transactions. When spouses are related and the genetic correlation among family members is, consequently, relatively high, kin-selected nepotistic altruism tends to be promoted. Thus, the intrafamilial willingness to cooperate increases, and in-law conflicts are reduced. Studies by Chagnon, Lynch, Shenk, Hames, and Flinn (2017) argued that cross-cousin marriage among the South American Yanomamö is beneficial for family members outside the consanguineous union. In particular, the brothers of consanguineous women benefit strongly from their kinship with their brothers-in-law in reproductive terms. According to the authors, the advantages of cross-cousin marriages among the Yanomamö ultimately accrue to the parents of the consanguineous spouses. The adaptive scenario of consanguinity also includes the likelihood that in-law conflicts within the intensive kin network would be reduced. It has, for example, been shown that mothers-in-law play different roles in familial reproduction depending on the degree of kinship (Willführ, Johow, & Volland, 2018). Research in behavioral ecology has found considerable evidence that in addition to encouraging monogamy (Kramer & Russell, 2015; Lukas & Clutton-Brock, 2012), consanguinity promotes cooperative reproductive strategies, which may have sparked the evolution of cooperative breeding systems. However, consanguinity may have also evolved because it conferred very direct genetic advantages. After all, an increase in homozygosity as a result of endogamous reproduction could prevent a breakup of co-adapted gene complexes. Denic, Nagelkerke, and Agarwal (2008) argued that among populations living in areas where malaria is endemic, alleles for  $\alpha$ -thalassemia are associated with noticeable survival benefits, and ensuring that offspring inherit these alleles could compensate for the costs of inbreeding depression. Moreover, co-adapted gene complexes might enable a population to mount an effective immune response to other locally prevalent pathogens. It is possible that these gene complexes would not work as well in individuals with foreign genetic material (Hoben, Buunk, Fincher, Thornhill, & Schaller, 2010).

In past centuries, malaria (known locally as “marsh fever”) was endemic in the Krummhörn (Knottnerus, 2002). Thus, because of the prevalence of malaria in the region, increased consanguinity may have conferred selective advantages via the mechanism described by Denic et al. (2008). Since these selective benefits are independent of land ownership and other social indicators, they would have been relevant for the whole population. If protection against malaria was the main reason for the practice of consanguineous marriage, we would expect to see no significant variation in the frequency of such marriages between different social groups. If, however, we assume as Bailey et al. (2014) – and previously also Van Den Berghe and Mesher (1980) – posited that consanguineous marriage is used to concentrate or secure resources, we would expect to observe a correlation between consanguinity and landholding, as well as an association between consanguinity and inheritance strategies. To examine these possible correlations, we use a family-tree based calculation of the inbreeding coefficients that estimates the percentage of women who gave birth to children in a

marriage with a medium or a high degree of consanguinity (i.e.,  $0.0625 > F \geq 0.0156$  or  $F \geq 0.0625$ ). We are particularly interested in exploring two questions: First, were there any socioeconomic differences in consanguinity patterns? Second, was there a preference for consanguineous marriages that can be linked to the inheritance of landholdings? To investigate the second question, we compare the intergenerational correlation in documented landholdings between marriages of first cousins ( $F = 0.0625$ ) and marriages with a lower degree of consanguinity ( $F < 0.0625$ ).

## 2. Data and methods

### 2.1. Data availability

We utilized the archive ZA8630: Familienrekonstitution der Krummhörn (Ostfriesland), 1720–1874 preserved under <https://doi.org/10.4232/1.12643> for this study. The files provide individual vital data, information on genealogical relationships, as well as other forms of information, such as data on place names (locations), land ownership, and occupations, for 34,708 reconstituted families who lived in the Krummhörn (Ostfriesland) in the 18th and 19th centuries. Parish records from a total of 33 parishes in the Krummhörn and various tax lists are our primary data sources. An overview of the methodology of this family reconstitution can be found in [Voland \(2000\)](#).

### 2.2. Assessment of the inbreeding coefficient $F$

To identify the consanguineous marriages in our sample, a family tree-based assessment of the inbreeding coefficient  $F$  is required. From the available data, 74,639 individuals could be allocated to a single genealogy (meaning they all had at least lateral genealogical connections to other members of the pedigree). This group represents about two-thirds of all of the individuals in the database. However, it is important to keep in mind most of the individuals who were not identified as belonging to the pedigree were mentioned in single entries that could not be attributed with sufficient certainty to the existing entries (i.e., because the names were common). We can therefore assume that many of these isolated individuals are actually unrecognized doubles of individuals included in the pedigree. For the descendants within the family tree under investigation, the inbreeding coefficient  $F$  was calculated using the function `calcInbreeding()` contained in the pedigree package ([Coster, 2013](#)) available for R ([R Core Team, 2017](#)). To create the graphics, the R-package `ggplot2` ([Wickham, 2016](#)) was used; the statistical modeling was done with the aid of the R-package `GJRM` ([Marra, Radice, Bärnighausen, Wood, & McGovern, 2017](#)) and `pscl` ([Zeileis, Kleiber, & Jackman, 2008](#)).

