Behav Ecol Sociobiol (1990) 26:65–72

Behavioral Ecology and Sociobiology

Differential reproductive success within the Krummhörn population (Germany, 18th and 19th Centuries)

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Received October 24, 1988 / Accepted July 29, 1989

Summary. On the basis of a family reconstitution study (Krummhörn, Germany, 18th und 19th centuries) it is shown how in one marriage cohort (1720–1750), family land ownership correlates with systematic fitness differentials. Farmers have a greater long-term fitness, on the average, than members of non-peasant population, and farmers possessing better than average wealth achieve a greater long-term fitness than farmers with medium-sized or small landholdings. The proximate causes herefore are to be found in both the varying patterns of marital fertility and in the differences in the marital and migration habits of the children from the various social groups. That is why the number of live births or even the number of surviving children is not the best estimate of a person's genetic contribution to the next generation of the local population. This can be shown by using a new algorithm for the assessment of long-term fitness differentials.

Introduction

Recent empirically solid studies reveal socio-ecological correlates of differential reproductive success in humans (e.g., Ajami 1976; Boone 1988; Borgerhoff Mulder 1987b; Crook & Crook 1988; Essock-Vitale 1984; Faux & Miller 1984; Flinn 1986; Hughes 1986; Irons 1979; Kaplan & Hill 1985; Mealey 1985; Shaikh & Becker 1985; Stys 1957; Turke & Betzig 1985). Three general points emerge from these analyses:

1. Despite the cultural diversity of the populations represented by these studies, "wealth" and "status" appear as regularly recurring cultural correlates of reproductive success. However, Vining (1986) presented considerable evidence that this relationship is not consistent in all cohorts of modern, post-transitory society. Furthermore, it was shown that "wealth" and "status" on their part may have a decisive effect on reproductive success and that by no means in all cases does the number of children determine a family's wealth due to the exploitation of their working power (Borgerhoff Mulder 1987b; Irons 1979).

2. First-generation differences in reproductive success result from three components, namely, by differences in total marital fertility, in offspring viability, and in mating success. From the male point of view, the last term refers to variance in males' ability to monopolize female fecundity, e.g., by simultaneous or serial multiple marriages. When male mating success as an explanatory variable was studied explicitly, it regularly proved to be a crucial proximate cause for differential reproductive success. On the other hand, the results with respect to the influence of differential marital fertility and infant and child mortality on reproductive success are not consistent.

3. In anthropology, substitute parameters such as age-specific fertility rates (Irons 1979; Turke & Betzig 1985) or – if data permit – the lifetime reproductive success of individuals, are utilized to estimate fitness. The latter usually refers to the number of surviving children among individuals who have completed genetic reproduction (Borgerhoff Mulder 1987a). Age-specific fertility rates can depend on tactical options of long-term life history strategies and may therefore only approximately reflect the actual reproductive success. On the other hand, the total number of surviving children losses every significance if a majority of them remain celibate (Kaplan & Hill 1986) or are forced to leave

the breeding population due to poor local living and reproductive chances. The European emigrants to America, for example, contributed nothing to their parents' fitness, regardless of how reproductively successful they might have been in their new homes. They left their natural population, and, as is known, by definition "fitness" measures the relative reproductive success within one's breeding population (Endler 1986). Beside differential long-range emigration, fitness, of course, depends on the number of children who marry and reproduce themselves.

The fate of surviving children (i.e., philopatry vs emigration and marriage vs celibacy) under rural and pre-industrial living conditions strongly depends on the ability of the parents to place their children in the community by means of legacies and bride-price and/or dowry payments. Accordingly, long-term fitness consequences do not necessarily have to correlate with first-generation measures of reproductive success (martial fertility, infant viability), and long-term effects of wealth for genetic persistence are, indeed, still largely unknown.

