Terje Bongard

Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period

Doctoral thesis
for the degree of doctor scientiarum

Trondheim, March 2005

Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
Department of Biology

NTNU

ISBN 82-471-6978-9 (printed ver.)
ISBN 82-471-6977-0 (electronic ver.)

Print: NTNU-trykk

Life history strategies, mate choice, and parental investment among Norwegians over a 300-year period.

Preface

The work presented in this thesis has been done in collaboration with students and supervisors at the Norwegian University of Science and Technology, Department of Biology, Trondheim. I am deeply grateful to my supervisor, professor Eivin Røskaft, who not only is a brilliant scientist, but also has the humane ability to inspire and be visionary when the going gets tough. Also thanks to my co-supervisor, professor Gunilla Rosenqvist, and to our co-authors, Anne Kristiansen, Lise Munkeby and Åslaug Viken. We thank the students in human behavioural ecology through the last decade for their contribution: Annelise Wara, Ann Elisabeth Djupvik, Linda Sedolfsen and Roger Hagen. A special thanks to my student colleague and wife for 25 years, Lise Munkeby. Was I lucky or clever?

This is the first PhD in human behavioural ecology in Norway (see Mysterud (2004) for a review of the wide array of different names for the research fields). It would not have been possible to complete this work without financial help from my employer, the Norwegian Institute of Nature Research (NINA), and I hereby thank my superior colleagues for their support.

Like most people, probably also including a lot of our ancestors with smaller brains than we are blessed with, I have always been interested in the eternal questions: Why are we here? Why are we the way we are? Why am I me? Sociobiologists claim that the new science of human behaviour is coming up with answers we can acknowledge, and that this research can provide us with tools to understand ourselves better. Answers and explanations that can be tested, scrutinized and understood by the very brain who construct the questions. Within social science there are many people that mix up scientific and moral truth. Also, the debate is bothered by debaters who have their maps already drawn, whatever the terrain might look like (Ridley, 1994; Ellis, 1996; Alcock, 1998b; Segerstråle, 2000). When I studied sociology at the University of Oslo, I was introduced to the full meaning of Machiavellian intelligence, and that the goal of a dispute not necessarily is a common quest for the truth, but to win a discussion (and thereby status). Our conversations about the value of human behavioural ecology might start with the understanding of this aspect, and thereby help us to put prestige aside. We must act as if every debater wants to contribute in making the world a better place, and not merely defend his or her own position. Truly an academic challenge.

My respect for the consequences of human behavioural ecology has two foundations: Firstly, that every human being has its eigenvalue, and secondly to the honor of truth, which is the principle above all and so often gets confused with wishful thinking and relativism. Evolutionary biology is contributing to understand the innate and often easy-triggered drivers behind egoism, ethnocentricity, violence, crime, divorce, anthropogenic environmental problems and psychiatric disorders. Likewise, our science also helps us figure out what the essence of good lives should be. Biology does not present any ethical or political values, but as individuals and society we can uphold such values if we want to: Solidarity and justice, creative cultural activity based on knowledge rather than superstition. Political control, care and welfare democratically distributed for the purpose of a better world, and not just filling up the accounts of the upper percent of capital stock owners. However, we need to know more about why these values and changes are so difficult to achieve in order to perform corrections.

Contents

List of papers 4
Abstract 5
Norsk sammendrag 7

Synopsis

Introduction 10
Hypotheses and predictions 11
Results and discussion 16
Conclusion 23
Perspectives 23
References 25
Paper I-VII 30

List of papers:

I Røskaft, E., Bongard, T., Viken, Å. Rosenqvist, G. 2005. Ecological conditions and life history variations in two Norwegian human populations during the period 1700-1900 CE. *Submitted.*

II Røskaft, E., Viken, Å., Bongard, T. 2005. Birth rank, family size, sex and life history; Data from a Norwegian human population during the period 1700-1900 CE. *Submitted.*

III Bongard, T., Røskaft, E. 2005. Optimal Birth Intervals, Life History and Sex Ratios at Birth; A Study of Two Human Populations in Central Norway 1700-1900 CE. *Submitted.*

IV Bongard, T., Rosenqvist, G., Røskaft, E.2005. Optimal genetic similarity in a Norwegian population from 1700-1900 CE. *Short communication manuscript.*

V Bongard, T., Kristiansen A., Røskaft, E. 2005. Do humans choose partners that physically resemble themselves? *Submitted.*

VI Bongard, T., Rosenqvist, G., Røskaft, E. 2005. Factors affecting the length of a relationship; A female perspective. *Submitted.*

VII Røskaft, E., Bongard, T., Munkeby, L. 2005. Parents experience higher conflict levels with their offspring in daily-life situations than do nursery school teachers. *Submitted.*

Abstract

In this thesis, seven papers concerning life history, mate choice and parental investment strategies are presented. Data was compiled from old church books from two parishes in Central Norway from 1700-1900, Soknedal and Smøla (Paper I-IV). Also the results of three questionnaires are presented (Paper V-VII). Results show that access to stable resources was the main predictor of number of children born and number of grandchildren produced within and between two human populations (Paper I). The two studied villages (Soknedal and Smøla) were at the same latitude, but had different resource foundation in that the coastal parish (Smøla) had access to year round fishing. This extra resource affected most life history traits of particularly low class women, who produced significantly more grandchildren than their sisters without this stable resource. Birth rank and family size also affected the life history of children (Paper II). Here we considered the survival rate, the probabilities of becoming married and migration rate from the home parish in relation to status of mother, family size, sex of the children, birth rank, sex ratio of siblings, year of birth and age of the mother. We found that the future reproductive value of boys was greatly affected by both family size and birth rank, in that boys from larger families and boys late in birth rank had a lower probability of getting married and a higher probability of migrating from the parish. No such relations were found for girls. We conclude that a difference in the access to parental resources during childhood affected the life history of boys, but not that of girls.

There was no support for longer birth intervals between the births of two boys compared to other sex combinations of children (Paper III). Short birth intervals (less than two years) between two children led to higher mortality among both the first-born and second-born in such combinations There were significant differences in birth interval between high and low status women in both parishes. Also the poorer parish of Soknedal had longer birth intervals than Smøla for both status groups. The survival rate increased significantly when birth intervals exceeded 2 years, both for a child and its next sibling. The optimal birth rate in Soknedal seems to be slightly over three years. In a multilinear regression analysis, the number of children of mother was, not surprisingly, the most

important variable in explaining the variation in birth interval. Laterborn children had longer birth intervals (Paper III).

In Paper IV we tested the inbreeding avoidance between related individuals in Soknedal parish, and found this to be significant. We found, however, no statistically significant differences in fertility between the three groups called non-locally, consanguineous and locally married couples.

Physical variables in human mate choice were tested on a sample of students (Paper V). There was a significant correlation between the age of a man and a woman and the height of the two individuals in a pair. However, none of the correlations or cross-correlations between height, weight, hair colour or eye colour were statistically significant. Within a pair there was a highly significant positive correlation between the attractiveness of a man and a woman. We also tested if strangers could pick out mates by facial looks. 101 test persons were presented a series of four photos, two males and two females and asked to pick out the pair. The pair was correctly picked out in about 40 % of the cases, which was higher than random. Altogether almost 90 percent of the test persons were able to pick out the pair more frequently than random. There was no significant difference between the sexes in their ability to pick out the right pair from photos. Paper VI presents results concerning female view of the male commitment into a relationship, his economic status variables and his ambition levels. We tested predictions derived from evolutionary biology concerning female mate choice through a questionnaire presented to female subscribers of a Norwegian magazine. The expectations of a stable economic wealth prior to engagement affected positively the length of relationships. The partner's economic stability, the respondent's perceived economic satisfaction and the partner’s investment in children from previous relationships were significantly higher in an ongoing than in a broken relationship. These factors are predicted to be crucial to mate choice and ultimately fitness-enhancing. Finally, in Paper VII phenotypic levels of daily-life parental-offspring conflicts in two different social contexts were studied; 1) between biological parents and their offspring at home, and 2) between the adults and the same children in the nursery school. Parents and nursery school teachers were asked how the children acted in conflicting situations that frequently occur during a day. Parents reported a higher level of conflict with their children than did teachers from nursery

schools. Parents did not experience differences in conflict level between boys and girls, while nursery school teachers did experience such differences. The results give support for the hypothesis that children have an innate and selected mechanism that guides them in different social contexts, and that they easily assess differences important for the level of care and attention they can expect to get. Children expect a higher investment from their parents than from their teachers, and therefore solicit more in the parent-offspring context. Such context-related behaviour among children will optimise their own social status and benefits in the form of resources and attention, and is the conceptual background for parent-offspring conflict.

Sammendrag

Denne doktoravhandlingen består av syv arbeider innenfor feltet human atferdsøkologi. I motsetning til sosiologisk tilnærming forsøker humanbiologien å finne universelle trekk som er like for alle. Medfødte trekk trenger ofte en utløsende miljøfaktor. Poenget er imidlertid at på et evolusjonært grunnlag følger det logisk å tro at alle individer vil respondere mer eller mindre likt. I forhold til noen atferdstrekk er dette lett å vise, som for eksempel smerte, latter, sjalusi eller sinne. Andre trekk kan bare testes statistisk, som for eksempel at barn maser mer på foreldrene sine enn på andre voksne, eller at trangen til å emigrere er større når en gutt fødes sent i fødselsrekka, slik jeg har vist her.

De fire første arbeidene er analyser av data fra kirkebøker fra Soknedal og Smøla mellom 1700-1900. De tre siste er resultater fra tre spørreundersøkelser foretatt i årene 1993-2002. Soknedal og Smøla har en biologisk relevant ulikhet i at Smølaboerne hadde tilgang på fiske året rundt, noe som stabiliserte mattilgangen. Denne ulikheten ga seg utslag i at lavstatuskvinner fra Smøla fikk flere barnebarn enn lavstatuskvinner fra Soknedal (Paper I). Blant høystatuskvinner var det ingen forskjell. Størrelsen på søskenflokken og nummer i fødselsrekkefølgen bestemte viktige livshistorieparametre (Paper II). Kjønnsforskjellene var store og ga seg utslag i at en senerefødt gutt hadde lavere sjanse for å overleve, lavere sjanse for å bli gift, men høyere sannsynlighet for å emigrere. Slik var det ikke for jentene. Dette er i tråd med seleksjonsprinsippene for arter

med høy foreldreinvestering ved at tidligfødte menn som arvet mest ressurser ble attraktive og fikk livsløp med større sjanser for etterkommere. Også fødselsintervallene betyr mye for livsløpet (Paper III). For korte mellomrom mellom fødslene gir lavere ressurstilgang til barna (både det som er født før og etter) og dermed lavere fitness, men samtidig bør total reproduktiv periode utnyttes. Dermed kan det beregnes et optimalt fødselsintervall som gir flest overlevende og attraktive etterkommere. Det finnes noe data på at det å få gutter er mer ressurskrevende, og vil øke det optimale intervallet, men materialet fra Midt-Norge viste ikke dette. I Paper IV så jeg på om beslektede individer unngikk å gifte seg med hverandre, hvilket de gjorde. Sannsynligheten for å gifte seg med en slektning var ganske stor på den tiden (24 %), men bare 9 % av høystatus- og 6 % av lavstatuskvinnene giftet seg med slektninger. Partnervalg er et område det er gjort ganske mye forskning på, og vi gjentok en del av de undersøkelsene som viser at vi ofte velger partnere som matcher oss i fysiske variabler (Paper V). Vi fant bare korrelasjon mellom alder og høyde, og ikke mellom høyde, vekt, hårfarge eller øyefarge. Vi fant en god korrelasjon i skjønnhetsscore. Vi la ut foto av to menn og to kvinner og lot ti personer velge ut hvem som var sammen av disse. Tilfeldig ville 25 % velge riktig, men forsøkspersonene klarte nesten 40 % rett. Dette støtter hypotesen om at vi ser etter tegn og trekk som er relevante for hvor attraktive vi er, og at dette er en universell egenskap hos mennesker. Disse egenskapene trenger ikke være fysisk utseende, men kan være atferdstrekk forbundet med omsorgsevne og økonomi. Bladet ”KK” betalte for en spørreundersøkelse blant sine abonnenter hvor vi blant annet spurte om økonomi, ambisjoner og innsats hos tidligere og nåværende mannlige partnere (Paper VI). Det var god korrelasjon mellom utilfredsstillende økonomi, manglende innsats og omsorg, lavt ambisjonsnivå og graden av skilsmisse og brudd i forholdene. Menn som viste ambisjoner, hadde felles økonomi, investerte i kvinnens tidligere barn og hadde økning i inntekt, ble sjeldnere skilt. Et interessant resultat var at menn som ble karakterisert som svært ambisiøse hadde økt sjanse for brudd med partneren. Dette kan ha flere grunner, hvorav to er nærliggende: 1) En overinvestering i karriere må nødvendigvis ta tid og krefter, og det vil gå utover investeringen i hjemmet. Her er det viktig å huske at det er den følelsesmessige reaksjonen hos partner som er viktig, og ikke nødvendigvis antall kroner som teller. 2) Menn med karriere er attraktive, og vil få flere tilbud og muligheter for andre partnere. I den siste undersøkelsen kartla vi ulikheter i hvordan biologiske foreldre og barnehageansatte oppfatter konflikter med barn (Paper VII). Ut fra evolusjonær biologi kan en predisere at barn vil være tilpasset å kreve mer av sine foreldre enn av andre voksne, og at dette vil gi seg utslag i et høyere konfliktnivå med det samme barnet, avhengig av hvem som i øyeblikket har omsorgen. Vi fant støtte for prediksjonen ved at i alle de undersøkte situasjonene med det samme barnet oppfattet den biologiske forelderen et høyere konfliktnivå enn den barnehageansatte.

Det er utgitt en svært omfattende bok på norsk som oppsummerer hva som er oppnådd hittil innen fagretningene sprunget ut av evolusjonær biologi (Mysterud, 2003). Boken anbefales til alle som arbeider med mennesker på alle plan. Evolusjonsbiologi er en del av naturvitenskapen, og er dermed logisk sammenhengende på en annen måte enn samfunnsvitenskapene. Evolusjonsbiologi er grunnleggende konsistent og sammenhengende med hele den menneskelige vitenskap, og det er derfor ikke logisk eller rasjonelt å velge å se bort fra de problematiske sidene av denne forskningen.

Synopsis

Introduction

Animal behaviour is logically interconnected through the various stages of life. Mate choice, life history strategies, parental investment and divorce strategies are different areas that involve decisions affecting fitness, the ultimate goal of life itself. Natural and sexual selection forces have shaped the behaviour of all animal species on earth, including humans. This doctoral thesis provides results concerning human life history strategies and choices, mate choice and retention of mates, and testing of parental investment mechanisms. All these areas are crucial for the maximization of individual and offspring fitness. An important aspect of evolutionary biology in general is based on how animals make decisions affecting their life history, and whether they will become ancestors or not. Decisions are usually led by environmental cues like the present resource situation and prospects of how it will become in the future, the number of siblings and peers competing at all times, proximate mechanisms like individual hormone levels and immune responses to parasite loads, and the number of potential mates available (Roff, 2002; Stearns, 1992). Decisions on when to start reproduction, and with whom, are extremely important. Mate choice and mating are depending on competition in most animal species. Mate choice, like all other life history strategies, is about optimising the result in the form of fitness. There are numerous examples of how individuals apply different strategies because of differences in the environment (Futuyma, 1998). Girls growing up without fathers experience earlier menarche, a strategy probably selected for in the past because this implies a more uncertain childhood (Quinlan, 2003; Chedraui et al., 2004; Jorm et al., 2004). An intriguing area of conflict is between parents and offspring. The fact that each individual is 100 percent related to itself, but only 50 percent to its mother, father and siblings, opens up an array of conflicting arenas for animals in general, and birds and mammals in particular (Kolliker & Richner, 2001; Royle et al., 2004). High parental investment selects for mechanisms that are sensitive to how these resources are distributed by parents, and also exploited by offspring (Lummaa et al., 1998).