### 2.3. Data selection

The “founding generation” refers to the individuals whose parents are unknown. Their children and grandchildren were excluded, as consanguinity cannot be confirmed for these cases ([Fig. 1](#), top). Our investigations take into account all marriages of women who were in a first marriage and gave birth to at least one child within the relatively well-documented period of 1720 to 1874 ( $N = 5835$ ). Our sample is thus restricted to generative marriages, and excludes “marriages for maintenance purposes,” which were typically entered into by elderly people after the death of a spouse. These marriages had no reproductive intent, and were often contracted for purely economic reasons, such as in order to maintain a household or to keep a business going. We imposed this restriction because  $F$ , our primary measurement of consanguinity, is only available for the offspring of a marriage. However, we also estimated the proportion of first-cousin marriages among (the relatively small fraction of) women who married at age 45 or older.

Furthermore, we applied the following selection criteria for the inclusion of mothers in the total sample of our study:

- Marriages with a pedigree depth of less than four were excluded.
- Marriages of remarried wives were excluded; thus, only marriages in which the woman was in her first marriage were selected.
- Marriages for which the exact year they were contracted is unknown were excluded.
- Marriages for which no birth date of an offspring is known were excluded.
- Marriages with a known offspring's birth date before 1720 or after 1874 were excluded.

Within our initial sample of 5835 marriages (“total”), we flagged 2253 marriages for which all eight grandparents of both spouses are documented (“known sample”).

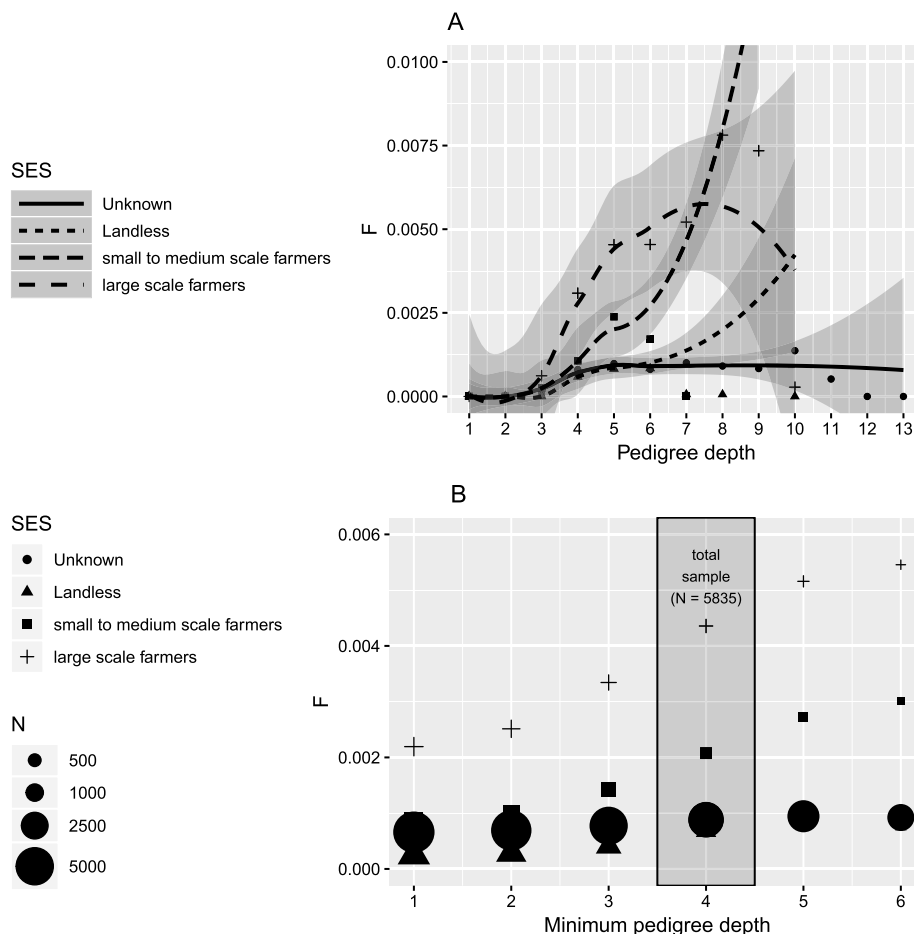
### 2.4. Evaluation of consanguinity and missing values

When calculating  $F$ -values, a minimum threshold value for  $F$  is obtained from the number of preceding generations, below which the following applies:  $F = 0$ . This corresponds to the unrealistic assumption of the perfect exogamy of the unknown ancestors. The lack of sensitivity for low consanguinity values due to the lack of data on longer-term accumulated endogamy leads to a general underestimation when calculating  $F$  based on family trees. However, the sensitivity and the specificity of the  $F$ -estimations are reduced to varying degrees with growing genealogical distance through partly missing values. For example, whereas a false negative recognition of first-cousin marriages ( $F = 0.0625$ ) can be ruled out with certainty only for those cases in which all eight grandparents of both spouses are completely known; even in cases for whom the grandparents and great-grandparents are not fully known, the likelihood that the positively recognized values (i.e.,  $F \geq 0.0156$ ) are accurate is relatively high. We account for such cases by adjusting the sample selection models to allow for incomplete observations when estimating the actual  $F$ -values and the prevalence of consanguineous marriages (see [Marra et al., 2017](#)).

Even after we excluded the founding generation and their children and grandchildren, we found that in the starting sample of all mothers of children born between 1720 and 1874, the share of married couples for whom all of the grandparents could be completely identified in the data was only around one-third ( $N = 11,682$ , corresponding to 33.7% of all documented marriages). If we applied the criterion of having full information on (at least) two times eight of the great-grandparents of both spouses, the percentage of known families in the starting sample would fall below 3%, and a social group-specific analysis of consanguinity differences would become impossible. However, even in families for whom only some of the great-grandparents of the spouses are known, consanguineous marriages can be identified, and incompletely documented families can be included in the analysis.