The present study tries to extend the generality of the previous results of the wealth/fitness research by providing another case. Is there any correlation between wealth and reproductive success in the Krummhörn population (Germany, marriage cohort 1720–1750)? And if so, by which components is differential reproductive success established? Are differences in the mean number of live births per family, in infant and child mortality, or in the social placement (with the effect of differential spatial and social mobility and nuptiality) of children primarily responsible for systematic fitness differentials between the social groups? Answers to these questions with respect to long term consequences of differential reproductive performance are of special interest. Thus, in this study an algorithm is proposed that tries to trace the genetic consequences of wealth stratification over more than one generation.

Material and Methods

The study population

This study is part of a larger historical demographic research project, the primary goal of which is the description of the factual reproductive performance of a population and its interpretation from a Darwinian point of view. We search for biological adaptations in the context of human demographic patterns, and we try to name the ecological and cultural constraints that were decisive for the development of specific reproductive strategies. The selected population lived at the "Krummhörn", a Northwestern German coastal region consisting of a total of 32 parishes with a cross-sectional population of about 14000 individuals. The settlement of the coastal marshes was completed early in history, so that since early modern times no more rural settlers have been able to establish themselves there. The Krummhörn is hence comparable to an animal population in a saturated habitat with only a limited amount of breeding places available. Correspondingly, in contrast to most parts of Europe (Flinn 1981), no noteworthy changes in the population density were observed from the 17th to the 19th centuries (Engel in preparation; Klöpper 1949). Most people were Protestants ("reformed"). Their subsistance was dominated by agriculture and dairy farming. The social stratification was very marked: There were exceedingly wealthy peasants who were clearly different from the great masses of agricultural workers in nearly every material and immaterial aspect of their lifestyles. The youngest son, as a rule, inherited the undivided property from his father. Furthermore, there were tradesmen (craftsmen and merchants) who satisfied the people's daily requirements and, depending on their particular branch of business, were able to achieve variable degrees of prosperity. Moreover, seafaring played a certain role in one village of the Krummhörn.

Data acquisition

The demographic data upon which this study is based were acquired utilizing the method of family reconstitution (e.g., Henry 1980). The main data sources were parish registers and a few civil records. Even though a few parish registers were begun in the 17th century, their data could not be reliably used – due to partial underregistration (especially of stillbirths and of children who died young) as well as due to other source-specific peculiarities – until the beginning of the 18th century. The entries were systematically collected until the year 1874, rearranged to family histories, and managed by means of the KLEIO data bank system (Thaller 1988). The data were analyzed with SPSS-x routines and our own software.

Information on the social backgrounds of the families (including land ownership) was drawn from tax lists.

Data analysis

According to the current state of data processing, information from 7 out of the 32 parishes was used in this study. The cohort studied consisted of all marriages contracted between 1 January 1720 and 31 December 1749, and the end of which – and thus the lifetime reproductive output – was known. This is given if the marriage date and the death dates of both spouses are exactly documented. Sterile marriages were excluded from the starting cohort because in this sample their frequencies did not systematically correlate with the families' social backgrounds. In total, the initial cohort consisted of $n=276$ families. Moreover, details on land ownership are known for 181 families.

The reproductive output or "fitness" (Φ) of all families is summed up for 100 years at 10-year intervals, beginning with the tenth year after marriage, and is computed according to the following formula:

$$\Phi_t = \sum_{i=1}^{n_t} (r * v_{x1}) \qquad (1)$$

The symbol Φ_t represents the measure of fitness of one marriage (or one person) at time t; n symbolizes the number of all of the direct descendants alive at time t; r is the coefficient of relatedness; and v_x is the residual reproductive value (Fisher