Natural and sexual selection operate on the basis of the fitness results of individual traits, decisions and mechanisms. The payment in evolutionary terms is always the number of ancestors. The level and importance of consciousness is of minor interest when it comes to animals, but is a matter of discussion in humans. I do not address this aspect.

This thesis is based on tests of human data of some of the predictions concerning life history decisions established as important for animal species. Human behavioural ecology is about testing the same hypotheses onto humans that apply on animals. Are we optimizing our fitness, just like any other animal? Are we born with skills and traits that, when triggered by environmental cues, lead to logically predicted behaviour? The challenge of human behavioural ecology is to look through the obscure and confusing cultural differences and peculiarities. The strength of the research is that the hypotheses generated are predicted to be present for all populations and samples, if overcoming stochastic noise. They are predicted to be human universals, often modified by cultural differences, but always present in some form or another (Hrdy, 1999; Low, 2000; Ridley, 1994; Buss, 1994; Pinker, 2002; Barkow et al., 1992).

Hypotheses and predictions

I have used data from both historical and contemporary sources. The last decades the western way of life is characterised by a surplus of food, medicine and the presence of contraception. The major problem with research on human behaviour is that novel societies are far from how the world was like when our ancestors were selected for. The most fundamental variables determining the outcome of fitness for all species is the access to resources, and to resist diseases, all for the ultimate goal of having viable and competing offspring.

In order to avoid the problems of our modern society's resource excess, I have analysed old life history data from two parishes in 17th century middle Norway (Røskaft et al., 1992). The data consists of life history variables from one inland parish (Soknedal), which is characterised by unstable resources, and a coastal parish (Smøla) with more stable and predictable outcome. The crucial difference between these two parishes was the access to near-shore fishing at Smøla, which was an insurance against crop failure and hunger that did not exist in the inland parish Soknedal. This insurance was first and foremost to the benefit of the low status people at Smøla.

The data was compiled from church books. In Soknedal data consisted of about 1870 men, 1920 women and 5600 children, and in Smøla the number of cases were about 600 of men and women each, and about 3600 children. The number of cases differs somewhat in each analysis depending on the completeness of the variable information for each case, limitation of years for analysis and according to which of the variables that are tested. The people in the parishes were further separated into a low and a high status group. The high status group was land owners and farmers who leased their land. The low status group was the working class who owned no land.

The data was used to test the outcome of decisions important for fitness (Roff, 2002). We analysed how the number of children and grandchildren were related to crucial factors in life, like the parental resource situation, the age of first marriage, age of spouse of first marriage, and number of children born, survived and married (Lummaa, 2001, Paper I). We controlled for mean birth interval and the mother's age of death in a linear regression analysis. Analyses were based on 1218 women from Soknedal and 706 women from Smøla.

In Paper II, the birth rank situation was also compared to survival, marriage and migration rate. The resources available for a child, and parental investment, are predicted to be closely related to the number of siblings competing, the sex of the child and the number in birth rank (Trivers, 1972; Salmon & Daly, 1998; Rohde et al., 2003). Linear regression analyses were used to test correlations between the status of the mother, family size, sex of child, birth rank and year of birth. Three predictions were tested:

- There should be an increase in the infant mortality rate of boys in relation to birth rank. However, since girls are cheaper to produce, and because the value of a girl is independent of her birth rank, no such increase should exist for girls.
- The firstborn boys in general would have higher probabilities of getting married than the lastborn boys. Similarly, family size should generally affect the probability of sons to become married. However, because girls do not have the same need of resource input to increase their attractiveness and enable them to get married, these relationships were not predicted for girls.
- Boys born early should tend to settle in their home parish at a higher frequency than their laterborn siblings. Furthermore, boys from large-sized families should show a greater tendency to migrate from home than boys from smaller-sized families. This pattern is not predicted for girls.

In Paper III, data was analysed to establish the influence of birth interval on the survival and success of offspring in the different resource situations. In mammals, variation in reproductive traits are usually easiest to detect among females, since they usually invest more than males both during and after pregnancy (Clutton-Brock, 1991a; Alcock, 1998a). We tested the following predictions on the female population:

- If costs of producing a son is higher than producing a daughter we predicted that birth interval after having a son should be longer than after having a daughter.
- Because resources and ecological conditions are important factors for a woman when reproducing, we predicted that high status women should have shorter birth intervals than low status women. In addition we predicted that women living in a rich and resource stable parish should have shorter birth intervals than women in a resource-unstable parish.
- If there is an optimal birth interval, we predicted that children born with shorter birth intervals should have a lower survival rate.

The data from the church books was also tested for one aspect of mate choice, namely the degree of consanguinity in the parishes (Paper IV). This is an area where human cultures are very diverse in how this is practiced and regulated, and all cultures investigated have some sort of regulations towards consanguinity (Hussain & Bittles, 1998; Hussain, 1999; Fuster & Colantonio, 2003; Alper et al., 2004; Fuster & Colantonio, 2004). Religion and legislation is often accommodated to the conflicts between the pros, that include offspring with more than 50 % kinship with parents and the advantages of building strong families, and the cons including genetic diseases from inbreeding. Although fertility might be high in some consanguineous unions, there are also reports describing hereditary disorders, congenital malformations, mental retardation and recessively transmitted diseases (Tuncbilek, 2001; Zlotogora, 2002; Koochmeshgi et al., 2002; Sureender et al., 2003; Jaber et al., 2004).

Mate choice is central to all animal species, and can be regarded as a series of decisions crucial for individual fitness. Both natural and sexual selection have been, and still are, working to shape the minds of men and women in a longer scale. What are the criteria we look for in a partner, and are there any selective advantages for choosing like we do? During the last decades these questions have been tested extensively, and some human universals have been revealed (Buss, 1994; Koyama et al., 2004). We tested physical traits like weight, height, hair color and age among student partners in Trondheim to see if there were correlations (Paper V). The data were obtained from 200 persons between 20 and 34 years of age. We also tested whether a group of ten test persons were capable of recognizing who is a pair from four photos. This has never been done before. The goal was to test if there is a general human ability to evaluate the mate value of a pair by their looks (Grammer et al., 2003; DeBruine, 2004; Simmons et al., 2004). Results that show some variation in preferences have been published, explained by environmental stress in the form of competitive conditions (McGraw 2002), or increased parasite load (Penton-Voak et al. 2004).

An equally important aspect of life history for humans is to retain a selected mate. Throughout evolutionary history, fitness success has been dependent on a stable partnership and investment in offspring from both parents. We wanted to examine the presence of resources and investment from a man as cues of attractiveness to a woman. The Norwegian female magazine “KK” was asked to finance a questionnaire that was sent to all their 22 000 subscribers, which gave us a database of 3400 women (Paper VI). They were asked questions about how their previous and present partners behaved and acted concerning the acquisition and contribution of their resources. Predictions included the probabilities of the pairs staying together or decide to leave each other, and were tested on the basis of factors like the degree of economic stability, sharing and satisfaction in economic matters, male investment, ambition level and career performance. From a female point of view, these factors are predicted to be important for safe child rearing and, ultimately, her fitness. Sexual competition in humans is expected to be high because of the high investment in the offspring by both fathers and mothers, and thereby quests for a high quality partner. The human male is adapted to commit himself to an unusual high degree of paternal effort compared to mammal species in general, although their investment is exceeded several folds by the females (Low, 2000). Not fulfilling the expectations is predicted to increase the divorce ratio. We tested the hypothesis that females will appreciate male stability, ambitions and willingness to invest. The following predictions were outlined:

- Perceived high commitment in the form of economic confidence, satisfaction and predictability are factors preventing divorce.

One aspect of this is how the spouses trust each other by having shared their economy. High confidence in each other was assumed to be a sign of a stable partnership.

- A high level of male ambition in relation to his career will prevent divorce.
- An increase in a man’s socioeconomic status from the day they met will prevent divorce.
- A perception of a fair outcome of who gets the last word in disputes will prevent divorce.

Debates and quarrels are strategies to win small fights over resources in daily lives, and solving them in a just way is crucial in well-functioning partnerships.

- A woman’s perception of high investment in her previous children will prevent divorce.

Finally, in the last paper (Paper VII) we tested how parental investment could be connected to differences in conflict levels and a child's expectance of different attention and care from biological parents in contrast to other grown-ups. The prediction was that the conflict level would be higher between a child and its biological mother than between other grown-ups. Conflicts in general are connected to disputes over resources in some way or another, whether these are time and commitment, food, or other signs of parental investment (Perezagote, 1986; Schudlich et al., 2004; Summerfield, 1998; Don-Yehiya, 1998). Also the lack of returning reciprocal help may be a source of conflict (Barkow et al., 1992). We compared the personal perception of conflict levels in eight different daily situations with the same child from the mother's and the preschool teacher's point of view. We also tested whether there were sex differences in the conflict levels, both for a male or a female teacher and also between boys or girls in the kindergarten.

Results and discussion

Paper I

All statistical tests on data from Soknedal and Smøla were based on the mother's status. As predicted, the women of high status gave birth to significantly more children than did low status women within both populations. Also, low status women gave birth to significantly more children in the stable resource parish Smøla than in the more unstable parish Soknedal. Furthermore, high status women had significantly more grandchildren only in Soknedal, and low status women in Smøla produced 66 % more grandchildren than low status women in Soknedal. These results support the prediction that stable access to resources is an important variable for the reproduction (Clarke & Low, 2001).

In spite of this, significantly more children survived in Soknedal, so that number of children married was quite similar. An optimal birth interval implies a trade-off between the contradictory forces of resource depletion and limited reproductive time. Because of a too short time between the previous or the next child, offspring may suffer from different kinds of shortages, like famine and lack of care. On the other hand, a woman's reproductive period is restricted. Previous research is not conclusive (El Shalakani, 1989; Low, 1991; Mace & Sear, 1997; Wilkinson et al., 1989). Twin boys are reported to be more expensive when it comes to parental investment (Lummaa et al., 2001)

The partial correlations performed in Paper I between the different life history traits and number of grandchildren, controlling for social status, gave quite similar results between Smøla and Soknedal. The year born was important in explaining the number of grandchildren. Number of childbirths in general went down in Norway during the time period studied. The correlation between number of grandchildren and number of childbirths was positive in Smøla while negative in Soknedal. This is probably due to the differences in the changing population densities, which had a higher impact in Soknedal.

Because some important life history traits examined, as the number of children born, survived and married inter-correlated at highly significant levels, only number of children who became married was used as an independent variable in the multivariate analysis in Paper I. Within both populations the multivariate patterns in life history variation was very similar; the number of children married turned out to be the most important variable in explaining the variation in number of grandchildren born. In addition, a woman's reproductive period, as well as the mean birth interval of her children was both important traits in explaining variation in number of grandchildren. On the other hand, the year a woman was born, her own age when she married, age of her spouse when they married and age when she died turned out to be insignificant additional variables in explaining the variation in number of grandchildren a woman produced.

Both women and their spouses married at an earlier age in Smøla than in Soknedal. On the other hand, women at Smøla died earlier (Paper I). We have only a speculative explanation for this, involving increased exposure to accidents and diseases. Travel and transport of goods and people took place mainly along the coast, which consequently increased the risk of contact with sickness. Also the rate of accidents like storms were higher along the coast.

Paper II

I analysed the probabilities of survival, marriage and migration correlated with status and birth rank. We found a linear relationship between each of the variables survival to adulthood, marriage probability and migration correlated with birth rank for boys, but not for girls. These findings support the prediction that boys compete more for resources within the family than girls do, and that their fitness is more connected to resource acquisition (Trivers & Willard, 1973). Indeed, the status of a mother turned out to be the most important factor in explaining survival rates for her male children, but not for her female children. The mere family size had a significant impact on a boy's probability of survival (negative), getting married (negative) and migrate (positive). Also, boys from larger families with a sibling sex ratio skewed towards boys had a lower survival probability. All these findings support the hypothesis that costs of producing boys are higher than that of producing girls (Clutton-Brock, 1991b).

Paper III

As expected, there was a significant correlation between mean birth interval and number of children born, in that the shorter the interval, the more siblings a child was likely to have. I found no differences in birth interval between the various combinations of sibling sexes, despite the findings of previous researchers (Low 1991, Lummaa 2001). There were, as predicted, significant differences in birth interval between high and low status women within both parishes, as well as between the two parishes, in that the poorer parish of Soknedal had longer birth interval for both status groups.

The optimal birth rate in Soknedal seems to be slightly over three years. If birth interval was lower, survival rate of children went down. If birth interval went up, the total number of children consequently went down. All differences were statistically significant.

In a multilinear regression analysis of birth interval as the dependent variable, the number of children of mother was, not surprisingly, the most important independent variable in explaining the variation in birth interval. A child's number in birth order explained a substantial part of the variation, whereas laterborn children had longer birth intervals.

Survival rate and status of mother were significant factors in explaining birth interval variance.

Paper IV

A random mating in the population would give a total of 24% marriages between relatives of more than 0.03 in coefficient of relatedness. The actual numbers for the high status group were 9 % and for the low status group under 6 %. The hypothesis of inbreeding avoidance is therefore supported in this material (Morris et al., 2002). There was however no difference in number of children born or number of surviving children between consanguineous or non-consanguineous marriages, which would have been the ultimate test of the fitness consequences of inbreeding.

Paper V

In the mate choice experiment, we found that age, height and physical attractiveness were significantly correlated between mates (Susanne, 1997; Hur, 2003). Weight and hair colour were randomly distributed. Even though there is clear evidence of human universal mate preferences, some cultural displacement exist between the known traits (McGraw, 2002).

We tested whether ten test persons were able to pick out a pair from four photos, and they did so in about 40 % of the cases, random chance was 25 %. Almost 90 % of the test persons picked out the right pair more frequently than random (Paper V). This result indicate a domain-specific psychological mechanism selected to evaluate mates by the facial attractiveness (Barkow et al., 1992). Several connections are described between fluctuating asymmetry, attractiveness and genetic quality, e.g. a correlation between facial attractiveness and semen quality, and between the degree of male masculinity and parasite load in the society (Thornhill & Gangestad, 1999; Soler et al., 2003; Penton-Voak et al., 2004).

The persons on the photos were about the same age, and all were Caucasian. According to the universal nature of the described mechanisms, racial differences should not have any influence on the results, but this prediction needs larger samples for testing. Independent of race or culture, the prediction is nevertheless that any subpopulation should have the same mate choice preferences.