Thus, when estimating consanguinity, the data selection method is subject to a trade-off between the objectives of maximum reliability and maximum validity. Our choice is between examining a larger number of cases with partly unknown grandparents, but among whom consanguineous marriages cannot always be identified; or analyzing a smaller sample for whom the parentage is fully known, but who may not be representative of the population ([Postma, Martini, & Martini, 2010](#)).

We deal with this dilemma in our study by adjusting the sample selection models to identify a subsample within the sample for whom the parentage of the offspring is completely known until the third generation of ancestors (i.e., the identity of all eight great-grandparents), and thus for whom at least the first cousins of the parents can be identified with absolute certainty. First, the sample selection method is used to estimate the relative social group-specific probability of being included in a sample with “completely” known parentage ( $N = 2253$  mothers) for the starting sample (with only partly known parentage,  $N = 5835$  mothers). Within the adjusted semiparametric sample selection models with a continuous outcome or a binary response (Copula



**Fig. 1.** Average F-values versus depth of the family tree (A: with loess-smooth and a t-based approximated 95% confidence interval) or a minimal depth of the family tree (B: corresponding to the excluding exclusion of preceding generations) differentiated by socioeconomic status (N total = 10,909). For the following investigations, cases with a family-tree depth of less than four were excluded (remaining cases: N = 5835).

regression models), the potentially non-random selection of our sample with known parentage is subsequently accounted for when estimating the effects for the population as a whole (Marra et al., 2017). Accordingly, the models are divided into an equation for the modeling of selection processes for the percentage under complete observation and an equation for modeling the respective outcome examined: namely, estimates of the inbreeding coefficient F or the percentage of marriages with medium ( $0.0625 > F \geq 0.0156$ ) or high degrees of consanguinity ( $F \geq 0.0625$ ).

**2.5. Copula regression models to evaluate the inbreeding coefficient F and the resulting percentage of consanguineous marriages**

The only partial observability of inbreeding events can affect the members of various social groups in different ways. It is therefore important that in assessments of differences in the inbreeding coefficient F, the possible effects of social group membership on selection in the sample with “known” parentage are modeled as a separate process. Copula distributions are well-suited for the task of separating the dependence on a non-random sample selection from the estimated effects of specific predictors. The distribution of the cases examined to the respective social groups is shown in Table 2.

For the selection equation, the social group affiliation is also incorporated as a predictor. We distinguished four categories: “unknown”, “landless”, “small- to medium-scale farmers”, and “large-scale farmers”. It should be noted, however, that based on the information about their occupations, most of the individuals assigned to the

unknown category were likely also landless, and were thus relatively mobile (see also Willführ & Störmer, 2015). Furthermore, a smooth function with a thin plate regression spline basis was also incorporated as a non-parametric term for the “birth period” (as the year of the first birth), which interacts with the social group affiliation. For the modeling of the inbreeding coefficient F (or the percentage of consanguineous marriages and marriages between first cousins), the social group affiliation served as a predictor. Based on model convergence criteria, we chose a Joe copula model with a bivariate error distribution rotated by 90 degrees.

**2.6. Zero-inflated negative binomial regression**

The zero-inflated binomial model used to model the inheritance of landholdings is similar to the previously described copula regression used to assess the inbreeding coefficient F, because it comprises two different components. Here, too, the difference between the distributions must be modeled using two separate processes: namely, the probability of the emergence of the qualitative circumstances of landlessness, and the probability of the emergence of quantitative differences between inheriting landholders (i.e., for quantitative differences among the heirs). When modeling the probability of zero (i.e., the risk of being a non-heir), we also included a categorical factor for both spouses that indicates whether a younger brother of the husband or any (i.e. younger or older) brother of the wife was alive at the time of marriage (based on documented death dates). Since ultimogeniture was commonly practiced among landholding families, a younger brother

would have represented a potential rival for the heir; thus, information about the presence of a (younger) brother should be included when estimating probabilities of land inheritance. Furthermore, we can expect to observe interaction effects between having no (younger) brother at the time of marriage and the known landholdings of the parental families of origin (scaled as logarithm of the sum with one).

However, estimating whether the younger brothers of the spouses were alive and were available as candidates for potential inheritance is difficult due to the large problem of unobserved migration. Thus, it cannot be assumed that just because a brother was not listed as deceased at a given point in time he was still part of the population. An additional problem arises because our ability to track individual heirship is significantly restricted by the limitations of our data, which contain observations of landholdings for different families, but not at the individual level. For example, while the economic contribution to the family of a specific spouse's (putative) heirship might be highly suggestive in some cases, there are also many cases in which individual contributions and their originating inheritors cannot be assumed with sufficient confidence.

Although this model can also be depicted as copula (So, Lee, & Jung, 2011), we have chosen to use the zero-inflated negative binomial model here, as any landholding can be represented by an integer, and the reliability of this model is far more established in comparable studies than that of the copula regression.

### 2.7. SES coding

The socioeconomic status was estimated in “grasen” based on documented landholdings, whereby one gras roughly corresponds to the area of 0.37 ha. Missing values were recorded as an independent category (“unknown”, 1805 cases in the sample with known parentage), and the existing information was allocated to one of three categories: “landless,” (with zero grasen, 215 cases), “small- to medium-scale farmers,” (with fewer than 75 grasen, 121 cases), or “large scale farmers” (with > 74 grasen, 112 cases). For each wife, we included in the analysis not just the documented maximum ownership of grasen of her first founded family, but the documented maximum ownership of her natal family. Furthermore, the maximum landholding of the natal family of the woman's spouse was taken into account. Our investigations were limited to the first marriages of women with at least one birth.