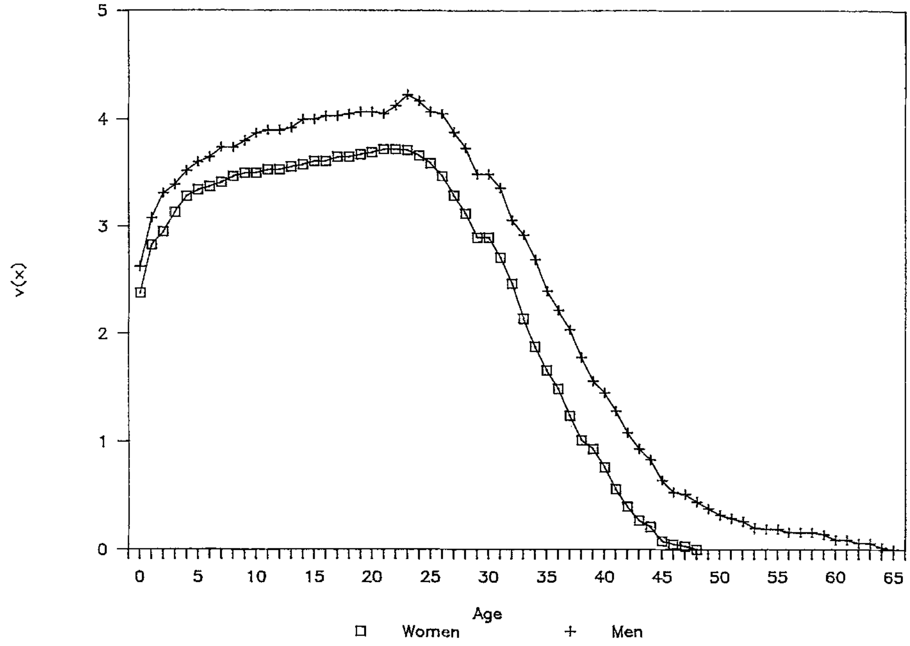

Fig. 1. Age-specific residual reproductive value (v_x) (Krummhörn, Germany, 18th–19th centuries)

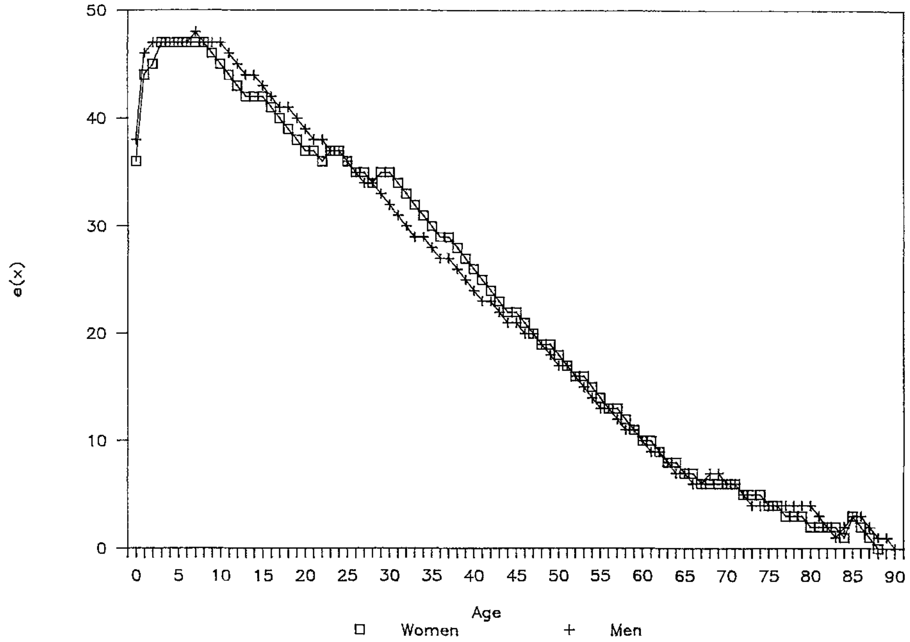

Fig. 2. Further life expectancy (e_x) (Krummhörn, Germany, 18th–19th centuries)

1930) at a certain age x reached by time t. Thus, Φ_t is calculated from the sum of the residual reproductive values of all of the living direct descendants at time t, weighted according to the corresponding coefficients of relatedness. Therefore, Φ is a combined measure of the number of descendants and their respective reproductive prospects.