Paper VI

The results from the questionnaire presented to the subscribers of "KK" supported all the predictions tested. Males are retained if they invest and show signs of commitment in the relationship. Economic satisfaction, predictability, sharing and a male's ambition level are all variables that are highly evaluated by a female. Two results from this study are particularly interesting. When women were asked who got the last word in disputes, it turned out that the stability of a relationship was significantly higher when a woman felt that disputes were equally shared, regardless of which of the two spouses dominated (Table 1B). Twice as many women from broken relationships reported that they won discussions. The respondents that reported an equal sharing of who got the last word in disputes were having lower divorce rates. It is OK to quarrel, if there is some justice in the outcome. Investment may here have the form of standing up for one's views. Not only is this a sign of strength in competition with other males, but also a sign of care and commitment: I am so involved in this relationship. A tilting of this balance either way increases the probability of divorce.

The other interesting result is the higher divorce rate among overambitious men (Figure 1). Ambition up to a certain level prevents divorce. Alas, beyond that, the career-hunters may fail to invest the results of their industriousness into the family, or they may have become more attractive and thereby facing tempting offers outside.

Paper VII

In the last paper we analysed if there was a correlation between a child's expectations of parental investment and conflict level between the biological mother and other grown-ups (Paper VII). We found that there was a statistically significant difference between the reported level of conflict between parents and kindergarten teachers in all eight context categories examined. The situations were during meals, when resting, during toilet visits, dressing and undressing, washing, indoor behaviour, outdoor behaviour and reactions to disciplinary warnings. Biological parents were always reporting a higher level of conflict. Also, the variation in level of conflict for each context was similar for parents and teachers. Teachers, but not parents, reported a significant difference between the sexes in the conflict levels. Boys were more troublesome than girls in the kindergarten, but not at home. Mothers and fathers did not report any significant difference in the level of conflict with their child, but among the teachers the female respondents reported a significantly higher level of conflict than the male respondents. A General Lineal Model analysis, in which conflict level was the dependent variable, shows that neither the sex of the parents nor the sex of the child had a significant influence of the conflict level. Among the teachers however, the sex of both the child and the adult contributed significantly to the conflict level.

Studies of parent-offspring conflicts on a phenotypic level have increased in recent years (Kilner & Johnstone, 1997; Mock & Parker, 1997; Kölliker et al., 1998; Kölliker et al., 1999). Particularly nestling birds may modify their solicitation behaviour according to the strategy of their parents (Kilner & Johnstone, 1997; Slagsvold, 1997; Kölliker et al., 1998; Kedar et al., 2000; Budden & Wright, 2001). Increased level of soliciting by an offspring may lead to a higher effort by the parents which under natural conditions may be more costly for them in terms of fitness loss. For instance in birds, parents frequently respond to increased begging call activity by increasing their feeding effort (Ottoson et al., 1997; Burford et al., 1998; Davies et al., 1998; Wright, 1998). Variation in soliciting activity is measured by the rate of peeping or begging in chicken (Webster & Hurnik, 1987; Kölliker et al., 2000). Similar results have been found among rodents (Graham & Letz, 1979; Brunelli et al., 1997). The crying of human babies induces physiological stress responses in their parents (Wiesenfeld & Zander Malatesta, 1983), and elicits caring behaviour (Lummaa et al., 1998). Intensity of crying of human neonates differ significantly between individuals (Korner, 1974; Furlow, 1997; Barr, 1999), a variation that may be triggered by individual differences in genetic variation, physiology and individual life history (Kölliker & Richner, 2001). A child which is being discontent increases the level of conflict towards the providers, which during evolutionary time usually have been its biological parents (Buijzen & Valkenburg, 2003). In order to test the hypothesis, we based our study on a questionnaire and not observations, because the individual persons’ feeling of conflict level is the variable directly responding to the child’s crying and whimpering. Systematic errors like the possibility that nursery teachers might have a different perception of a conflict than parents seem highly unlikely, because the level of conflict reported by the adult person correlate between the different settings. The reported variation was similar for parents and school teachers being relatively high during meals, what was called typical indoor situations and when the adult person was correcting the behaviour of the child. The lowest conflict levels were reported from both groups during toilet visits and the outdoor situations. The parent's perception is that the children during their daily life are more difficult to handle than the nursery school colleagues perceive it to be. We claim that the observed difference in conflict levels are a measure of higher demands for attention and care from the children at home than in similar contexts in the nursery school. The results give support for the hypothesis that children have an innate and selected mechanism that guides them in different social contexts, and that they easily assess differences important for the level of care and attention they can expect to get. Children expect a higher investment from their parents than from their teachers, and therefore solicit more in the parent-offspring context.

Conclusion

The results from the analyses performed in the papers of this thesis support the hypothesis that life history variables important for animals are also important for humans. Predictions derived from evolutionary biology applied on animals are fruitful in revealing the consequences of human behaviour. Unconscious choices made by parents and offspring had, and still have, crucial impacts on fitness and the number of descendants from each acting individual. Decisions concerning how to behave when being in an unstable environment in contrast to living in abundance have vital effects on the number of surviving offspring. Finding an optimal mate, and currently evaluate his or her qualities, are behaviour that is rewarded with increased fitness. A child that was reluctant and quiet was disregarded by a craving and demanding sibling. We have tested data from 300 years ago, and from today, and have found support for predictions derived from evolutionary biology, in the form of life history decisions that are expected to be present as human universals.

Perspectives

Sexual selection is one of the most challenging views and the most powerful explanation concept for the peculiarities encumbered with us as a species. The significance of the male and female differences, the resulting mate choice and status seeking are interwoven with small and large decisions taken in everyday life, policy-making on small and large scale, and also the diverse cultural expressions found all over the world. Together with analyses of conflicts in general, psychic health is one of the fields that probably will profit most from this new insight. An evolutionary way of diagnosing psychic disorders is to quantify a patient’s emotional reaction as too much or too little compared to a mean. Speculation concerning the perspectives from evolutionary biology soon brings us far away. Two areas are of special interest to me:

- To help building sustainable and democratic societies for the third world on their own premises, without destroying the environment, is one of the areas where humanity has the largest challenge. Policy-makers are often neglecting the fact that societies consist of individuals, and that the individual behaviour in sum constitute the reaction to whatever the measures would imply.

- The Western world overconsumption, and the connection to the innate drivers of wanting to have more, regardless of how much each has. This is a problem that must be dealt with politically, because the prediction from our evolutionary past is that this behaviour will emerge in all societies who have the chance.

Evolutionary biology presents more insight. It is our responsibility to use it correct.

References

Alcock, J. 1998a. *Animal Behavior: An Evolutionary Approach*. Sunderland, Massachusetts: Sinauer.

Alcock, J. 1998b. Unpunctuated equilibrium in the natural history essays of Stephen Jay Gould. *Evolution and Human Behavior*, **19,** 321-336.

Alper, O. M., Eregin, H., Manguoglu, A. E., Bilgen, T., Cetin, Z., Dedeoglu, N. & Luleci, G. 2004. Consanguineous marriages in the province of Antalya, Turkey. *Annales De Genetique*, **47,** 129-138.

Barkow, J. H., L. Cosmides & Tooby, J. 1992. *The Adapted Mind*. New York: Oxford University Press.

Barr, R. G. 1999. Infant crying behavior and colic: an interpretation in evolutionary perspective. In: *Evolutionary Medicine* (Ed. by Trevathan, W. R., Smith, E. O. & McKenna, J. J.), pp. 27-51. New York: Oxford University Press.

Brunelli, S. A., Vinocur, D. D., Soo-Hoo, D. & Hofer, M. A. 1997. Five generations of selective breeding for ultrasonic vocalization (USV) responses in N:N IH strain rats. *Developmental Psychobiology*, **31,** 255-265.

Budden, A. J. & Wright, J. 2001. Begging in nestling birds. *Current Ornithology*, **16,** 83-118.

Buijzen, M. & Valkenburg, P. M. 2003. The effects of television advertising on materialism, parent-child conflict, and unhappiness: A review of research. *Applied developmental psychology*, **24,** 437-456.

Burford, J. E., Friedrich, T. J. & Yasukawa, K. 1998. Responses to playback of nestling begging in the red-winged blackbird, *Agelaius phoeniceus*. *Animal Behaviour*, **56,** 555-561.

Buss, D. M. 1994. *The Evolution of Desire. Strategies of Human Mating*. New York, USA: Basic Books.

Chedraui, P. A., Hidalgo, L. A., Chavez, M. J. & Miguel, G. S. 2004. Determinant factors in Ecuador related to pregnancy among adolescents aged 15 or less. *Journal of Perinatal Medicine*, **32,** 337-341.

Clarke, A. L. & Low, B. S. 2001. Testing evolutionary hypotheses with demographic data. *Population and Development Review*, **27,** 633-+.

Clutton-Brock, T. 1991a. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Clutton-Brock, T. H. 1991b. The Evolution of Parental Care. Princeton, New Jersey: Princeton University Press.

Davies, N. B., Kilner, R. M. & Noble, D. G. 1998. Nestling cuckoos, Cuculus canorus, exploit hosts with begging calls that mimic a brood. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265,** 673-678.

DeBruine, L. M. 2004. Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271,** 2085-2090.

Don-Yehiya, E. 1998. Rituals of conflict: Religion, politics and public policy in Israel. *American Political Science Review*, **92,** 492-493.

El Shalakani, M. H. 1989. Estimation of fertility and mortality of the Kuwaiti population. 21: . *Journal of Biosocial Science*, **21,** 433-442.

Ellis, L. 1996. A discipline in Peril: Sociology's future hinges on Curing its Biophobia. *Amer. Sociol.*, **27,** 21-41.

Furlow, F. B. 1997. Human neonatal cry quality as an honest signal of fitness. *Evolution and Human Behavior*, **18,** 175-193.

Fuster, V. & Colantonio, S. E. 2003. Inbreeding coefficients and degree of consanguineous marriages in Spain: A review. *American Journal of Human Biology*, **15,** 709-716.

Fuster, V. & Colantonio, S. E. 2004. Socioeconomic, demographic, and geographic variables affecting the diverse degrees of consanguineous marriages in Spain. *Human Biology*, **76,** 1-14.

Futuyma, D. 1998. *Evolutionary biology*. Sunderland, Mass. : Sinauer Associates, c1998.

Graham, M. & Letz, R. 1979. Within-species variation in the development of ultrasonic signaling of preweaning vrats. *Developmental Psychobiology*, **12,** 129-136.

Grammer, K., Fink, B., Moller, A. P. & Thornhill, R. 2003. Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Reviews*, **78,** 385-407.

Hrdy, S. B. 1999. *Mother nature : a history of mothers, infants, and natural selection*. New York: Pantheon Books.

Hur, Y. M. 2003. Assortative mating for personality traits, educational level, religious affiliation, height, weight, and body mass index in parents of Korean twin sample. *Twin Research*, **6,** 467-470.

Hussain, R. 1999. Community perceptions of reasons for preference for consanguineous marriages in Pakistan. *Journal of Biosocial Science*, **31,** 449-461.

Hussain, R. & Bittles, A. H. 1998. The prevalence and demographic characteristics of consanguineous marriages in Pakistan. *Journal of Biosocial Science*, **30,** 261-275.

Jaber, L., Karim, I. A., Jawdat, A. M., Fausi, M. & Merlob, P. 2004. Awareness of folic acid for prevention of neural tube defects in a community with high prevalence of consanguineous marriages. *Annales De Genetique*, **47,** 69-75.

Jorm, A. F., Christensen, H., Rodgers, B., Jacomb, P. A. & Easteal, S. 2004. Association of adverse childhood experiences, age of menarche, and adult reproductive behavior: Does the androgen receptor gene play a role? *American Journal of Medical Genetics Part B-Neuropsychiatric Genetics*, **125B,** 105-111.

Kedar, H., Rodriguez-Girones, M. A., Yedvab, S., Winkler, D. W. & Lotem, A. 2000. Experimental evidence for offspring learning in parent-offspring communication. *Proceedings of the Royal Society of London, Series B*, **267,** 1723-1727.

Kilner, R. & Johnstone, R. A. 1997. Begging the question; are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, **12,** 11-15.

Kolliker, M. & Richner, H. 2001. Parent-offspring conflict and the genetics of offspring solicitation and parental response. *Animal Behaviour*, **62,** 395-407.

Koochmeshgi, J., Bagheri, A. & Hosseini-Mazinani, S. M. 2002. Incidence of phenylketonuria in Iran estimated from consanguineous marriages. *Journal of Inherited Metabolic Disease*, **25,** 80-81.

Korner, S. F. 1974. The effect of the Infant's state, level of arousal, sex, and ontogenetic stage on the caregiver. In: *The Effect of the Infant on its Caregiver* (Ed. by Lewis, M. & Rosenblum, L. A.), pp. 105-121. New York: J. Wiley.

Koyama, N. F., McGain, A. & Hill, R. A. 2004. Self-reported mate preferences and "femimst" attitudes regarding marital relations. *Evolution and Human Behavior*, **25,** 327-335.

Kölliker, M., Brinkhof, M. W. G., Heeb, P., Fitze, P. S. & Richner, H. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proceedings of the Royal Society of London, Series B*, **267,** 2127-2132.

Kölliker, M. & Richner, H. 2001. Parent-offspring conflict and the genetics of offspring solicitation and parental response. *Animal Behaviour*, **62,** 395-407.

Kölliker, M., Richner, H., Werner, I. & Heeb, P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour*, **55,** 215-222.

Kölliker, M., Richner, H., Werner, I. & Heeb, P. 1999. Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour*, **55,** 215-222.

Low, B. S. 1991. Reproductive life in nineteenth century Sweden: An evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, **12,** 411-448.

Low, B. S. 2000. *Why Sex Matters: A Darwinian Look at Human Behavior*. Princeton: Princeton University Press.

Lummaa, V. 2001. Reproductive investment in pre-industrial humans: The consequences of offspring number, gender and survival. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **268,** 1977-1983.

Lummaa, V., Jokela, J. & Haukioja, E. 2001. Gender difference in benefits of twinning in pre-industrial humans: boys did not pay. *Journal of Animal Ecology*, **70,** 739-746.

Lummaa, V., Vuorisalo, T., Barr, R. G. & Lehtonen, L. 1998. Why cry? Adaptive significance of intensive crying in human infants. *Evolution and Human Behavior*, **19,** 193-202.

Mace, R. & Sear, R. 1997. Birth interval and the sex of children in a traditional African population: An evolutionary analysis. *Journal of Biosocial Science*, **29,** 499-507.

McGraw, K. J. 2002. Environmental predictors of geographic variation in human mating preferences. *Ethology*, **108,** 303-317.

Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford, New York, Tokyo: Oxford University Press.

Morris, R. D., Morris, K. L. & Morris, J. A. 2002. The mathematical basis of sexual attraction. *Medical Hypotheses*, **59,** 475-481.

Mysterud, I. 2003. *Mennesket og moderne evolusjonsteori*. Oslo: Gyldendal akademisk.

Mysterud, I. 2004. One name for the evolutionary baby? A preliminary guide for everyone confused by the chaos of names. *Social Science Information*, **24,** 95-114.

Ottoson, U., Bäckman, J. & Smith, H. G. 1997. Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca*. *Behavioural Ecology and Sociobiology*, **41,** 381-384.

Penton-Voak, I. S., Jacobson, A. & Trivers, R. 2004. Populational differences in attractiveness judgements of male and female faces: Comparing British and Jamaican samples. *Evolution and Human Behavior*, **25,** 355-370.

Perezagote, A. 1986. The Role of Religion in the Definition of a Symbolic Conflict - Religion and the Basque Problem. *Social Compass*, **33,** 419-435.

Pinker, S. 2002. *The blank slate : the modern denial of human nature*. New York: Viking.