Efficiency in the intergenerational transmission can be quantified on the basis of the regression coefficient  $\beta$  between the maximum landholdings in the parental and in the filial generation (Borgerhoff-Mulder et al., 2009 for log of wealth in two generations). Accordingly, values with  $\beta < 1$  result in a decrease in prosperity differences across subsequent generations within a population; whereas values with  $\beta > 1$  result in an increase in the concentration of inheritable property; i.e., to an increase in inequality of prosperity.

The landholding of a family was depicted in a zero-inflated negative binomial model to enable us to separate the probability that the landholding was even documented for a family from the statistical effects that may be associated with the size of the holding. Our primary interest here was to investigate the question of whether landholdings in marriages with a low/medium or a high degree of consanguinity correlate differently with the landholdings in male and female natal families.

### 3. Results

When we applied the definition of a consanguineous marriage based on an inbreeding coefficient of at least  $F \geq 0.0156$  – i.e., the spouses were related at the level of second cousins or closer (Barakat & Basten, 2014) – we found that at least 132 out of a total of 5835 women were in a consanguineous marriage during the 1720–1874 period (Table 1). Thus, out of all marriages studied, about 2.3% were shown to be

**Table 1**  
Distributions of marriages according to the mean F-value and form of marriage.

	Full sample	Known great-grandparents
low ( $F < 0.0156$ )	5703 (97.74%)	2148 (95.34%)
medium ( $0.0156 \leq F < 0.0625$ )	50 (0.86%)	43 (1.91%)
high ( $F \geq 0.0625$ )	82 (1.41%)	62 (2.75%)

**Table 2**  
Frequencies of marriages by social-group affiliation.

	Full sample	Known great-grandparents
Unknown	4418 (75.72%)	1805 (80.12%)
Landless	734 (12.58%)	215 (9.54%)
small to medium scale farmers	428 (7.34%)	121 (5.37%)
large scale farmers	255 (4.37%)	112 (4.97%)

consanguineous. When the study was restricted to those wives for whom all four grandparents are known for both spouses ( $N = 2253$ ), 105 consanguineous marriages, or about 4.7% of all marriages studied, were identified. In both samples, the majority of the consanguineous marriages had a high degree of consanguinity ( $F \geq 0.0625$ ) through a union with a patrilineal parallel cousin (i.e., a woman marrying her father's brother's son FBS) or a first-degree cross cousin.

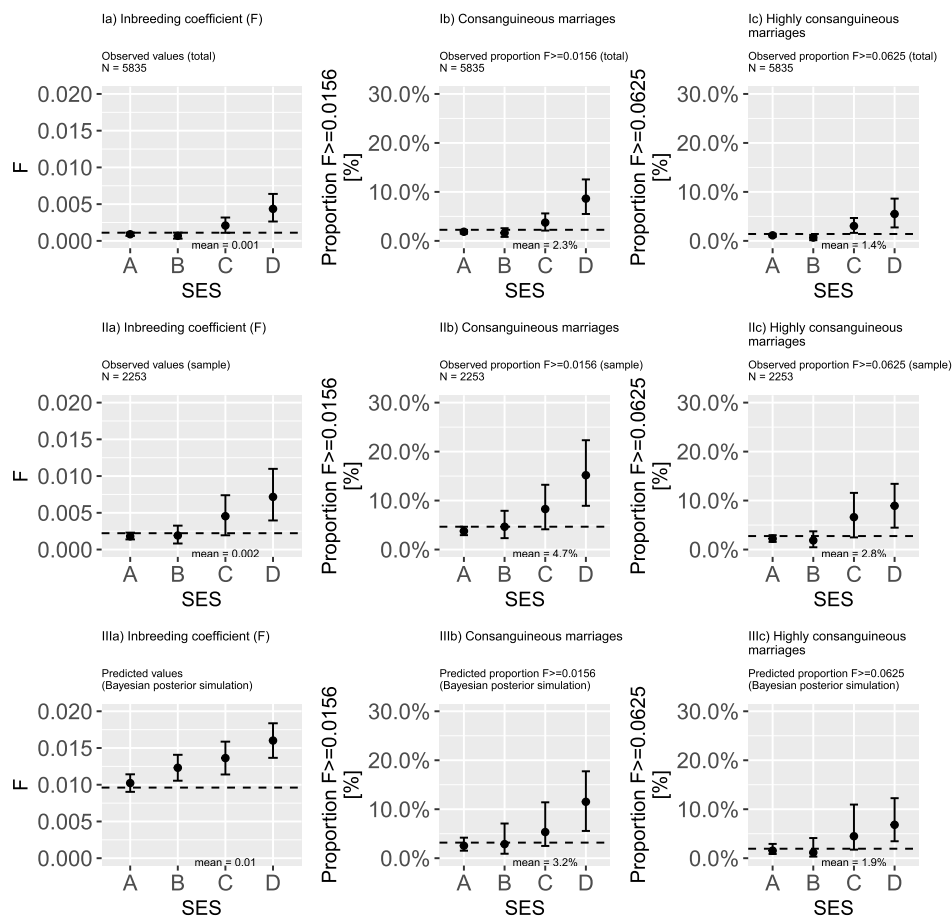
### 3.1. Socioeconomic differences in the mean inbreeding coefficient and the relative frequency of consanguineous marriages and cousin marriage types