The value v_x was ascertained separately for men and women from a sample taken from our total data collection, excluding emigrants (Fig. 1).

The sample was balanced out according to the following population parameters: 16% infant mortality; 18% child mortality; 13% celibate adults; and 3% permanently childless married individuals (the percentages refer to live births).

A serious methodological problem emerges from the assessment of the offspring whose dates of death are not known, that is, of regionally mobile persons. Their existence within the population at a particular critical point in time t can only be suspected with a certain degree of probability. If the age distribution of the emigrants is unknown, one proceeds as follows: These persons are included in the fitness computation (Φ) of their ancestors by ascertaining their further life expectancy (e_x) at the time of the last definitive record of their life. Thus, the statistically probable date of death is used as a substitute date for the missing actual date of death. The last evidence of a person's existence is frequently an entry in the confirmation or marriage register or (in unfavourable cases) the documentation of his/her baptism. Figure 2 shows the further life expectancy, ignoring social differences.

According to the entries in the tax lists, we distinguish three social groups, namely the landless families (*non-possessors*, $n=102$), the *smallholders* (who own 1–75 *Grasen*, 1 *Gras* ≈ 0.37 ha; $n=63$) and the *farmers* (75+ *Grasen*; $n=19$). The 75-*Grasen*-limit is a border-line which, in a certain way, is arbitrary. Yet we are of the opinion that it serves as a rather reliable distinction between full-time farmers and the smallholders. If there were changes of land ownership, we classified the respective families as belonging to that group that corresponds to the largest property. The group of non-possessors consists, for the most part, of agricultural workers (mostly day laborers) and members of the simple rural trades (e.g., shoemakers, tailors, weavers). The group of smallholders is rather heterogenous. Frequently, the families derive their main livelihood primarily from a medium- or higher-skilled trade (e.g., millers, bakers, smiths) with relatively good income prospects. The group of farmers consists of full-time peasants.

Results

Fitness differentials

Table 1 contains the mean fitness (Φ) of families from three social groups for the first 100 years after marriage.

On the average, land-owning farmers achieved a higher long-term fitness than the smallholders and they, in turn, achieved a higher long-term fitness than the landless. Insofar, the results correspond to the evolutionary biology prediction that resource control translates into fitness gains for humans as well, even if there is no complete separation of the 95% confidence intervals for the single means due to the high standard deviations. The reason for the population mean being lower than for the three groups lies in the fact that some reproductively less successful families (due to their short time of existence, e.g.) do not appear in the tax lists and, therefore, cannot be allocated to any one social category.

The continuous decline in the Φ values after 30 years (Table 1) is mainly due to the constant "displacement" of the gene replicates from the initial cohort because of immigration and not because of a decrease in total population. The biological consequences of this diluting effect will not be discussed any further here, as the primary concern is the ratio of the average Φ values among the three social groups and not the changes in their absolute values.

In Fig. 3 the farmers' fitness is shown in relation to the population mean.

Table 1. $\Phi(\bar{x}, \sigma)$ by social group, 10–100 years after marriage (Krummhörn, Germany, marriage cohort 1720–1750)

Years after marriage	Total $n=276$	Non-possessors $n=102$	Small-holders $n=63$	Farmers $n=19$
	$\bar{x}$ (σ)	$\bar{x}$ (σ)	$\bar{x}$ (σ)	$\bar{x}$ (σ)
10	4.30 (2.11)	4.52 (2.13)	4.24 (2.17)	4.70 (2.07)
20	5.70 (3.35)	6.10 (3.62)	5.85 (3.45)	6.33 (3.13)
30	5.78 (3.66)	6.29 (4.06)	6.15 (3.84)	6.64 (4.06)
40	4.51 (3.67)	4.95 (4.09)	5.21 (3.85)	5.50 (4.07)
50	3.22 (3.71)	3.67 (4.21)	3.86 (4.12)	4.39 (4.03)
60	2.86 (3.62)	3.29 (3.96)	3.53 (4.09)	3.96 (3.97)
70	2.45 (3.41)	2.86 (3.79)	3.05 (4.03)	3.25 (3.72)
80	1.95 (3.22)	2.78 (3.49)	2.48 (3.93)	3.30 (4.26)
90	1.64 (3.06)	1.85 (3.26)	2.23 (3.67)	2.97 (4.02)
100	1.50 (3.00)	1.69 (3.05)	2.13 (4.16)	2.87 (4.66)