Quinlan, R. J. 2003. Father absence, parental care, and female reproductive development. *Evolution and Human Behavior*, **24,** 376-390.

Ridley, M. 1994. *The Red Queen: Sex and the evolution of human nature*. Penguin books.

Roff, D. A. 2002. *Life history evolution*. Sunderland, Mass.: Sinauer.

Rohde, P. A., Atzwanger, K., Butovskaya, M., Lampert, A., Mysterud, I., Sanchez-Andres, A. & Sulloway, F. J. 2003. Perceived parental favoritism, closeness to kin, and the rebel of the family: The effects of birth order and sex. *Evolution and Human Behavior*, **24,** 261-276.

Royle, N. J., Hartley, I. R. & Parker, G. A. 2004. Parental investment and family dynamics: interactions between theory and empirical tests. *Population Ecology*, **46,** 231-241.

Røskaft, E., Wara, A. L. & Viken, Å. 1992. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, **13,** 443-461.

Salmon, C. A. & Daly, M. 1998. The impact of birth order on family sentiment: Middleborns are different. *Evolution and Human Behavior*, **19,** 299-312.

Schudlich, T. D. D. R., Shamir, H. & Cummings, E. M. 2004. Marital conflict, children's representations of family relationships, and children's dispositions towards peer conflict strategies. *Social Development*, **13,** 171-192.

Segerstråle, U. 2000. *Defenders of the truth : the battle for science in the sociobiology debate and beyond*. Oxford: Oxford University Press.

Simmons, L. W., Rhodes, G., Peters, M. & Koehler, N. 2004. Are human preferences for facial symmetry focused on signals of developmental instability? *Behavioral Ecology*, **15,** 864-871.

Slagsvold, T. 1997. Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Animal Behaviour*, **54,** 1357-1368.

Soler, C., Nunez, M., Gutierrez, R., Nunez, J., Medina, P., Sancho, M., Alvarez, J. & Nunez, A. 2003. Facial attractiveness in men provides clues to semen quality. *Evolution and Human Behavior*, **24,** 199-207.

Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.

Summerfield, D. 1998. Protecting children from armed conflict - Children affected by war must not be stigmatised as permanently damaged. *British Medical Journal*, **317,** 1249-1249.

Sureender, S., Ramachandran, S., Subbiah, A. & Ravishankar, A. K. 2003. Consanguineous marriages and pregnancy wastage. *Indian Journal of Social Work*, **64,** 533-540.

Susanne, C. 1997. Heritability of anthropological characters. *Human Biology*, **49,** 573-580.

Thornhill, R. & Gangestad, S. W. 1999. The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior*, **20,** 175-201.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man1871-1971* (Ed. by Campbell, B. G.), pp. 136-179. Chicago: Aldine Publishing Co.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179,** 90-92.

Tuncbilek, E. 2001. Clinical outcomes of consanguineous marriages in Turkey. *Turkish Journal of Pediatrics*, **43,** 277-279.

Webster, A. B. & Hurnik, J. F. 1987. Heritability of the peep vocalization in white leghorn-type chicks. *Applied Animal Behaviour Sciences*, **19,** 157-168.

Wiesenfeld, A. R. & Zander Malatesta, C. 1983. Assessing caregiver sensitivity to infants. In: *Symbiosis in Parent-Offspring Interaction* (Ed. by Rosenblum, L. A. & Moltz, H.), pp. 173-188. New York: Plenum.

Wilkinson, G. S., Nagoshi, C. T., Johnson, R. C. & Honbo, A. M. 1989. Perinatal mortality and sex ratios in Hawaii. *Ethology and Sociobiology*, **10,** 435-447.

Wright, J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from the play-backs of chick begging. *Behavioural Ecology and Sociobiology*, **42,** 423-429.

Zlotogora, J. 2002. What is the birth defect risk associated with consanguineous marriages? *American Journal of Medical Genetics*, **109,** 70-71.

Paper I

PAPER I

Ecological conditions and life history variations in two Norwegian human populations during the period 1700-1900 CE

EIVIN RØSKAFT, TERJE BONGARD, ÅSLAUG VIKEN AND GUNILLA ROSENQVIST

Norwegian University of Science and Technology (NTNU), Department of Biology, Realfagbygget, N-7491 Trondheim, NORWAY

Abstract

In this study we report results showing that access to stable resources was the main predictor of number of children born and number of grandchildren produced within and between two human populations in Central Norway from 1700-1900. Our main objective was to test whether resources per se could be more important than other factors for the reproductive success of a woman. We measured the total number of children born and the number of grandchildren produced as well as differences in other important life history traits. The two studied villages were at the same latitude, but had different resource foundation in that the coastal parish had access to year round fishing. This extra resource affected most life history traits of these latter women, particularly low class women produced significantly more grandchildren than their sisters without this stable resource.

Key-words; human life history, reproductive success, resource access, social status

Introduction

Different life history traits, such as age at maturity or at the first reproductive event, reproductive life span, interval between the reproductive events, number of offspring and offspring survival are all responsible for variances in reproductive success (Stearns, 1992; Roff, 2002). Number of offspring that survive to reproductive age and number of grandchildren produced is the ultimate goal favoured by natural selection (Smith & Fretwell, 1974; McGinley & Charnov, 1988; Käär et al., 1996; Käär & Jokela, 1998; Lummaa, 2001; Jones & Marlowe, 2002; Tracer, 2002; Helle et al., 2002). The distribution and quality of resources are important ecological factors which will influence the evolution of life history traits (Stearns, 1976; Roff, 2002). Delayed onset of first reproduction and longer time between the reproductive events, have for instance been found to follow from resource limitations (Waynforth et al., 1998; Covas et al., 2004). In agrarian human societies where resources are inherited, differences in reproductive strategies can be due to differences in lineage access to resources. Families with greater or lesser access to resources are expected to follow different life history strategies, which are typically phenotypic plastic responses to different environments (Käär et al., 1996), and access to resources have also been recorded to correlate positively with reproductive success in humans (Betzig, 1986; Clutton-Brock, 1991; Røskaft et al., 1992). However, changes in life history strategies due to different access to resources between families have not to our knowledge been reported earlier.

The present study tested whether individuals from two Norwegian villages followed different life history strategies based on their differences in access to resources. In one village the people had access to fishing in addition to their agricultural activities. We analysed how resource aquisition within and between these two human populations during the period 1700 to 1900 affected life history traits. Particularly, we tested individual variation in female lifetime reproductive success measured as the total number of children and grandchildren born. The prediction tested was that more stable resources should have a higher impact on reproductive success particularly in the low status group, given that other life history parameters were kept constant.

Materials and methods

The two populations in our study from Central Norway differed in their resource situation, but apart from this they were quite similar. Soknedal (63° N 10° E, the farming parish), is a small (435 km^2) agricultural parish situated between 200 and 600 m above sea level. It is a typical inland parish with mountains and valleys, and had through the study period a very uniform structure because most people were more or less occupied by farming. In addition, most people were able to carry out small game hunting, and some fishing in lakes and rivers. The larger game moose (*Alces alces)* was the property of the landowner. There were good conditions for cultivated pasture and harvest, but the northern climate and the altitude made limitations for farm production. None of the farms in the parish were particularly large, but did vary in size.

The other population Smøla (63° N 8° E, the fishing parish) is an island (275 km^2) located off the coast of central Norway. Smøla has a maximum altitude of 70 m above the sea level. During the 16th and 17th century there was some land clearing on the island and the typical Smøla man became both a farmer and a fisherman. During the late 17th and 18th century farming became increasingly more important as a contribution when fishing gave uncertain income. The output capacity from the farms met the daily requirements (2600 kcal per person) for only 140 of 600 inhabitants in 1650. In 1865 the farms where able to feed 1300 of 2400 inhabitants (Leivdal & Fredly, 1997).

The data were obtained from transcripts made from parish registers and from local history books (Haukdal, 1971; Berg, 1981; Leivdal & Fredly, 1997). These books provide good demographic data for people who lived in the populations, including widespread information about the living conditions, economic basis and life in general. The demographic data in the books are based on primary sources such as church registers, local tax lists, land registers, population censuses and the electoral register. We chose local history books from these populations for several reasons. First, we found that these data had high quality, as there was complete information on all family members in most families. Second, the two populations were comparable with respect to ecological conditions and the predictability of resources, with an important variable being the difference in access to resources for the low status people. The inshore fishing at Smøla represented a stable and predictable income of food rich in protein. Norway has a dramatic variation in climate changing from the arctic north to the boreonemoral south, but both studied parishes are located at the same latitude (63° N), with quite similar climate conditions. The distance between them is about 120 kilometres, and the Atlantic coast situated only about 80 kilometres away from the farm parish.

Several researchers, as demographers (Bongaarts, 1978), economists (Mosk & Johansson, 1986), Darwinian anthropologists (Boone, 1986; Boone, 1988), evolutionary psychologists (Buss, 1989) and behavioural ecologists (Low, 1989; Low, 1990; Low, 1991; Low & Clarke, 1991; Low, 1992; Low & Clarke, 1992; Clarke, 1993) have studied the demographic transition in humans, described as the observed decrease in fertility with an increase of wealth in the western world. This change arose mainly during the last century and can be viewed as a consequence of evolutionary optimisation of the human life history strategy of resource allocation (Mace, 2000; Mulder, 2000; Low, 2000; Teriokhin et al., 2003). We avoided the demographic transition by choosing our study period before number of children per family started to decline. Even though the data extended back as far as the 17th century, the period 1700 - 1900 was chosen for two reasons. Before 1700, the quality of the data was precarious, and after 1900, the social structure in the societies became less uniform and unstable because of the demographic transition and an increasing proportion of paid professions.

The majority of the population in the farming parish (Soknedal) belonged to one of four different social groups (Røskaft et al., 1992);

1) Bønder; farmers who owned their farms,

2) Leilendinger; farmers who leased their farm from landowners,

3) Husmenn; people who worked for the farmers, but usually had a small house on their own, and were able to feed a cow, and some sheep, and

4) Inderst; farm servants, and other people who temporary worked for farmers.

The difference between "Bønder" and "Leilendinger" is more a historical than a social phenomenon and the two groups are therefore defined as high-status people with relatively stable access to food resources. "Inderst" and "Husmenn", who owned no land, were regarded as the low-status group, consisting of people with lesser access to food resources (Haukdal, 1971).

In the fishing parish (Smøla) the four social groups were equivalently present. In addition to them, there was another group called pure fishermen. As in the farming parish, the social groups were classified into high-status and low-status groups. Furthermore, both populations had traders, priests and teachers, but all these groups are excluded from the study. The major difference between the two parishes was that everybody on Smøla was able to harvest from the sea, and consequently low status people had more reliable access to food resources (Leivdal & Fredly, 1997).

All statistical tests were based on the mothers in the two populations. The tests are two-tailed unless otherwise stated. The total database consists of 1218 women from the farming parish Soknedal and 706 women from the fishing parish Smøla.

The number of children and grandchildren a woman produce is dependent on many factors, as number of children born, number of children who grew up, number of children that became married, age of her own first marriage, age of her spouse of first marriage, reproductive period and year she was born (Røskaft et al., 1992). In addition to these variables, we controlled for mean birth interval and the mother's age of death in a linear regression analysis (Roff, 2002;

Lahdenperä et al., 2004). Number of grandchildren of a woman was defined as number of children born times number of children married.

Results

High status women gave birth to significantly more children than did low status women within both populations. Furthermore, low status women gave birth to significantly more children in the fishing parish Smøla than in the farming parish Soknedal (Table 1). Although high status women had more grandchildren in both parishes, the difference between the two classes was statistically significant only in Soknedal. Low status women in Smøla produced 66 % more grandchildren than low status women in Soknedal (Table 1).

Most of the life history variables differed between the women from Smøla and Soknedal. However, significantly more children survived in Soknedal, while number of children married was quite similar. This fact is connected to the shorter mean birth interval in Smøla (Table 2). Both women and their spouses married at an earlier age in Smøla than in Soknedal. On the other hand, women at Smøla died earlier (Table 2).

The partial correlations between the different life history traits and number of grandchildren, controlling for social status, was relatively similar between Smøla and Soknedal (Table 3). The year born was important, although positive in Smøla while negative in Soknedal (Table 3). Because some important life history traits examined, as the number of children born, survived and married intercorrelated at highly significant levels, only number of children who became married was used as an independent variable in the multivariate analysis (Table 4). Within both populations the multivariate patterns in life history variation was very similar; the number of children married turned out to be the most important variable in explaining the variation in number of grandchildren (Table 4). In addition, a woman's reproductive period, as well as the mean birth interval of her children was both important traits in explaining variation in number of grandchildren. On the other hand, the year a woman was born, her own age when she married, age of her spouse when they married and age when she died turned out to be insignificant additional variables in explaining the variation in number of grandchildren a woman produced (Table 2).

Discussion

Women of high social status, or with more reliable access to resources, gave birth to more children than women of the lower social status in both populations. Previous studies from other parts of Scandinavia have shown that stable access to resources leads to higher fertility (Low, 1990; Low, 1991; Low & Clarke, 1991; Low, 1992; Low & Heinen, 1993; Clarke, 1993; Clarke & Low, 2001). We found that there was a difference between high and low status female reproductive success when comparing the two parishes Soknedal and Smøla. The results indicate that the ecological factor of fishing was important for the reproduction at Smøla, because women of both social status groups gave birth to more children than did women with similar status in the farming parish Soknedal (Table 1). The difference between the high and low status groups in Soknedal was significant, compared to the difference at Smøla. Thus, people of low status benefited relatively more than high status people by the extra resources from the sea at the coastal community. These results support our prediction.

The survival rate of children born in Smøla was significantly lower, probably due to accidents and diseases more common along the coast where travel and transport in Norway generally took place. The difference in numbers of grandchildren produced between the fishing and the farming parish among low status women was nevertheless in favour of Smøla (Table 1). Grandchildren are normally a more reliable measure of reproductive success than number of children born to a woman. In humans, a post-reproductive grandmother may also have significant impact on her fitness through her investment (Lahdenperä et al., 2004). The reproductive periods of the women from the two different populations were quite similar, but women in the coastal area had shorter life spans and produced more children per unit time than their sisters in the inland, supported by their significant lower mean birth interval. A negative correlation between fertility and longevity among women has been found among 153 different cultures (Thomas et al., 2000). This study showed that young mothers and/or mothers with high number of children bear the cost of shorter life spans. In a study of three pre-modern human populations in Finland, results show that a woman’s lifetime reproduction schedule and distribution of resources is crucial for her individual fitness (Käär & Jokela, 1998). They found that a female giving birth to four children at a young age might actually have a higher fitness than a female giving birth to six children at a higher age. This fact might not entirely be due to a shorter generation time.

As previously shown by Røskaft et al. (1992), a decline in fertility in both social groups was observed at Soknedal over the 200 year period. This decline was explained by an increase in population density, which caused a more limited access to resources for each individual. At Smøla this pattern was opposite, as number of grandchildren increased over the 200-year period. The fertility therefore seemed to be density dependent in the inland community, but not in the coastal community where fishing was an important factor. These differences might be a result of the access to fishing resources and, through the 18th century, better fishing tools and methods that improved catchment. On the other hand, women in Smøla died earlier than in Soknedal. This fact may have a similar explanation as the child mortality, as people were more exposed to accidents and diseases along the coast.