Table 2 shows the frequencies of medium and highly consanguineous marriages according to social group affiliation for the initial sample (total), and for those cases for whom all grandparents of the spouses are known completely (known sample). It is noticeable here that in the minority of cases for whom landownership is documented (i.e., whose social group is not specified as unknown), the relative shares of small- to medium-scale farmers and large-scale famers decreases with increasing landholdings. Moreover, in the sample for whom all of the grandparents of both spouses are known completely, the share with unknown social group affiliation rises; and in cases for whom the landholdings are known, the large-scale farmers appear to be slightly overrepresented relative to the landless and the small- to medium-scale farmers.

When we look at the differences in the distribution of cousin marriage types between the social groups in the known sample, we find that among the large-scale farmers, patrilineal parallel cousin marriage (i.e., a woman marrying her father's brother's son) was observed most frequently. However, given the small number of cases examined, these differences should be treated with caution.

Fig. 1 shows the average F-values differentiated by family tree depth (on the top) or the change in the total average when excluding preceding generations (on the bottom) differentiated by social group affiliation. With an increasing number of generations, a sigmoidal rise in F is ascertainable for the generation numbers one to seven. At the same time, however, the number of cases decreases (and the uncertainty in the assessment of the mean value clearly rises for cases that are lower on the family tree). A minimum family tree depth of four appears to us to be an acceptable compromise of the reliability of the F-values and the validity of the sample size.

In the overall sample with a generation number of at least four, and in the subsample selected from this sample consisting of cases for whom all great-grandparents of the children born are completely documented, the mean inbreeding coefficient, the percentage of consanguineous marriages ( $F \geq 0.0156$ ), and the percentage of marriages with a high degree of consanguinity ( $F \geq 0.0625$ ) are associated in the same way, albeit sometimes at different levels, with the family's documented landholdings: the mean inbreeding coefficient and the percentage of



**Fig. 2.** Average inbreeding coefficient (left column) and the percentage of marriages with a medium (middle column) or a high degree of consanguinity (right column), each within the initial sample (at the top with bootstrapped 95% confidence intervals: Ia–Ic), in the sub-sample for whom the grandparents of the spouses are completely known (in the middle, with bootstrapped 95% confidence intervals: IIa–IIc), or in model predictions under the assumption of non-random sample selection (at the bottom, with 95% confidence intervals based on the Bayesian posterior simulation: IIIa–IIIc). Factor levels for socioeconomic status (SES) are A: unknown; B: landless; C: small- to medium-scale farmers, D: large-scale farmers.

consanguineous marriages ( $F \geq 0.0156$ ), and the percentage of marriages with high consanguinity ( $F \geq 0.0625$ ), are significantly higher among large farmers than among the landless population (Fig. 2).

**3.2. Proportion of consanguineous marriages among wives marrying age 45 or above**

When we compare the proportions of fertile and non-fertile marriages (for maintenance purposes) that are consanguineous, we see that levels of consanguinity are (slightly) higher among women who married at age 45 or older: while about 2.1% of the 14,584 marriages in the total sample are consanguineous, 2.6% in the 317 marriages in which the bride was older than 45 are consanguineous.

**3.3. Modeling of socioeconomic consanguinity differences with a non-random sample selection**

The probability that all eight great-grandparents of the children born are documented in the available data could vary across the socioeconomic groups examined here. This would mean that the selection criterion for inclusion in the sample does not apply to all studied cases in the same way, and that the rate of identification of consanguineous marriages between social groups differs, which would make a direct comparison problematic. To counter this risk and to depict the process of sample selection adequately in terms of statistics, we adjusted the corresponding sample selection models in Tables 3–8.

When evaluating these models, we found that large-scale farmers could be incorporated into the sample with a higher probability (see Table 3). But while the estimated overall level of consanguinity was increased about two times, the relative differences between socioeconomic groups did not differ significantly between the actual

**Table 3**  
Best fit estimates for parametric selection terms used in models for inbreeding coefficients and proportions of consanguineous marriages or marriages between first cousins.

	Estimate	Std. error	z value	Pr(>  z )
(Intercept)	-0.37	0.02	-16.72	*** < 0.001
Landless	0.13	0.06	2.11	* < 0.05
Small to medium scale farmers	0.09	0.08	1.06	0.2879
Large scale farmers	0.33	0.09	3.52	*** < 0.001

**Table 4**  
Best fit estimates for non-parametric selection terms used in models for inbreeding coefficients and proportions of consanguineous or first-cousin marriages.

	edf	Ref.df	Chi.sq	p-value
Smooth (year of first birth): SES unknown	2.81	3.53	105.65	*** < 0.001
Smooth (year of first birth): landless	1.00	1.00	27.30	*** < 0.001
Smooth (year of first birth): small to medium scale farmers	3.00	3.76	20.80	*** < 0.001
Smooth (year of first birth): large scale farmers	1.00	1.00	5.72	* < 0.05
Smooth (pedigree depth)	2.78	3.46	220.23	*** < 0.001

inbreeding coefficient and the coinciding prevalence of consanguineous marriages (Fig. 2 at the bottom: panels IIIa–IIIc), or from our “naïve” assessments that did not take into consideration the sample selection within the sample with completely known grandparents (Fig. 2 middle: panels IIa–IIc). The results of our outcome models confirmed our assumption that in the large-scale farmer families, both the average inbreeding coefficients (Table 5) and the percentage of consanguineous