Only 10 years after marriage the farmers began to have higher fitness, which increased continuously until the end of the observation period. One hundred years after marriage, that is about the great-grandchild generation, the proportion of the gene replicates from a particular farmer family was almost twice as high (1.91), on the average, as those from a family with an average reproductive success.

Proximate mechanisms

Which demographic factors led to these differences? Table 2 demonstrates – as is already known for other pre-modern European agrarian societies (Hughes 1986; Stephan 1983; Stys 1957) – that the farmers in this cohort also produced more children per family then the members of the other groups in the population.

Even if infant and child mortality tended to level out the reproductive "lead" associated with a higher number of live births, the farmers still raised one child more per family, on the average, to adulthood (15 years and older) than the smallholders.

The number of celibates rose with social rank, as expected (Bourdieu 1962; D'Argemir 1987); however, these differences never reached statistical significance.

Clear differences are found in the distribution of emigrants and married persons: the probability of emigration for a surviving child from the group of non-pocessors was approximately 1.8 times higher than for any farmer child. Also, farmer chil-

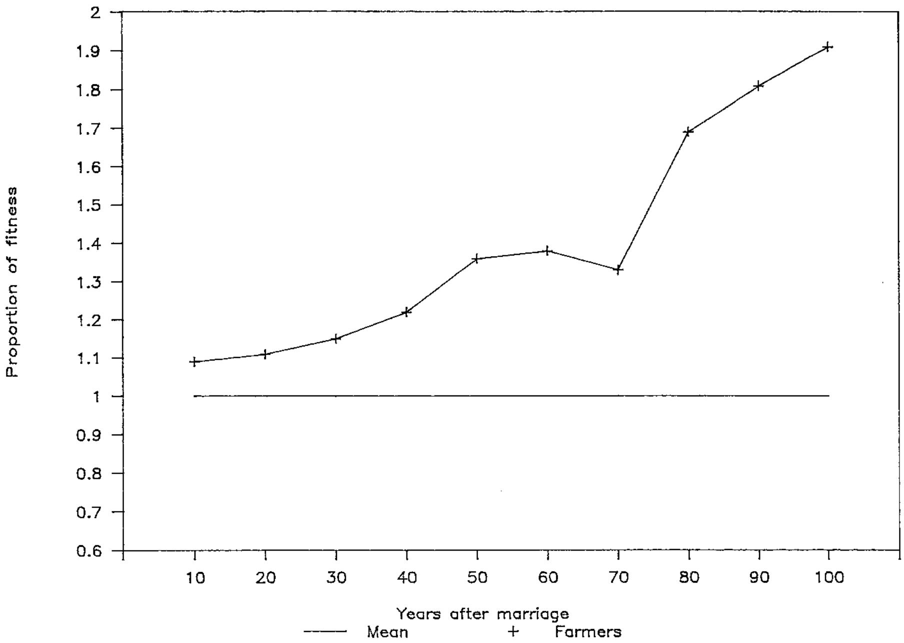

Fig. 3. Proportion of farmers' fitness vs population mean (Krummhörn, Germany, marriage cohort 1720–1750)

Table 2. Demographic parameters in three social groups (Krummhörn, Germany, marriage cohort 1720–1750)