The age of first marriage of a woman was very important for her fertility both at Soknedal and at Smøla. However, the importance of age disappeared in the linear regression analysis, because other variables as number of children who became married were more important. The women at Smøla were younger than women at Soknedal when they first married. Despite of this, when controlling for their age of marriage and social status, the overall differences between the two populations in both fertility rate and length of fertile periods could still be explained by the differences in access to resources between the two parishes.

Acknowledgments

We are indebted to Bobbi S. Low and Alice L. Clarke for valuable discussions. The results are partly based on the master theses of Annelise Wara and Anne Elisabeth Djupvik.

References

Berg, G. F. 1981. *Smøla Bygdebok*. Trondheim, Norway (in Norwegian): Rune Forlag.

Betzig, L. 1986. *Despotism and Differential Reproduction: A Darwinian View of History*. New York: Aldine de Gruyter.

Bongaarts, J. 1978. A framework for analyzing the proximate determinants of fertility. *Population and Demographic Review*, 4, 105-132.

Boone, J. L. I. 1986. Parental investment and elite family structure in preindustrial states: A case study of late medieval-early modern Portuguese genealogies. *American Anthropologist*, 88, 859.

Boone, J. L. I. 1988. Parental investment, social subordination and population processes among the 15th and 16th century Portuguese nobility. In: *Human Reproductive Behaviour: A Darwinian Perspective* (Ed. by Betzig, L., Borgerhoff Mulder, M. & Turke, P.), pp. 201-219. Cambridge, U K: Cambridge University Press.

Buss, D. M. 1989. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12, 1-49.

Clarke, A. L. 1993. Women, resources, and dispersal in nineteenth-century Sweden. *Human Nature*, 4, 109-135.

Clarke, A. L. & Low, B. S. 2001. Testing evolutionary hypotheses with demographic data. *Population and Development Review*, 27, 633-+.

Clutton-Brock, T. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Covas, R., Doutrelant, C. & du Plessis, M. A. 2004. Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 271, 827-832.

Haukdal, J. 1971. *Busetnad og Folkeliv i Soknedal. Gard og grend. Bind 1-4*. Støren, Norway: Midtre Gauldal, (in Norwegian).

Helle, S., Käär, P. & Jokela, J. 2002. Human longevity and early reproduction in pre-industrial Sami populations. *Journal of Evolutionary Biology*, 15, 803-807.

Jones, N. B. & Marlowe, F. W. 2002. Selection for delayed maturity - Does it take 20 years to learn to hunt and gather? *Human Nature*, 13, 199-238.

Käär, P. & Jokela, J. 1998. Natural selection on age-specific fertilities in human females: Comparison of individual-level fitness measures. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 265, 2415-2420.

Käär, P., Jokela, J., Helle, T. & Kojola, I. 1996. Direct and correlative phenotypic selection on life-history traits in three pre-industrial human populations. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 263, 1475-1480.

Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature, London*, 428, 178-181.

Leivdal, N. T. & Fredly, K. 1997. *Smøla Bygdebok. Bind 5-6*. Kristiansund, Norway: Expresstrykkeriet og Reklameservice AS (in Norwegian).

Low, B. S. 1989. Human responses to environmental extremeness and uncertainty: A cross-cultural perspective. In: *Risk and Uncertainty in Tribal and Peasant Economics*, pp. 229-255: Weslow Press.

Low, B. S. 1990. Occupational status and reproductive behavior in nineteenth-century Sweden: Locknevi parish. *Social Biology*, 36, 83-101.

Low, B. S. 1991. Reproductive life in nineteenth century Sweden: An evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, 12, 411-448.

Low, B. S. 1992. Sex, coalitions, and politics in preindustrial societies. *Politics and the Life Sciences*, 9, 1-18.

Low, B. S. 2000. *Why Sex Matters: A Darwinian Look at Human Behavior*. Princeton: Princeton University Press.

Low, B. S. & Clarke, A. L. 1991. Family patterns in nineteenth-century Sweden: Impact of occupational status and landownership. *Journal of Family History*, 16, 117-138.

Low, B. S. & Clarke, A. L. 1992. Resources and the life course: Patterns through the demographic transition. *Ethology and Sociobiology*, 13, 463-494.

Low, B. S. & Heinen, J. T. 1993. Population, resources, and environment: implications of human behavioral ecology for conservation. *Population and Environment*, 15, 7-42.

Lummaa, V. 2001. Reproductive investment in pre-industrial humans: The consequences of offspring number, gender and survival. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 268, 1977-1983.

Mace, R. 2000. Evolutionary ecology of human life history. *Animal Behaviour*, 59, 1-10.

McGinley, M. A. & Charnov, E. L. 1988. Multiple resources and the optimal balance between size and number of offspring. *Evolutionary Ecology*, 2, 11-20.

Mech, L. D. 1987. At home with the arctic wolf. *National Geographic*, may 1987, 562-592.

Mosk, C. & Johansson, S. R. 1986. Income and mortality: evidence from modern Japan. *Population and Development Review*, 12, 415-40.

Mulder, V. B. 2000. Optimizing offspring: the quantity-quality tradeoff in agropastoral Kipsigis. *Evolution and Human Behavior*, 21, 391-410.

Roff, D. 2002. *Life History Evolution*. Sunderland MA: Sinauer.

Røskaft, E., Wara, A. & Viken, Å. 1992. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, 13, 443-461.

Smith, C. C. & Fretwell, S. D. 1974. The optimal balance between size and number of offspring. *American Naturalist*, 108, 499-506.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *The Quarterly Review of Biology*, 51, 3-47.

Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.

Teriokhin, A. T., Thomas, F., Budilova, E. V. & Guegan, J. F. 2003. The impact of environmental factors on human life-history evolution: an optimization modelling and data analysis study. *Evolutionary Ecology Research*, 4, 1199-1221.

Thomas, F., Teriokhin, A. T., Renaud, F., De Meeus, T. & Guegan, J. F. 2000. Human longevity at the cost of reproductive success: evidence from global data. *Journal of Evolutionary Biology*, 13, 409-414.

Tracer, D. P. 2002. Somatic versus reproductive energy allocation in Papua New Guinea: Life history theory and public health policy. *American Journal of Human Biology*, 14, 621-626.

Waynforth, D., Hurtado, A. M. & Hill, K. 1998. Environmentally contingent reproductive strategies in Mayan and Ache males. *Evolution and Human Behavior*, 19, 369-385.

Table 1. Number of children born and number of grandchildren produced for women of high (HS) and low (LS) statuses in the fishing parish Smøla and the farming parish Soknedal.

	Number of children born			Number of grandchildren		
	HS	LS		HS	LS	
parish	Mean ± SD (*n*)	Mean ± SD (*n*)	*P* =	Mean ± SD (*n*)	Mean ± SD (*n*)	*P* =
Smøla	5.9 ±2.7(435)	4.4 ±2.7 (191)	0.002	19.3 ±18.8 (409)	16.3 ±22.1 (176)	0.081
Soknedal	5.1 ±3.0 (717)	3.8 ±2.6 (406)	0.000	20.0 ±20.7 (687)	9.8 ±12.3 (378)	0.000
P =	ns	0.007		ns	0.000	

Table 2. Differences between life history variables among women in the fishing parish Smøla and the farming parish Soknedal.

Variables	Smøla Mean ± (SD)	Soknedal Mean ± SD)	$N_{Smøla}$	$N_{Soknedal}$	F	*P* =
Age of first marriage	26.5 ± (5.6)	28.1 ± (6.2)	652	1209	30.31	0.000
Age of spouse of first marriage	29.5 ± (6.5)	31.5 ± (7.1)	648	1210	35.43	0.000
Age of death	65.5 ± (17.0)	69.1 ± (16.9)	655	1187	19.17	0.000
Number of children born	5.0 ± (2.7)	4.6 ± (2.9)	705	1217	7.89	0.005
Number of children survived	3.5 ± (2.2)	3.9 ± (2.3)	699	1125	15.56	0.000
Number of children married	2.9 ± (2.0)	2.8 ± (1.9)	694	1085	0.95	ns
Reproductive period	11.7 ± (6.6)	11.8 ± (7.1)	668	1109	0.123	ns
Mean birth interval	3.0 ± (1.5)	3.7 ± (1.6)	496	790	12.26	0.000
Number of grandchildren	18.7 ± (20.2)	16.5 ± (18.9)	695	1175	5.69	0.017

Table 3. Partial correlations controlling for status between number of grandchildren and different life history variables among women in the fishing parish Smøla and the farming parish Soknedal ($df_{Smøla}$ = 374, $df_{Soknedal}$ = 756).

	Smøla		Soknedal	
Variables	r	*P* =	r	*P* =
Age of first marriage	-0.360	0.000	-0.418	0.000
Age of spouse of first marriage	-0.205	0.000	-0.235	0.000
Age of death	0.202	0.000	0.135	0.000
Number of children born	0.835	0.000	0.829	0.000
Number of children survived	0.860	0.000	0.842	0.000
Number of children married	0.924	0.000	0.921	0.000
Reproductive period	0.705	0.000	0.678	0.000
Mean birth interval	-0.213	0.000	-0.303	0.000
Year born	0.114	0.027	-0.073	0.045

Table 4. A stepwise linear regression analysis explaining the variation in number of grandchildren born in Smøla ($r^2 = 0.902$, df = 7, 365, p = 0.000) and Soknedal parishes ($r^2 = 0.899$, df = 7, 751, p = 0.000).

Source of variation	Smøla		Soknedal	
	t	*P* =	t	*P* =
Number of children married	32.4	0.000	48.1	0.000
Reproductive period	10.6	0.000	16.0	0.000
Mean birth interval	-8.79	0.000	-8.39	0.000
Age of death	-1.38	ns	-1.29	ns
Age at first marriage	-1.01	ns	1.14	ns
Age of spouse at first marriage	0.53	ns	0.62	ns
Year born	-0.30	ns	0.68	ns

Paper II

PAPER II

Birth rank, family size, sex and life history;

Data from a Norwegian human population during the period 1700-1900 CE

EIVIN RØSKAFT, ÅSLAUG VIKEN AND TERJE BONGARD

Department of Biology

Norwegian University of Science and Technology

Realfagbygget, N-7491 Trondheim, NORWAY

Abstract

Birth rank and family size may affect the life history of children. In the present study we considered the survival rate, the probabilities of becoming married and migration rate from the home parish in relation to status of mother, family size, sex of the children, birth rank, sex ratio of siblings, year of birth and age of the mother when giving birth for a Norwegian farming parish during the period 1700 - 1900. We found that the future reproductive value of boys was greatly affected by both family size and birth rank, in that boys from larger families and boys late in birth rank had a lower probability of getting married and a higher probability of migrating from the parish independent of social status of the mother. No such relations were found for girls. We conclude that a difference in the access to parental resources during childhood affected the life history of boys, but not that of girls.

INTRODUCTION

Trivers (1972; 1985) defined parental investment (PI) as any investment by the parents in an individual offspring that increases that offspring's chance of surviving (and hence reproductive success) at the cost of the parents ability to invest in other offspring. Resources are limited, and each offspring can not be regarded as unaffected by the other, which means that the investment in one offspring may decrease the investment in another.

A significant factor that influences the parental investment is the relationship between the reproductive value (RV) of the parents and their young (Fisher, 1930; Williams, 1966; Trivers, 1972; Pianka & Parker, 1975). A baby has a lower RV than e.g. an adolescent because there is higher probability that an infant will not reach reproductive age. At sexual maturity an individual reaches its maximum RV. At menopause a woman's RV becomes zero, although her investment in grandchildren is reported to be of significance for her fitness (Hawkes, 2003; Lahdenperä et al., 2004). Trivers (1972) suggested that parental investment increase with the parent's age, because of the continually decreasing RV caused by the dwindling probability of being able to produce another offspring (Williams, 1966; Pianka & Parker, 1975). Thus, parental investment in the firstborn is predicted to be low compared to investment in the lastborn. On the other hand, the RV of a child increases with its age. An early born offspring which reaches puberty first has a higher RV than that of its smaller sisters or brothers. For the parents it is therefore more beneficial to invest in their oldest children up to the time that their RV declines and the sibling's RV catch up (Fisher, 1930; Charlesworth & Leon, 1976; Schulman & Chapais, 1980). Another factor is that parents are usually inexperienced when they produce their first child. This may involve both a higher reproductive effort and a higher mortality rate of their young (Røskaft et al., 1983; McClureMartinez & Cohn, 1996; Hipfner & Gaston, 2002) . Thus, birth rank may be a very important determinant of life history traits.

In humans, birth rank has been shown to be important predictors of family dynamics, creative lives and personality (Sulloway, 1996). Birth rank and sex may therefore be strong predictors of family sentiments. For instance, middle born receive less parental investment (Salmon & Daly, 1998; Salmon, 1999) and may for this reason be less faithful towards their kin(Salmon, 2003) . The firstborn appear to be more status oriented (Davis, 1997), while parents most frequently seem to favour the last born child (Rohde et al., 2003).

In the present study we chose a life history approach to these questions (Stearns, 1992; Strassmann & Gillespie, 2002; Roff, 2002). We considered survival rate, probabilities of becoming married and migration probabilities in relation to status of mother, family size, sex of a child, birth rank, year of birth and age of the mother when giving birth to the child in question in a Norwegian farming parish during the period 1700-1900. The heritage system in this parish was patrilineal, i.e. the parental property was distributed among their sons.

We predicted that the firstborn child in a family would receive more parental resources than the laterborn. At the beginning of their reproductive life, the parents will have more resources to invest in each offspring than later on when the family size is bigger. This influences the amount of resources given to the offspring born later. Furthermore, the children in large families will receive fewer resources per individual (Trivers & Willard, 1973). Investment should be relatively higher in boys if parents possess large amounts of resources and relatively higher in girls when parents are poorer in resources. This implicates that parents should invest more in their firstborn boys than in laterborn sibling boys.

According to Trivers and Willard (1973) it will pay parents to terminate investment in an individual offspring if its chance of survival for some reason is estimated as low. On the other hand, Maynard Smith (1980) argued that this termination of parental investment would have to take place immediately after birth if it were to pay the parents to do so. Because boys are more expensive to rear (Clutton-Brock, 1991), and because boys have a higher value among the first-born children in a family, we predicted that: 1). There should be an increase in the infant mortality rate of boys in relation to birth rank. However, since girls are cheaper to produce, and because the value of a girl is independent of her birth rank, no such increase should exist for girls.

A relationship between access to resources and the reproductive success of men has been demonstrated in many human societies (Voland, 1984; Essock-Vitale, 1984; Betzig, 1986; Betzig & Turke, 1986; Boone, 1986; Boone, 1988; Hill & Kaplan, 1988; Low, 1990a; Low, 1990b; Voland, 1990; Voland & Engel, 1990; Røskaft et al., 1992). Thus, the access to resources by the parents should affect the RV of their sons. Because parents invest more in their firstborn sons, we predicted that: 2). The firstborn boys in general would have higher probabilities of getting married than the lastborn boys. Similarly, family size should generally affect the probability of sons to become married. However, because girls do not need to receive greater resources to enable them to get married, these relationships were not predicted for girls.