**Table 5**  
Best fit estimates for parametric outcome terms modeling inbreeding coefficients.

	Estimate	Std. error	z value	Pr(>  z )
(Intercept)	0.00953	0.000269	35.43	*** < 0.001
Landless	−0.00120	0.000676	−1.78	0.075
Small to medium scale farmers	0.00014	0.000853	0.17	0.8682
Large scale farmers	0.00371	0.000945	3.93	*** < 0.001

**Table 6**  
Best fit estimates for non-parametric outcome terms modeling inbreeding coefficients.

	edf	Ref.df	Chi.sq	p-value
Smooth (year of 1st birth)	7.59	8.38	76.47	*** < 0.001
Smooth (pedigree depth)	4.27	5.07	55.79	*** < 0.001

**Table 7**  
Best fit estimates for parametric outcome terms modeling the overall proportion of consanguineous marriages ( $F \geq 0.0156$ ).

	Estimate	Std. error	z value	Pr(>  z )
(Intercept)	−1.95	0.12	−16.59	*** < 0.001
Landless	0.05	0.16	0.34	0.7333
Small to medium scale farmers	0.34	0.18	1.94	0.0518
Large scale farmers	0.75	0.15	4.95	*** < 0.001

**Table 8**  
Best fit estimates for parametric outcome terms modeling high consanguinity (proportion  $F \geq 0.0625$ ).

	Estimate	Std. error	z value	Pr(>  z )
(Intercept)	−2.16	0.14	−15.05	*** < 0.001
Landless	−0.11	0.21	−0.52	0.6026
Small to medium scale farmers	0.46	0.19	2.42	* < 0.05
Large scale farmers	0.67	0.18	3.78	*** < 0.001

(Table 7) or highly consanguineous marriages (Table 8) were noticeably increased.

### 3.4. Zero-inflated negative-binomial model for land-inheritance

Model estimates (Table 10) are in consistence with an increased correlation between the landholding of a couple and the landholding of the husband's natal family found for highly consanguineous marriages as shown in Fig. 3. This model only considers marriages for whom the landholdings of the families of origin are known  $N = 237$ ). In Table 9, the estimated effects on the probability for landlessness are documented. As we could ascertain no significant effects of the consanguinity of a marriage or the interaction between consanguinity and the landholdings of the family of origin of both spouses, these terms were excluded from the model. In order to account for the locally prevalent heirship system of ultimogeniture in which the youngest son generally inherits the parents' farm, we instead included a factor for the wife and her husband, respectively, that indicates whether a younger brother of the husband or any brother of the wife could be estimated as being alive at the time of marriage.

Table 10 shows model estimates for predictors of counts as obtained from zero-inflated negative binomial regression of the landholding of the husband's or the wife's family of origin (log. 1 + grasen) and the consanguinity of the marriage on the absolute landholdings for those families for whom the landholding was documented as being larger than zero. We can see that the model estimates also assume a varying correlation of marital landholdings with the landholdings of the

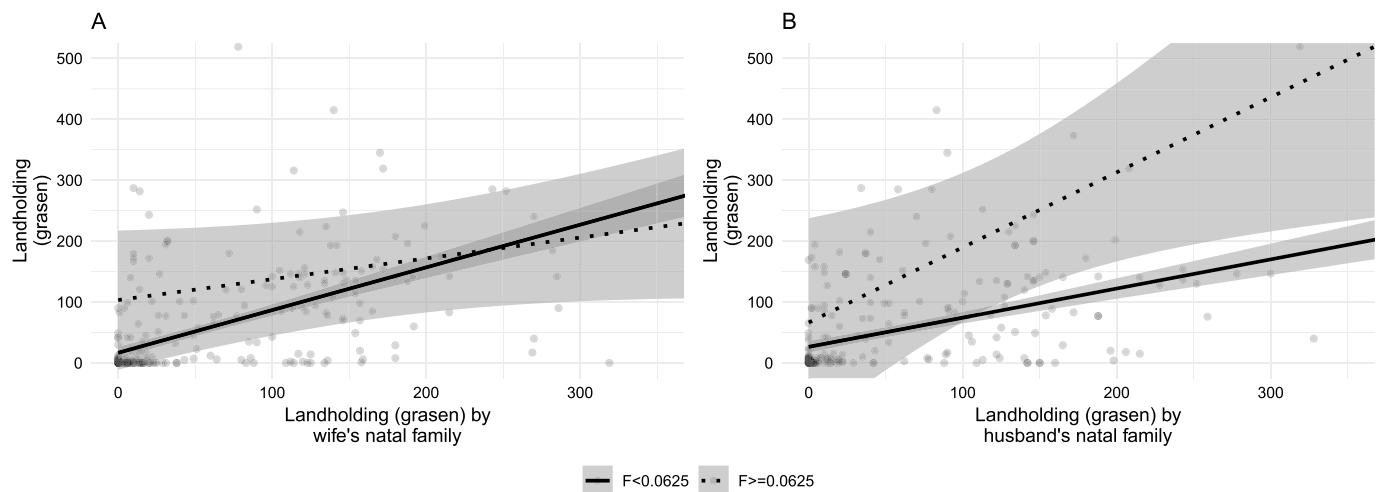
families of origin of both spouses depending on whether the marriage was between first cousins or had a lower degree of consanguinity. In summary, it could be ascertained that patrilineally inherited landholdings in highly consanguineous marriages (i.e.  $F \geq 0.0625$ , almost exclusively between first cousins) were, on average, larger than those in marriages with a low (i.e.  $F < 0.0156$ ) or a medium (i.e.  $0.0156 \leq F < 0.0625$ ) degree of consanguinity. However, no similar increase can be estimated for highly consanguineous marriages in case of the effect of landholdings of the wife's family of origin.