	Non-possessors	Small-holders	Farmers
n completed Families	102	63	19
n live borns ($\chi^2 = 7.9$, $df = 2$, $P < 0.05$)	492	274	113
$\bar{x}$ live births/ completed family	4.8	4.3	5.9
n surviving children ($\chi^2 = 6.1$, $df = 2$, $P < 0.05$)	393	201	79
l_{15}	0.799	0.734	0.699
$\bar{x}$ surviving children/ completed family	3.9	3.2	4.2
of which			
remained celibate (in %) (n.s.)[a]	8.7	10.0	12.7
emigrated (in %) ($\chi^2 = 6.2$, $df = 2$, $P < 0.05$)[a]	51.7	48.8	29.1
married (in %) ($\chi^2 = 5.4$, $df = 2$, $P < 0.1$)[a]	39.7	41.3	58.2
$\sum =$	100.1%	100.1%	100.0%

[a] χ^2-test has been done for the frequencies; however, for better comparability, the % values are shown

dren had better marriage (and thus reproduction) prospects than children of smallholders or the landless.

In summary, it can be stated that farmers achieved long-term fitness advantages due to their higher marital fertility and the better social placement of their offspring. On the other hand, infant and child mortality tended to smooth the effects stemming from differential marital fertility.

The influence of social placement on fitness differentials

Between 30 and 40 years after marriage, the Φ values of the smallholders exceeded those of the non-possessors (Table 1). Thus, with a lower number of both live births and of surviving children, the smallholders were able to achieve a higher long-term fitness than the landless. The strategic "trick" was the more successful social placement of the comparatively fewer children. Table 3 illustrates the social mobility of 236 married children from marriages of the initial cohort (both sexes combined).

The overwhelming majority of married non-possessor children (75.6%) remained socially consistent, i.e., they were again confronted with the worst reproductive chances in the Krummhörn. On the contrary, smallholder children had a certain

Table 3. Social mobility (Krummhörn, Germany, children from the marriage cohort 1720–1750, both sexes combined)

Natal status	Acquired status			
	Non-possessors	Small-holders	Farmers	Total
Farmers				
n	8	16	16	40
row %	20.0	40.0	40.0	
col %	15.0	20.5	64.0	
Smallholders	35	36	6	77
	45.5	46.8	7.8	
	26.3	46.2	24.0	
Non-possessors	90	26	3	119
	75.6	21.8	2.5	
	67.7	33.3	12.0	
Total	133	78	25	236

chance to make the social climb to the group of farmers (7.8%) and thus a certain prospect of reproductive histories with an above average success. In a more extensive sample (marriage cohort 1720–1874), the upward social mobility of the smallholder daughters was even more pronounced, i.e., 18% in comparison with 4.1% for the non-possessor daughters (Voland & Engel, in press).

Still in need of clarification, however, is whether there really was a causal relationship between reduced fertility and increased social chances for the children or whether the smallholders could not have pursued their strategy of an upwardly oriented social placement just as effectively with more children.

Discussion

The ranking order with respect to the long-term fitness (Φ) (i.e., farmers > smallholders > non-possessors) differs from the ranking orders with respect to the number of live births as well to the number of surviving children (i.e., in both cases: farmers > non-possessors > smallholders). Social group differences in the fate of the surviving children (migration, nuptiality, social mobility) had made a significant contribution to the differential fitness of the parents.

To be sure, fertility rates and measures of lifetime reproductive success are important and indispensible approaches to the description of fitness differentials, particularly because multiple-generation data are very hard to obtain in anthropological field research. It should not be overlooked however, that these measures do not necessarily or perfectly mirror the long-term genetic contribution of one person or family to the gene pool of the population. Both parameters (fertility and lifetime reproductive success) have one decisive disadvantage when studying human populations, namely, that at best only the single-generation effects of the various behavioral strategies can be measured (Borgerhoff Mulder 1987a; Kaplan & Hill 1986). Under conditions of a well-established *r*-selection, the proportion of surviving offspring may be a valid estimate of fitness, because here growth rates (*r*) are maximized. In human societies, under conditions of a more or less marked *K*-selection, the number of children can be a very inappropriate, and perhaps even misleading, indicator of reproductive fitness. Under *K* conditions, the advantageous social and ecological placement of one's children in the population, i.e., the best possible equipping of one's offspring with fitness-relevant resources or with high-quality mates, correlates with long-term reproductive success because these attributes are especially efficient in the permanent displacement competition of *K*-selection.