Among mammals, the male is normally the sex that migrates from its natal grounds while the opposite pattern is found in birds (Clark, 1978; Greenwood, 1980; Clutton-Brock et al., 1982;

Dobson, 1982; Clutton-Brock, 1989; Clarke, 1993; Clarke et al., 1997). In many human societies, however, it has been found that the females show higher emigration rates than the males (Koenig, 1989; Clarke & Low, 1992; Clarke, 1993). Therefore, in societies with patrilineal heritage it is a reasonable prediction that the girls will have a higher emigration rate than the boys. Furthermore, because a minimum amount of property is necessary to keep a family alive, it will be better to share the property among a few than between many sons. Thus, we predicted that: 3). Boys born early should tend to settle in their home parish at a higher frequency than their laterborn siblings. Furthermore, boys from large-sized families should show a greater tendency to migrate from home than boys from smaller-sized families. This pattern is not predicted for girls.

MATERIALS AND METHODS

The data were obtained from transcripts made from the parish registers and printed in books on local history compiled by Haukdal (1971). These provide demographic data for year of birth, marriage, death and the number of children born (equal to family of siblings, in the analyses described as family size). Also, data including the number of children who survived to adulthood, the number of children who became married, and either stayed or migrated from the parish were provided for most of the families (see Røskaft et al. (1992) for a more detailed description of the sources). The parish studied was Soknedal, a small parish in South Trøndelag County, in Central Norway, about 70 km south of Trondheim (61°N 10°E). Soknedal is an agricultural parish situated between 200 and 600 m above sea level close to higher mountains. The people in the parish were mostly farmers. The period 1700-1900 was selected for this study, because this was a period during which the social structure was relatively stable, and the quality of the data was good (see Røskaft et al. (1992) for further details about the choice of study area and period).

We analysed the data for 1217 married women, who altogether gave birth to 5601 children, of which 2873 were boys and 2728 girls. All children born were recorded, whether born alive or dead. During the study period, patrilineal heritage was the rule in Norway. Therefore we chose to analyse family size and birth rank of the children from the mother's point of view. Family size varied between 0 and 15, the most common family size being three to five children (Figure 1). For statistical analyses of birth rank and family size we pooled families with more than 10 children. In some of the analyses the relevant variables are converted into ratios in order to avoid pseudo-replication.

The survival rate is based on the survival to 20 years of age. For those who survived, we recorded the numbers who later became married or those who remained unmarried, those who migrated from (during 1850-1900 a substantial migration to North America took place) and those who stayed in the parish. For some of the children, no information of their marital status as adults was available. These are removed from the further analyses.

An inherent weakness in the kind of material of the present study is that the data have been collected at third hand. Nevertheless, since we only chose families for which full data sets were available, we feel confident that there are no systematically errors in the data. Minor errors are probably not significant either, due to the large sample size. We analysed the pooled data for the entire 200-year period, but in the multiple analyses birth year was used as an independent variable because Røskaft et al. (1992) found a decrease in family size during the study period.

Furthermore, Røskaft et al. (1992) found that differences in family size existed between different status groups in the society studied, indicating that the smaller-sized families were significantly more frequent among low-status people. Thus, social status was used as an independent variable in the multiple regression analyses. Landowners were considered high status, while landless people were coded as low status. Altogether, age of mother when giving birth to a certain child as well as sex ratio of the children in a family in some cases were of significant value, these variables were insignificant in the total regression analysis and were therefore removed from the final regression analyses.

RESULTS

Survival

Of the total number of children recorded as born (N = 5601), 81 % of the girls and 78 % of the boys survived to the age of 20 years (Table 1). Although there was no statistically significant difference in this survival pattern in relation to birth rank for neither of the sexes (Table 1), there was a significant linear tendency for the laterborn boys to have a higher mortality risk (Table 1).
In a multiple linear regression analysis we found that survival rate of boys in general significantly declined with family size and with increasing number of brothers among the siblings (Table 2). It was furthermore, as predicted, positively correlated with the mother's social status (Table 2). This was not the case for the girls where variation in survival rate was not explained by any of the variables tested for (Table 2). When sex of a child, as well as year of birth of a child were introduced into the linear regression analysis, only the status of the mother turned out to be a significant variable in explaining survival rate of a child (Table 3).

Marriage

Of the surviving children, 77 % of the girls and 79 % of the boys got married (Table 1). There was a significant decline in marriage probability with increasing birth rank for boys, but not for girls (Table 1).

The multiple linear regression analysis revealed that, for both sexes, the mother's social status turned out to be a significant predictor of the probability of getting married (Table 2). In addition, family size was a significant variable in explaining marriage probability for boys. This was not the case for girls (Table 2). Sex ratio in the family of siblings had no effect on marriage probabilities for either sex. When the sex of a child as well as year of birth were introduced into the linear regression analysis, the social status of the mother, birth rank as well as the year a child was born, turned out to be significant in explaining the probability of getting married (Table 3).

Migration

Of the surviving children, 24 % of the girls and 25 % of the boys migrated from the parish (Table 1). A positive relationship between birth rank and the probability of migration was found among boys, but not among girls (Table 1).

In the multiple linear regression analysis for both sexes, both girls and boys that remained in the parish came from smaller families with more high status mothers compared to those who migrated (Table 2). Family sex ratio on the other hand had no significant impact on migration rate for either boys or girls.

When the sex of a child and year of birth was included into the multiple regression analysis, the social status of the mother, the sex of the child, birth rank and year of birth all turned out to be of significant value for predicting migration of a child (Table 3).

DISCUSSION

Survival

We found a linear relationship between survival to adulthood and birth rank for boys, but not for girls. These findings support the prediction that boys compete more for resources within the family than girls do. The status of a mother, which correlates with resource access for her children, turned out to be the most important factor in explaining survival rates for her offspring. Boys who died also came from larger families with a sex ratio skewed towards boys, supporting the hypothesis that costs of producing boys are higher than that of producing girls. The evolutionary explanation for this is that reproductive success is more connected to the acquisition of resources and status for boys than for girls (Trivers & Willard, 1973; Clutton-Brock et al., 1983; Clutton-Brock et al., 1984) .

However, this is not a direct indication that the survival rate of children in larger families was lower than for smaller families. It could equally well indicate that the parents with large families were more willing to replace a child who died relatively soon after its death. When considering the relationship between birth rank and infant mortality, on the other hand, it could be argued that if a firstborn child died, family size could not have affected this child's death. The lastborn children who died during the first two years of their lives were born into larger families than those who survived. In such cases, differences in sibling competition within large and small families could explain the inequality of death rates among children (Mock & Parker, 1997) .

The above findings support studies from 1550 -1900 in France (Cohen, 1975), and in the 18th-19th century Germany (Voland, 1984), who found similar results. This pattern is well known also among animals (Rajpurohit & Sommer, 1991). Other studies have found that the infanticide pattern among high status people was biased towards girls in India, China and Western Europe (Kohl, 1978). Such a pattern of infanticide has resulted in a higher survival rate of boys (Dickemann, 1979). Johansson (1984) points at the fact that infant mortality rate for girls was higher than for boys in Sweden and in other European societies during the 19th century. These sex differences are probably related to a boy's higher potential of having descendants, and an evolutionary unconscious fitness enhancing behaviour among parents. A discrimination against girls is not necessarily a consequence of cultural bias favouring male children per se.

Marriage

We found that in this Central Norwegian agricultural parish, a significant relationship existed between the birth rank of boys and the probability of getting married. The oldest boys had a much higher probability of becoming married, as predicted. Occasionally, a farmer did split the farm between his two oldest sons. Further subdivision would probably have destroyed the income basis for all in the family. The youngest boys therefore, had to find some other way of surviving when adult. Landless men frequently married widows older than themselves, but who provided them with access to the necessary resources (Sundt, 1855; Riise, 1947; Drake, 1969; Haukdal, 1971; Visted & Stigum, 1971).This could be one way for the youngest boys in a family to survive. However, migration from the parish, or remaining unmarried, seemed to be the most actual alternatives for most of these boys.

Although the status of the mother was of significant importance, family size was a good predictor as to whether a boy would become married or not. This pattern was found for all the boys in the study regardless of birth rank. One explanation for why even the oldest boys in large families had a lower probability of becoming married was probably due to the fact that their parents were relatively young when they were born. When reaching adulthood, these boys had to wait longer to take over the farm, a circumstance that might have affected their attractiveness as husbands. Thus the life history of the boys was more dependent on access to resources during their childhood than it was for the girls, i.e. both birth rank and family size proved to be good life history predictors for boys. No relationship was found between birth rank or family size and the probability of girls becoming married.

Migration

As predicted, we found that there was a relationship between the migration rate and birth rank for boys, but not for girls. In addition, family size affected the migration rate for both boys and girls. Both the youngest boys and the boys from larger families tended to migrate at higher rates than both firstborn boys and boys from smaller families. Low and Clarke (1991) and Clarke and Low (1992) found similar results in that birth rank affected the migration rate of boys in Sweden during the mid-19th century. However, Towner (2001) did not find such relationships in Massachusetts during the 18th and 19th Century.

Dobson (1982) showed that the migration patterns of the males and females of monogamous animal species were the same, whereas among polygynous or promiscuous species the males tended to migrate at a higher rate. The human population in Soknedal was monogamous during the study period, but human cultures in general are more polygynous (Buss, 1994). Other studies made on industrialised societies have shown either that migration rates have been equal between the two sexes, or that the migration rate of men was higher than that of females (Spuhler & Clark, 1961; Shryock, 1964; Hollingsworth, 1970). On the other hand, in non-industrialised, agricultural societies a tendency has been found that women migrate at higher rates than men (Tindale, 1953; Wood et al., 1985). According to Greenwood (1980) migration rate of females will be higher in populations where males compete for available inherited resources.

To conclude; we have shown that family size and birth rank affect life history traits as survival rate, probability of getting married and migration rate among boys but not for girls. These results hold even when controlling for the mother's social status. We therefore conclude that costs of producing boys are higher than producing girls in terms of parental investment.

REFERENCES

Betzig, L. 1986. *Despotism and Differential Reproduction: A Darwinian View of History*. New York: Aldine de Gruyter.

Betzig, L. L. & Turke, P. W. 1986. Parental investment by sex on ifaluk. *Ethology and Sociobiology*, **7,** 29-37.

Boone, J. L. I. 1986. Parental investment and elite family structure in preindustrial states: A case study of late medieval-early modern Portuguese genealogies. *American Anthropologist*, **88,** 859-878.

Boone, J. L. I. 1988. Parental investment, social subordination and population processes among the 15th and 16th century Portuguese nobility. In: *Human Reproductive Behaviour: A Darwinian Perspective* (Ed. by Betzig, L. L., Borgerhoff Mulder, M. & Turke, P.), pp. 201-219. Cambridge, U K: Cambridge University Press.

Buss, D. M. 1994. *The Evolution of Desire. Strategies of Human Mating*. New York, USA: Basic Books.

Charlesworth, B. & Leon, J. A. 1976. The relation of reproductive effort to age. *American Naturalist*, **110,** 449-459.

Clark, A. B. 1978. Sex-ratio and local resource competition in a Prosimian primate. *Science*, **201,** 163-165.

Clarke, A. L. 1993. Women, Resources, and Dispersal in 19th-Century Sweden. *Human Nature-an Interdisciplinary Biosocial Perspective*, **4,** 109-135.

Clarke, A. L. & Low, B. S. 1992. Ecological Correlates of Human Dispersal in 19th-Century Sweden. *Animal Behaviour*, **44,** 677-693.

Clarke, A. L., Saether, B. E. & Roskaft, E. 1997. Sex biases in avian dispersal: A reappraisal. *Oikos*, **79,** 429-438.

Clutton-Brock, T. H. 1989. Female transfer and inbreeding avoidance in social mammals. *Nature, London*, **337,** 70-72.

Clutton-Brock, T. H. 1991. The Evolution of Parental Care. Princeton, New Jersey: Princeton University Press.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature, London*, **308,** 358-60.

Clutton-Brock, T. H., Guiness, F. E. & Albon, S. D. 1983. The cost of reproduction to red deer hinds. *Journal of Animal Ecology*, **52,** 367-383.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer, Behaviour and Ecology of two Sexes*. Edinburgh: Edinburgh University Press.

Cohen, J. E. 1975. Childhood mortality, family size and birth order in pre-industrial Europe. *Demography*, **12,** 35-55.

Davis, J. N. 1997. Birth order, sibship size, and status in modern Canada. *Human Nature*, **8,** 205-230.

Dickemann, M. 1979. Female infanticide, reproductive strategies, and social stratification: A preliminary model. In: *Evolutionary Biology and Human Social Behaviour. An Anthropological Perspective* (Ed. by Chagnon, N. A. & Irons, W. G.), pp. 321-367. North Scituate, MA: Duxbury Press.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30,** 1183-1192.

Drake, M. 1969. *Population and Society in Norway 1735-1865*. Cambridge: University Press.

Essock-Vitale, S. M. 1984. The reproductive success of wealthy Americans. *Ethology and Sociobiology*, **5,** 45-49.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28,** 1140-1162.

Haukdal, J. 1971. *Busetnad og Folkeliv i Soknedal. Gard og grend. Bind 1-4*. Støren, Norway: Midtre Gauldal, (in Norwegian).

Hawkes, K. 2003. Grandmothers and the evolution of human longevity. *American Journal of Human Biology*, **15,** 380-400.

Hill, K. & Kaplan, H. 1988. Tradeoffs in male and female reproductive strategies among the Ache: parts I and II. In: *Human Reproductive Behavior. A Darwinian Perspective* (Ed. by Betzig, L. L., Borgerhoff Mulder, M. & Turke, P.), pp. 277-305. New York: Cambridge University Press.

Hipfner, J. M. & Gaston, A. J. 2002. Growth of nestling Thick-billed Murres (Uria lomvia) in relation to parental experience and hatching date. *Auk*, **119,** 827-832.

Hollingsworth, T. H. 1970. Migration: A study based on Scottish experience between 1939 and 1964. In: *University of Glasgow, Social and Economic Studies Occional Papers*. Glasgow, Scotland.

Johansson, S. R. 1984. Deferred infanticide: Excess female mortality during childhood. In: *Infanticide: Comparative and Evolutionary Perspectives* (Ed. by Hausfater, G. & Hrdy, S. B.). New York: Aldine de Gruyter.

Koenig, W. D. 1989. Sex-biased dispersal in the contemporary United States. *Ethology and Sociobiology*, **10,** 263-278.

Kohl, M. 1978. *Infanticide and the Value of Life*. Prometheus Books.

Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature, London*, **428,** 178-181.

Low, B. S. 1990a. Marriage systems and pathogen stress in human societies. *American Zoologist*, **30,** 325-339.

Low, B. S. 1990b. Occupational Status, Landownership, and Reproductive Behaviour in 19th- Century Sweden: Tuna Parish. *American Anthropologist*, **92,** 457-468.

Low, B. S. & Clarke, A. L. 1991. Family Patterns in 19th-Century Sweden - Impact of Occupational-Status and Landownership. *Journal of Family History*, **16,** 117-138.

Maynard Smith, J. 1980. A new theory of sexual investment. *Behavioral Ecology and Sociobiology*, **7,** 247-251.

McClureMartinez, K. & Cohn, L. D. 1996. Adolescent and adult mothers' perceptions of hazardous situations for their children. *Journal of Adolescent Health*, **18,** 227-231.

Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford, New York, Tokyo: Oxford University Press.

Pianka, E. R. & Parker, W. S. 1975. Age-specific reproductive tactics. *American Naturalist*, **109,** 453-464.