## 4. Discussion

The data we presented show that in our study population, there was a correlation between landholdings and the frequency of consanguineous marriages. Similar findings have been reported for various populations (e.g. Bras, Van Poppel, & Mandemakers, 2009; Egerbladh & Bittles, 2011), as well as for the historical population of the Krummhörn region. While marriages between male and female cousins were extremely rare (1–2%) among the landless population during the period under study (the 18th and 19th centuries), they accounted for a significant share of large-scale farmer marriages (5–10%) (Fig. 2). Given the relatively large social group-specific differences ascertained here, we can surmise that consanguinity in the historic Krummhörn was a conditional reaction to local resource competition among the families of large-scale farmers (e.g. Egerbladh & Bittles, 2011 for a coastal population in northern Sweden). Although cousin marriages are rather rare in our data ( $N = 82$  cases of a total of 5835 marriages) it is important to note, that a marriage between patrilateral parallel cousins would be consistent with the wealth retention/consolidation strategy of an heir marrying his son (or possibly inheriting only daughter) to the daughter (or son) of one of his own non-inheriting brothers. Given a trade-off between potentially beneficial socioeconomic effects of consanguinity and the associated reproductive cost (i.e. inbreeding depression), also a higher level of consanguinity among (post- or non-generative) women marrying age 45 and above as we have found can be expected. However, we found no support in our data for the hypothesis that consanguinity in the Krummhörn was an adaptive reaction to pathogenic stress due to malaria or other endemic infectious diseases.

Theoretically, the noticeably higher frequency of consanguineous marriages found among the landholding population can be traced back to the benefits of such a union for certain family members. On the one hand, consanguinity could be an expression of the conditional reproductive strategies of both spouses for whom consanguinity increases the chances of reproductive success to varying degrees depending on their socioeconomic milieu (e.g. Boone, 1986; Low, 1990; Thornhill, 1991); through, for example, the transmission of concentrated wealth (Do, Iyer, & Joshi, 2013; Dow, Reed, & Woodcock, 2016). Whenever a family's socioeconomic status (and thus future reproductive prospects of its descendants) is linked to wealth or title, unigeniture becomes preferred over partible inheritance (Hrdy & Judge, 1993). In case of zero population growth, ultimogeniture can be seen as an adaptive strategy in order to preserve the family estate: Since taking-over of the farm will be experienced comparably later for farmers inheriting their enterprise to their youngest son instead of their oldest son (if compared to primogeniture), this enables the intergenerational transmission of property being delayed for a certain period of time. For a given period, this results in a lengthening of generational cycles between subsequent inheritances and thereby reducing the risk of economic divisions. However, marrying consanguineously could also serve as a tool of wealth retention and consolidation in this context.

On the other hand, consanguinity may result from intrafamilial conflicts in which reproductive disadvantages are more or less forced upon consanguineous couples in order to benefit other family members. Studies by Chagnon et al. (2017) have suggested that in the case of the Yanomamö, who live in the Amazon region, the widespread practice of marrying cross-cousins reproductively benefits the brothers of



**Fig. 3.** Known landholdings in established families between 1720 and 1874 and known landholdings in parental families of origin (measured in grasen, A: wife's natal family; B: husband's natal family) distinguished by the level of consanguinity. Shaded areas represent the 95% confidence level interval for predictions from a linear model.

consanguineous women in particular – even though this society lacks the form of inheritable wealth prevalent in Europe. The authors showed that this benefit that favors the brothers can lead to parent-offspring conflicts about consanguineous unions. Whereas the parents are able to increase the production of grandchildren by deploying a strategy that enhances the reproductive success of their sons; this strategy is to the detriment of the daughters, who suffer from the greater likelihood that their offspring will die due to inbreeding depression. It is also possible that the starting point of this parent-child conflict depends on the socioeconomic conditions, as the parents may be able to guide their offspring's mate selection decision through the pressure point of granting or withholding economic resources (Apostolou, 2010; Apostolou, 2011). The possibility that the correlation between landholding and the frequency of consanguineous marriages that we have also described in this study is fueled by a parent-offspring conflict cannot be ruled out a priori. However, analyses of this question have not yet been undertaken.

Inheritable resources obviously influence mate selection in multiple ways. Exogamy not only threatens the effectiveness and persistence of co-adapted gene complexes; it can lead to the fragmentation of tangible family property, and thus to the loss of economic supremacy and its associated social privileges. As we mentioned above, consanguinity can have reproductive costs, since exogamy produces more offspring per ancestor than consanguineous relationships. However, the large-scale farmers in our study might have found these costs acceptable, because under the local resource competition regime they were already pursuing strategies to reduce the number of potential heirs (Goody, 1976; Hrdy & Judge, 1993). The association between the number of older brothers alive and increased mortality of male newborns can be seen as a manifestation of such strategies (Voland & Dunbar, 1995). Consanguinity works along the same lines (Chapais, 2009). Shenk et al. (2016) have argued that consanguineous marriages function as the

**Table 10**

Best fit estimates for landholding transmission model (count).