This is why socio-cultural reproductive strategies associated with most important consequences for the local living chances of one's adult children are to be expected for the Krummhörn population. Efforts to place one's offspring socially as advantageously as possible by means of legacies and marriages probably played a central role in parental social reproductive behavior.

The decisive problem that at present can neither be satisfactorily solved in terms of research strategy nor in terms of theory is the evaluation of the emigrants. What was their contribution to the fitness of their parents? Even if natural selection is usually against dispersal (Horn 1983), there is still a series of ecological and genetic reasons for parents to encourage *short-distance emigration* of their offspring, even when the risks of mortality and other kinds of reproductive failure for emigrants are extremely high (Comins et al. 1980; Greenwood 1983; Hamilton & May 1977; Shields 1982).

On the other hand, *long-distance emigration*, that is, dispersal without genetic returns to the breeding population, can be extremely advantageous to the emigrant, for example, if he/she thereby participates in the foundation of a new, possibly expanding population. However, this reproductive success does not count towards the fitness of the parents. If, however, long-distance emigration has a positive influence upon the reproductive success of the resident kin-group, e.g., the brothers and sisters stay behind – with the result that the inheritance remains undivided or intrafamilial resource competition is reduced – the genetic basis of behavioral inclinations towards migration can spread in the sedentary population via kin selection. Should such an effect actually exist, it would manifest itself, however, by increased fitness of the remaining not emigrating children and is correspondingly contained in the figures presented in Table 1.

Resource control leads to fitness advantages. This result of the study was worked out on the basis of the reproductive results of marriages and not of individuals. The underlying pragmatic assumption that one's genetic contribution to the population originated only from the marriages "under observation", of course, must not apply to all individuals involved. If one takes into consideration that in the traditional Western European society the probability of remarriage was dependent on one's social position, at least for men (Dupâquier et al. 1981), then the fitness advantages of farmers accumulate through their multiple marriages to a larger degree than for men from other social groups. The bias stemming from ignoring multiple marriages, however, tends to work against the hypothesis, and insofar, the results underestimate the actual reproductive variance of all the men who had ever been married. This aspect will be examined in a later analysis with an expanded data base; it will then also be possible to compute mean fitness differences between men and women.

Do the present results allow any generalizations? Preliminary analyses revealed clearly pronounced cohort differences with respect to some demographic parameters in the history of the Krummhörn population (Engel, in preparation). The increasing agricultural modernization at the end of the 18th century created new living conditions and thus reproductive possibilities, which in other parts of Western Europe have triggered a demographic take-off (Flinn 1981) and to which the Krummhörn population likewise reacted with social-group-specific changes in demographic patterns. Therefore, it must be taken into account that the fitness differentials presented in this study cannot be found completely unchanged in the marriage cohorts after 1750.

For the period under investigation, however, the land-owning farmers were more likely to achieve higher fitness than other sectors of the population. Accordingly, socio-cultural strategies may be expected that were primarily aimed at securing and raising one's status (i.e., at cultural success), because this proxy would have been the best maxim for life leading to reproductive fitness maximization. Insofar, the social striving of the Krummhörn population can be regarded as a biological adaptation, just as many details of the whole functional system of traditional rural society are becoming more and more understandable from a Darwinian point of view (Voland 1989).

Acknowledgements. I wish to thank my colleagues of the *Arbeitsgruppe Krummhörn* for assistance in data collection and Claudia Engel, Eckhard W. Heymann, Werner Mesner, and Manfred Thaller for support in data processing. My thanks also go to Claudia Engel, K. Eduard Linsenmair, Volker Sommer, Christian Vogel, Paul Winkler, and two anonymous reviewers for their critical review of the manuscript and constructive comments. With financial support of the Deutsche Forschungsgemeinschaft.

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