Rajpurohit, L. S. & Sommer, V. 1991. Sex-Differences in Mortality among Langurs (Presbytis-Entellus) of Jodhpur, Rajasthan. *Folia Primatologica*, **56,** 17-27.

Riise, O. J. 1947. *Oppdalsboka. Historie og folkeminne. Bind 1*. Trondheim, Norway: Johan Grundt Tanums Forlag (in Norwegian).

Roff, D. A. 2002. *Life history evolution*. Sunderland, Mass.: Sinauer.

Rohde, P. A., Atzwanger, K., Butovskaya, M., Lampert, A., Mysterud, I., Sanchez-Andres, A. & Sulloway, F. J. 2003. Perceived parental favoritism, closeness to kin, and the rebel of the family: The effects of birth order and sex. *Evolution and Human Behavior*, **24,** 261-276.

Røskaft, E., Espmark, Y. & Järvi, T. 1983. Reproductive effort and breeding success in relation to age by the rook (*Corvus frugilegus*). *Ornis Scandinavica*, **14,** 169-174.

Røskaft, E., Wara, A. L. & Viken, Å. 1992. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, **13,** 443-461.

Salmon, C. 2003. Birth order and relationships. Family, friends, and sexual partners. *Human Nature*, **14,** 73-88.

Salmon, C. A. 1999. On the impact of sex and birth order on contact with kin. *Human Nature*, **10,** 183-197.

Salmon, C. A. & Daly, M. 1998. The impact of birth order on family sentiment: Middleborns are different. *Evolution and Human Behavior*, **19,** 299-312.

Schulman, S. R. & Chapais, B. 1980. Reproductive value and rank relations among Macaque sisters. *American Naturalist*, **115,** 580-593.

Shryock, H. S. 1964. Population mobility within the United States. Chicago: University of Chicago,Community and Family Study Center.

Spuhler, J. N. & Clark, P. J. 1961. Migration into the human breeding population of Ann Arbor, Michigan, 1900-1950. *Human Biology*, **33,** 223-236.

Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.

Strassmann, B. I. & Gillespie, B. 2002. Life-history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269,** 553-562.

Sulloway, F. J. 1996. *Born to Rebell, Birth Order, Family Dynamics, and Creative Lives*. London: Little, Brown and Company.

Sundt, E. 1855. *Om Dødeligheten i Norge. Om giftermål i Norge*. Oslo/Gjøvik: Christiania: Mallings Bogtrykkeri (in Norwegian).

Tindale, N. B. 1953. Tribal and intertribal marriage among Australian aborigines. *Human Biology*, **25,** 160-190.

Towner, M. C. 2001. Linking dispersal and resources in humans - Life history data from Oakham, Massachusetts (1750-1850). *Human Nature*, **12,** 321-349.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man1871-1971* (Ed. by Campbell, B. G.), pp. 136-179. Chicago: Aldine Publishing Co.

Trivers, R. L. 1985. *Social Evolution*. Menlo Park, California: Benjamin/Cummings Publishers Company.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179,** 90-92.

Visted, K. & Stigum, H. 1971. *Vår Gamle Bondekultur. Bind 1*. Oslo, Norway: Cappelens Forlag (in Norwegian).

Voland, E. 1984. Human sex-ratio manipulation: Historical data from a German parish. *Journal of Human Evolution*, **13,** 99-107.

Voland, E. 1990. Differential reproductive success with the Krummerhorn population (Germany, 18th and 19th centuries). *Behavioral Ecology and Sociobiology*, **26,** 65-72.

Voland, E. & Engel, C. 1990. Female choice in humans: A conditional mate selection strategy of the Krummerhörn women (Germany 1720-1874). *Ethology*, **84,** 144-154.

Williams, G. C. 1966. *Adaptations and Natural Selection*. Princeton: Princeton University Press.

Wood, J. W., Smouse, P. E. & Long, J. C. 1985. Sex-specific dispersal patterns in two human populations of highland New Guinea. *American Naturalist*, **125,** 747-768.

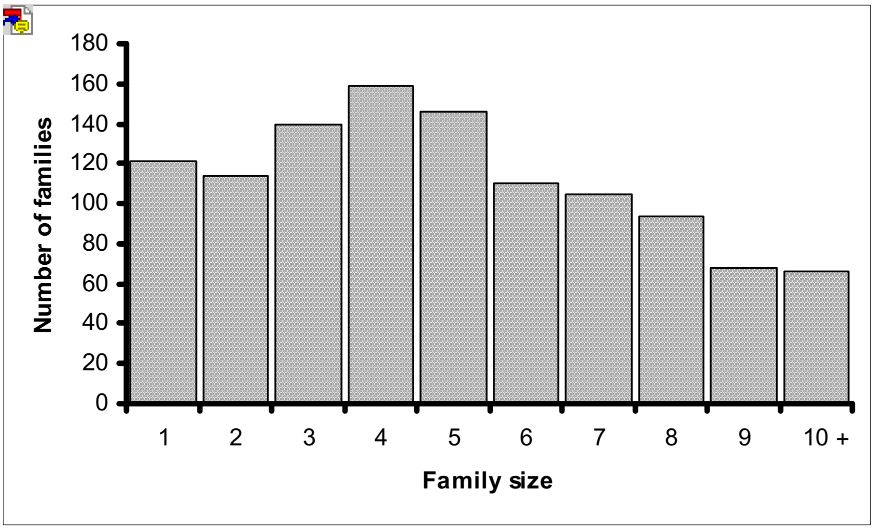


Figure 1

Numbers of different sized families (children) in Soknedal parish during the study period 1700-1900 CE.

Table 1

Differences in the percentages of some important life history variables in relation to birth rank of children from Soknedal.

Variable	% survived to adulthood		% married		% migration	
Sex	Girls (N)	Boys (N)	Girls (N)	Boys (N)	Girls (N)	Boys (N)
Birth rank						
1	80 (520)	77 (603)	79 (381)	86 (413)	20 (400)	18 (452)
2	79 (491)	81 (510)	77 (354)	81 (360)	21 (373)	20 (405)
3	82 (427)	81 (461)	81 (314)	80 (323)	26 (333)	24 (369)
4	83 (370)	78 (378)	74 (278)	77 (248)	23 (290)	27 (291)
5	79 (298)	73 (290)	76 (203)	71 (183)	30 (227)	26 (208)
6	82 (225)	77 (218)	74 (162)	76 (143)	30 (173)	31 (163)
7	82 (171)	77 (162)	78 (127)	72 (96)	24 (136)	36 (121)
8	80 (108)	79 (120)	74 (78)	78 (81)	22 (85)	37 (94)
9	82 (60)	73 (74)	89 (44)	77 (47)	19 (48)	43 (54)
10+	72 (58)	63 (57)	64 (39)	86 (28)	20 (40)	37 (35)
Mean	81 (2728)	78 (2873)	77 (1980)	79 (1922)	24 (2105)	25 (2192)
χ^2 (df)	5.6 (9)	19.4 (9)	13.5 (9)	26.9 (9)	16.5 (9)	51.3 (9)
p =	0.775	0.085	0.143	0.001	0.056	0.000
Linearity *p* =	0.184	0.034	0.156	0.000	0.122	0.000

Table 2

Linear regression analyses of the probabilities of a boy or a girl surviving to 20 years of age, getting married, and probability of migrating as dependent variables. Social status of mother, family size (siblings only), and sex ratio of the family of siblings were entered into the analyses as independent variables.

	Boys			Girls		
	Survival to adulthood	Marriage	Migration	Survival to adulthood	Marriage	Migration
r^2	0.034	0.023	0.056	0.003	0.046	0.031
F	11.7	7.3	18.8	1.1	14.5	9.8
p =	0.000	0.000	0.000	0.365	0.000	0.000
N =	1009	949	960	967	900	911
p value of independent variables: (- indicate negative relation)						
Status of mother	0.043	- 0.000	0.000	- 0.096	- 0.000	0.000
Family size	- 0.000	- 0.000	0.000	- 0.407	0.970	0.009
Sex ratio	- 0.000	- 0.332	0.368	- 0.877	- 0.070	0.442

Table 3

Linear regression analyses of the probabilities of a child surviving to 20 years of age, getting married, and the degree of migration as dependent variables. Social status of their mother, family size, sex of child, birth rank, sex ratio of the family of siblings, year of birth and age of the mother at birth were entered as independent variables.

	Survival to adulthood	Marriage	Migration
r^2	0.005	0.058	0.026
F	2.73	31.32	14.94
df =	7	7	7
N =	2800	2783	2794
p =	0.018	0.000	0.000
p value of independent variables: (- indicate negative relation)			
Status of mother	- 0.030	- 0.000	0.022
Family size	- 0.615	0.205	0.204
Sex of child	0.177	- 0.570	0.000
Birth rank	- 0.217	- 0.006	0.002
Year of birth	0.126	- 0.000	0.007

Paper III

PAPER III

Optimal Birth Intervals, Life History and Sex Ratios at Birth

A Study of Two Human Populations in Central Norway 1700-1900 CE.

TERJE BONGARD AND EIVIN RØSKAFT

Department of Biology, Norwegian University of Science and Technology, Realfagbygget N-7491 Trondheim, NORWAY

Abstract

Life history data from 1700-1900 were used as a basis for analyses of optimal birth intervals related to life history variables of children among women from two parishes in Central Norway. The coastal parish Smøla had access to year-round fishing and by that a more stable resource situation than the inland parish Soknedal. There was no support for longer birth intervals between the births of two boys compared to other sex combinations of children. There were significant differences in birth interval between high and low status women in both parishes. Also the poorer parish of Soknedal had longer birth intervals than Smøla for both status groups. The survival rate increased significantly when birth intervals exceeded 2 years, both for a child and its next sibling. The optimal birth interval seems to be close to three years. In a multilinear regression analysis, the number of children of mother was the most important variable in explaining the variation in birth interval. Laterborn children had longer birth intervals.

INTRODUCTION

Humans have one of the most intense and longest durations of parental care among mammals by investing in overlapping offspring over several years, leading to high costs for the parents (Daly & Wilson, 1983). Therefore a reliable access to resources is important for a successful reproduction for both men and women (Borgerhoff Mulder, 1987; Borgerhoff Mulder, 1988; Røskaft et al., 1992; Bereczkei & Csanaky, 1996). Life-history theory argues that reproduction has a cost in the sense that it extracts resources from a limited pool of total reproductive investment (Williams, 1966; Trivers, 1972; Calow, 1979; Clutton-Brock, 1991; Krebs & Davies, 1991; Roff, 1992; Stearns, 1992; Roff, 2002). Therefore, there is a trade-off between current reproductive effort and expected post-breeding survival and future reproduction. Costs of reproduction can be measured as an increase in mortality risk, e.g. Madsen et al. (1992) or reduced female condition and future fecundity, e.g. Boyd et al. (1995). In iteroparous species, natural selection will therefore benefit those individuals that balance current and future reproduction to give the optimal number of lifetime offspring (Williams, 1966). Start of reproduction is depending on each individual’s genetic predisposition and current state as a result of environmental conditions. If reproduction starts too early in life, it may reduce both the survival of the individual, offspring survival and future reproductive success. Costs of rearing offspring may therefore be greater for inexperienced adults, and it may affect low status individuals more than high status individuals (Røskaft et al., 1983; Clutton-Brock et al., 1984; Pyle et al., 1997). The quality of the young is dependent on the quality of the parents. Male offspring are frequently more expensive to produce and rear than female offspring in dimorphic mammal species (Trivers & Willard, 1973; Clutton-Brock et al., 1986; Wolff, 1988; Clutton-Brock, 1991). Studies have shown that male offspring in general are more resource demanding during pregnancy, are carried slightly longer *in utero*, and are bigger at birth (Djazeyery, 1993; Thompson et al., 1994; Guihard Costa et al., 1997). Furthermore, male offspring nurse larger amounts of milk and are weaned later than female offspring (Clutton-Brock et al., 1981; Lee & Moss, 1986; Le Boeuf et al., 1989; Berube et al., 1996). If parents invest equally in the offspring regardless of sex (Fisher, 1930), male offspring might therefore suffer a higher mortality rate (Røskaft & Slagsvold, 1985; Slagsvold et al., 1986).

The increased costs by producing males may result in a longer recovering period and a longer birth interval (Clark et al., 1990; Kojola & Eloranta, 1989). For instance, in humans there are some indications that birth intervals varies in relation to the sex of the offspring (El Shalakani, 1989; Low, 1991; Mace & Sear, 1997), and normally a short interbirth period is followed by a much longer one (Wilkinson et al., 1989). However, results are not conclusive, and production of sons may not necessarily be more expensive than production of daughters, unless when producing twins (Lummaa, 2001). Trivers and Willard (1973) argued that in a polygynous species, females in relatively good condition or of high social status should be more likely to have sons. Vice versa, females in relatively poor condition or of low social status should have daughters (Clutton-Brock et al., 1981; Betzig & Turke, 1986; Arnbom et al., 1994). However, if older females of higher status are in poorer condition than younger ones, older females should more likely give birth to daughters.

In mammals, variation in reproductive traits are usually easiest to detect among females, since they usually invest more than males both during and after pregnancy (Clutton-Brock, 1991; Alcock, 1998). We tested the following predictions on women from Soknedal and Smøla, Central Norway, during the period 1700-1900 CE:

1) If costs of producing a son is higher than producing a daughter we predicted that birth interval after having a son should be longer than after having a daughter.
2) Because resources and ecological conditions are important factors for a woman when reproducing, we predicted that high status women should have shorter birth intervals than low status women. In addition we predicted that women living in a rich and resource stable parish should have shorter birth intervals than women in a resource-unstable parish.
3) If there is an optimal birth interval, we predicted that children born with shorter birth intervals should have a lower survival rate.

MATERIAL AND METHODS

We collected data from two parishes in Central Norway during the years 1700 – 1900 CE. The first area, Soknedal (435 km^2) is an inland parish in South Trøndelag County (63^0 N, 10^0 E). The farms in Soknedal were spread in both flat and steep terrain at an altitude of 200 to 600 meters. In 1701 about 700 persons lived in Soknedal, in 1801 the population counted 1367 persons while in 1900 the number had increased to 2042 persons. Analyses show that the soil offered good conditions for the most common cultivated plants, and the soil was also resistant against drought. Nevertheless, the tough climate and the height above sea level naturally limited which plant species to grow successfully (Haukdal, 1971). During the study period the population in Soknedal was uniform; a typical peasant community where almost everybody in the parish worked as farmers, and made a living from the soil. The main production was fodder to keep domestic animals, like cattle and sheep (Haukdal, 1971). The agriculture was to a small degree supplemented with hunting and inland fishing (Try, 1979).

The second area, Smøla (275 km^2) is a group of islands in Møre and Romsdal County (63^0 N, 8^0 E). In 1701 about 600 persons lived on Smøla, this number increased to 1166 persons in 1801 and in 1865 there were 2366 persons living on the islands (Berg, 1981). The soil is mostly marshy and shallow, but in some areas agriculture is possible. Smøla's geographical location gave the population access to year round fishing, which still is the main livelihood. The majority of the population combined fishing with farming. However, fishing was without doubt the most important factor in order to make a living. Around 1650 only 25 % of the Smøla population could survive solely by farming, but in 1850 this proportion had increased to 55 % (Berg, 1981). Farming and fishing as the two main bases of existence at Smøla supplemented each other, and acted as food insurances if one of them should fail.