	Estimate	Std. error	z value	Pr(>  z )
(Intercept)	2.821	0.2358	11.96	*** < 0.001
A – medium consanguinity ( $0.0156 \leq F < 0.0625$ )	1.363	1.9348	0.70	0.4812
B – High consanguinity ( $F \geq 0.0625$ )	–2.161	1.7075	–1.27	0.2057
C – Log. (1 + grasen in husband's family-of-origin)	0.158	0.0646	2.45	* < 0.05
D – Log. (1 + grasen in wife's family-of-origin)	0.274	0.0650	4.21	*** < 0.001
Interaction A:C	–0.292	0.5340	–0.55	0.5848
Interaction A:D	0.065	0.3626	0.18	0.8583
Interaction B:C	0.584	0.1890	3.09	** < 0.01
Interaction B:D	–0.058	0.3670	–0.16	0.8738
Log (theta)	0.013	0.1266	0.11	0.9155

“glue” of an intensive kinship network, and thus reinforce family structures inwardly against external threats; whereas extensive kinship is oriented toward the expansion and the integration of other original external resources. Just as there is a life history tradeoff between a qualitative and a quantitative reproduction strategy, it may be possible to achieve economic success by pursuing a conservative strategy that provides protection against external disruptions, whereas pursuing a more “progressive” and adaptive approach to investments in kinship could prove much more profitable, but also riskier in the prevailing local resource competition system.

Within kin networks, consanguineous marriage allows for a more efficient transmission of family property to the following generations, because the “dilution” of the differences in prosperity levels due to marriages with economically disadvantaged non-kin is reduced

**Table 9**

Best fit estimates for landholding transmission model (probability of zero).

	Estimate	Std. error	z value	Pr(>  z )
(Intercept)	1.116	0.6639	1.68	0.0929
A – No husband's younger brother alive at time of marriage	–0.676	0.6888	–0.98	0.3266
B – Log. of 1 + grasen in husband's family-of-origin	–0.759	0.2408	–3.15	** < 0.01
C – No wife's brother alive at time of marriage	1.292	0.9384	1.38	0.1685
D – Log. of 1 + grasen in wife's family-of-origin	–0.084	0.3261	–0.26	0.7979
Interaction A:B	0.267	0.2711	0.98	0.3249
Interaction C:D	–0.417	0.3441	–1.21	0.2261



(Borgerhoff-Mulder et al., 2009). As for other non-industrial societies (von Rueden & Jaeggi, 2016), the correlation between tangible wealth and reproductive success – measured by fertility and the relative proportion of married descendants in the following generation – is well-documented for the Krummhörn (Johow & Volland, 2012; Klindworth & Volland, 1995; Volland, 1990; Volland & Dunbar, 1995). However, this association could lead to intensified sibling competition, in particular because consanguinity theoretically increases the negative fitness correlation between brothers due to the preferred transmission of family property through inheritance to sons who marry consanguineously. Whereas among the large-scale farmers we studied marrying a female cousin might have led to the takeover of the joint parental farm by the bridegroom, her brothers would have been paid off at best, and would have owned no share in the upward trajectory of landholdings and prosperity driven by consanguinity. Thus, the competition among brothers for inheritable landholdings, as was described by Gibson and Gurmu (2011) for an Ethiopian population, might be intensified by increased mating competition, especially if suitable first cousin marriage partners are scarce.

In addition to contributing to the preservation of a family's prosperity and protecting the heirs from non-kin accessing the family's property, another potential benefit of consanguineous marriage deserves consideration. Consanguinity could increase in various ways the willingness to cooperate within families, and could thus reduce the potential for intrafamily conflicts. Willführ et al. (2018) found that the influence of mothers-in-law on the mortality of their reproductive daughters-in-law is stratified by social group: i.e., the risk of death was found to be lower among large farmers than among members of other social groups. This finding is consistent with the differences of potential heirs in the effects of consanguinity that we have described, and it also corresponds on average to a higher degree of genetic kinship between daughter-in-law and mother-in-law. After all, in a marriage between first cousins, a genetic niece could be the daughter-in-law of her aunt. Hence, consanguinity differences could also correlate with varying tendencies in cooperative behavior. On the one hand, the chances of in-law conflict are mitigated significantly by the kinship of the spouses; as, for example, a spouse's parent-in-law may also be his or her biological uncle or aunt. On the other hand, consanguinity could also lead to a longer-term coalition of different genetic lines. Ohling (1929, 55–61) described how the preference of marsh farmers for marrying kin led to “clan thinking,” which was ultimately reflected in a fixed clan name. While this case, which happened in early modern times, supplemented the patronymic tradition (and did not replace it), it was limited to the social group of large farmers, and thus corresponds to the pattern of consanguinity ascertained here. According to Ohling (1929), even if there is “alienation” within a clan, kin can reconcile after “one hundred years,” and diverging genealogical lines can be merged once again through a renewal of consanguineous marriage. It was plausibly recognized by the people and established as a cultural norm that the social closure of the wealthy farmers was maintained by generation-spanning family networks that had been formed through intermarriage, but also through repeated and, possibly, reciprocal marriage relationships (Lorenzen-Schmidt, 2003). Ohling saw the function of this strategy in the creation of “friendship” in the clan, which corresponds to the “glue” of an intensive kinship described by Shenk et al. (2016) in the terminology of behavioral ecology.

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