Parish books from Smøla and Soknedal (Haukdal, 1971; Berg, 1981; Leivdal & Fredly, 1997) contain life-history information about reproductive success and social status for both men and women (Røskaft et al., 1992). From these books married individuals with complete information about their life history were registered for further statistical analyses. Unmarried men and women were excluded, because of insufficient data. Men or women who emigrated from the parish during their reproductive period were also excluded. Among these persons there was probably a surplus of poor, low status persons. Individuals were registered with information about sex, year of birth, age of death, and age of marriage. Their children were recorded with information about parental age, sex, birth order, age of death, marital status (married/unmarried) and whether the child emigrated out of the parish or not. Families were classified as either high or low status (Røskaft et al., 1992). The high status group contained persons who owned the farmland they were using, or tenant farmers who did not, but had the right to use the farmland through a leasing contract. The low status group contained cottiers and lodgers. Cottiers were persons who used a house, with or without farmland, in exchange for an agreed amount of working days on the landowner's farm. Lodgers were persons who rented just a bed or a room, often on farms. They were usually craftsmen (e.g. shoemakers, blacksmiths), construction workers, seasonal labour workers at farms, newly married couples waiting to get their own place to stay, or sick or old persons.

The data from Soknedal consisted of 1123 married women; 717 of these were high status women and 406 were low status women. High status women gave birth to 3648 children; 1858 boys and 1790 girls, while low status women gave birth to 1499 children; 785 boys and 714 girls. On Smøla, 626 married women were registered; 435 were high status women and 191 were low status women. High status women gave birth to 2211 children; 1104 boys and 1107 girls. Low status women gave birth to 819 children; 409 boys and 410 girls. All statistical tests are two-tailed.

RESULTS

As expected, there was a significant correlation between mean birth interval and number of children born to a woman (Pearson correlation, r = -0.367, N = 2580, p = 0.000). The shorter the birth interval, the more siblings a child was likely to have. There were no differences in birth interval between the various combinations of sibling sexes (Table 1), neither when controlling for status nor parish. Sex of a child was therefore not considered in the further analyses. There were, on the other hand, significant differences in birth interval between high and low status women in both parishes (Table 2). The difference was larger in Soknedal than in Smøla. Significant differences were also found between the two parishes, in that the poorer parish of Soknedal had longer birth intervals for both status groups (Table 2). The survival rate increased significantly when birth intervals exceeded 2 years, both for a child and its next sibling (Table 3). The low survival rate for 0 years birth interval was due to the fact that one or both twins died at an early age. Twins are randomly presented as first- or secondborn in the two columns, hence the similarity in survival rate (Table 3).

A closer look at the differences between the status groups in Soknedal indicated that the mean birth interval for a child that survived was 0.6 years longer for both high and low status mothers (Table 4). The equivalent time difference for the next sibling was less pronounced, being 0.3 years for low status, and only about 0.1 year for high status mothers (Table 4). All differences were statistically significant.

An optimal birth rate for Soknedal therefore seems to be slightly over three years for low status mothers, and slightly below three years for high status mothers. No such difference was found at Smøla.

We carried out a multilinear regression analysis and entered as independent variables the number of children of mother, the child's number in birth order, survival rate, status of mother**,** parish, sex of next sibling and survival rate of next sibling (Table 5). The number of children of a mother was the most important variable in explaining the variation in birth interval. A child's number in birth order explained a substantial part of the variation, whereas laterborn children had longer birth intervals. As shown above (Table 3 and 4), survival rate turned out to be a significant factor in explaining birth interval variance. Also status of mother was a significant factor in the linear regression analysis of birth interval variance (Table 5). The other variables had no significant effect on the variation in birth order.

DISCUSSION

We have shown that the optimal birth interval was connected to the resource situation for women at the two parishes examined. Better access to resources led to shorter birth intervals, and consequently a higher number of descendants (Røskaft, submitted). These findings are in accordance with previous studies on the relationship between short birth spacing and high child mortality in humans (Low, 1991; Wilkinson et al., 1989). The difference in the resource situation between Soknedal and Smøla gave, as predicted, significant differences in mean birth intervals. Also, mean birth interval in relation to survival rates between children born to high and low status mothers were different at Soknedal, but not at Smøla. An optimal birth interval is presumably the result of a trade-off between the opposite forces of resource depletion and number of children born within a woman's reproductive period. The low survival rate for one year birth interval for the first sibling was probably connected to stillborn and infant death. The lower survival rate of a child growing up with a one year older sibling was probably due to the effects from the resource competition. When a birth interval between two children was very short, costs in terms of high child mortality were recorded, which indicate that women with very short spacing between children did not manage to give the necessary care to both. This difference was dependent of the mother’s social status. High status mothers had the opportunity to, and indeed got, more children (Røskaft, submitted).

The linear regression analysis showed that the most important variables in explaining birth interval variations were number of siblings and the child’s number in birth order. The later in a family of siblings a child was born, the longer the birth interval lasted. The explanations for this might be lower fertility with increasing age, or resource impoverishment from a larger family of siblings.

We found no differences in birth intervals between any combinations of sibling sexes, and sex as independent variable had no influence on the variation in birth intervals. Low (1991) found from her study in the nineteenth century Sweden that a boy-boy birth interval was significantly longer than all other sex combinations. She suggested higher costs related to production of boys. However, her data was recorded in months. The information on birth intervals from the parish books used in the present study was recorded in years, and the data from Soknedal and Smøla might not be precise enough to reveal any minor difference. Lummaa (2001) also experienced difficulties in finding any effects on the mother after the production of a single son in Finland, but found strong effects when producing son twins.

To conclude, we found no support for the prediction that any possible higher cost in producing a son would affect birth intervals. The prediction that high status women should have shorter birth intervals was supported. In addition, the dissimilarity in birth intervals found between Soknedal and Smøla parishes was predicted on the background of the more unstable resource situation at Soknedal. Finally, as predicted, we found a lower survival rate for children born with shorter birth intervals.

REFERENCES

Alcock, J. 1998. *Animal Behavior: An Evolutionary Approach*. Sunderland, Massachusetts: Sinauer.

Arnbom, T., Fedak, M. A. & Rothery, P. 1994. Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. *Behavioral Ecology and Sociobiology*, **35,** 373-378.

Bereczkei, T. & Csanaky, A. 1996. Mate choice, marital success, and reproduction in a modern society. *Ethology and Sociobiology*, **17,** 17-35.

Berg, G. F. 1981. *Smøla Bygdebok. Bind 1-4*. Trondheim, Norway: Rune Forlag (in Norwegian).

Berube, C. H., Festa-Bianchet, M. & Jorgenson, J. T. 1996. Reproductive costs of sons and daughters in Rocky Mountain big horn sheep. *Behavioral Ecology*, **7,** 60-68.

Betzig, L. L. & Turke, P. W. 1986. Parental investment by sex on ifaluk. *Ethology and Sociobiology*, **7,** 29-37.

Borgerhoff Mulder, M. 1987. Resources and reproductive success in women with an example from the Kipsigis of Kenya. *Journal of Zoology, London*, **213,** 489-505.

Borgerhoff Mulder, M. 1988. Reproductive success in three Kipsigis cohorts. In: *Reproductive Success* (Ed. by Clutton-Brock, T. H.), pp. 419-435. Chicago: Chicago University Press.

Boyd, I. L., Croxall, J. P., Lunn, N. J. & Reid, K. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology*, **64**.

Calow, P. 1979. The cost of reproduction; A physiological approach. *Biological Reviews of the Cambridge Philosophical Society*, **54,** 23-40.

Clark, M. M., Bone, S. & Galef, B. G. 1990. Evidence of sex-biased postnatal maternal investment by Mongolian gerbils. *Animal Behavior*, **39,** 735-744.

Clutton-Brock, T. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Clutton-Brock, T., Albon, S. D. & Guinness, F. E. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature, London*, **289,** 487-489.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature, London*, **308,** 358-60.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1986. Great expectations: Dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour*, **34,** 460-471.

Daly, M. & Wilson, M. 1983. *Sex, Evolution and Behaviour*. Boston: Willard Grant.

Djazeyery, A. 1993. Nutritional-status of neonates at birth in Ardebil, Iran. *Ecology of Food and Nutrition*, **29,** 207-217.

El Shalakani, M. H. 1989. Estimation of fertility and mortality of the Kuwaiti population. 21: . *Journal of Biosocial Science*, **21,** 433-442.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Guihard Costa, A. M., Grange, G., Larroche, J. C. & Papiernik, E. 1997. Sexual differences in anthropometric measurements in French newborns. Vol.72, Nr.3: . *Biology of the Neonate*, **72,** 156-164.

Haukdal, J. 1971. *Busetnad og Folkeliv i Soknedal. Gard og grend. Bind 1-4*. Støren, Norway: Midtre Gauldal, (in Norwegian).

Kojola, I. & Eloranta, E. 1989. Influences of maternal body weight, age, and parity on sex ratio in semidomesticated reindeer. *Evolution*, **43,** 1331-1336.

Krebs, J. R. & Davies, N. B. 1991. Behavioural Ecology. An Evolutionary Approach. Oxford, England: Blackwell Scientific Publications.

Le Boeuf, B. J., Condit, R. & Reiter, J. 1989. Parental investment and the secondary sex ratio in northern elephant seals. *Behavioral Ecology and Sociobiology*, **25,** 109-117.

Lee, P. C. & Moss, C. J. 1986. Early maternal investment in male and female African elephant calves. 18: . *Behavioral Ecology and Sociobiology*, **18,** 353-361.

Leivdal, N. T. & Fredly, K. 1997. *Smøla Bygdebok. Bind 5-6*. Kristiansund, Norway: Expresstrykkeriet og Reklameservice AS (in Norwegian).

Low, B. S. 1991. Reproductive life in nineteenth century Sweden: An evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, **12,** 411-448.

Lummaa, V. 2001. Reproductive investment in pre-industrial humans: the consequences of offspring number, gender and survival. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268,** 1977-1983.

Mace, R. & Sear, R. 1997. Birth interval and the sex of children in a traditional African population: An evolutionary analysis. *Journal of Biosocial Science*, **29,** 499-507.

Madsen, T. & Shine, R. 1992. Determinants of reproductive success in female adders, *Vipera berus*. *Oecologia*, **92,** 40-47.

Pyle, P., Nur, N., Sydeman, W. J. & Emslie, S. D. 1997. Cost of reproduction and the evolution of deferred breeding in the western gull. *Behavioral Ecology*, **8,** 140-147.

Roff, D. A. 1992. *The Evolution of Life Histories*. New York: Chapmann and Hall.

Roff, D. A. 2002. *Life history evolution*. Sunderland, Mass.: Sinauer.

Røskaft, E., Bongard, T., Viken, Å. Rosenqvist, G. 2005. Ecological conditions and life history variations in two Norwegian human populations during the period 1700-1900 CE. *Submitted to Journal of Evolutionary Biology.*

Røskaft, E., Espmark, Y. & Järvi, T. 1983. Reproductive effort and breeding success in relation to age by the rook (*Corvus frugilegus*). *Ornis Scandinavica*, **14,** 169-174.

Røskaft, E. & Slagsvold, T. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. *Journal of Animal Ecology*, **54,** 261-266.

Røskaft, E., Wara, A. & Viken, Å. 1992. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, **13,** 443-461.

Slagsvold, T., Røskaft, E. & Engen, S. 1986. Sex-ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care; Fisher's theory applied to birds. *Ornis Scandinavica*, **17,** 117-125.

Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.

Thompson, J. M. D., Mitchell, E. A. & Borman, B. 1994. Sex specific birthweight percentiles by gestational age for New Zeeland. *New Zeeland Medical Journal*, **107,** 1-3.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man1871-1971* (Ed. by Campbell, B. G.), pp. 136-179. Chicago: Aldine Publishing Co.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179,** 90-92.

Try, H. 1979. *To Kulturer en Stat 1851-1884. Bind 11: Norges Historie*. Oslo, Norway: J.W. Cappelens Forlag A.S (in Norwegian).

Wilkinson, G. S., Nagoshi, C. T., Johnson, R. C. & Honbo, A. M. 1989. Perinatal mortality and sex ratios in Hawaii. *Ethology and Sociobiology*, **10,** 435-447.

Williams, G. C. 1966. *Adaptations and Natural Selection*. Princeton: Princeton University Press.

Wolff, J. O. 1988. Maternal investment and sex ratio adjustment in american bison calves. *Behavioral Ecology and Sociobiology*, **23,** 127-133.

Table 1. Birth intervals in years for women in Soknedal and Smøla (± SD) in relation to various sex combinations of children. High and low status groups are pooled. Repeated measurements; the same woman is likely to appear in several groups (one-way ANOVA test, F = 1.10, p = 0.347,).

Birth order	Birth interval	SD	N
Boy-boy	2.9	1.8	1806
Boy-girl	2.9	1.7	1871
Girl-girl	2.9	1.7	1707
Girl-boy	3.0	1.6	1861
Total	2.9	1.7	7245

Table 2. Mean birth intervals for high and low status women within and between Soknedal and Smøla parishes (±SD, p is the significance of a one-way ANOVA test).

	High status	Low status	N_{total}	F	p
Soknedal	2.9 ± 1.6	3.2 ± 1.9	4453	34.5	0.000
Smøla	2.8 ± 1.6	3.0 ± 2.3	2456	6.30	0.012
F	5.40	5.46			
p =	0.020	0.020			

Table 3. Child survival rates in relation to different birth intervals for a child and its next sibling. (Data from both Soknedal and Smøla).

Birth interval	Survived to adulthood %	N_{total}	Next sibling survived to adulthood %	N_{total}
0 year (twins)	60.0	140	63.1	141
1 year	43.5	575	68.1	546
2 years	71.0	2152	73.6	2157
3 years	81.4	2076	77.6	2099
4 years	82.1	758	75.5	777
5 years or more	83.0	643	76.7	656
Total	74.2	6344	74.8	6376
$P_{chi\text{-}square\ test}$ =		0.000		0.000
$P_{linearity}$ =		0.000		0.000

Table 4. Mean birth intervals between a child and its next sibling in relation to whether they died before, or survived to, the age of 20 (Only data from Soknedal is entered, p is the significance of a one-way ANOVA test).

	Low status	N	High status	N
Child:				
Dead before the age of 20	2.7	254	2.4	706
Survived to 20	3.3	949	3.0	2554
F =	18.9		93.0	
p =	0.000		0.000	
Next sibling:				
Dead before the age of 20	3.0	237	2.8	688
Survived to 20	3.3	966	2.9	2572
F =	5.41		4.26	
p =	0.020		0.039	

Table 5. Linear regression analysis of birth interval between a child and its next sibling as the dependent variable. Number of children of mother, the child's number in birth order, survival rate, status of mother, parish, sex of next sibling and survival rate of next sibling were entered as independent variables ($r^2 = 0.106$, F = 87.1, df =7, N = 5162, p = 0.000).

	t =	p =
Number of children of mother	-23.2	0.000
The child's number in birth order	10.6	0.000
Survival rate	3.4	0.001
Status of mother	2.5	0.012
Parish	-1.2	n.s
Sex of next sibling	1.1	n.s
Survival rate of next sibling	0.5	n.s

Paper IV

PAPER IV

Short communication:

Optimal genetic similarity in a Norwegian population from 1700-1900 CE

TERJE BONGARD, GUNILLA ROSENQVIST AND EIVIN RØSKAFT

Norwegian University of Science and Technology (NTNU), Department of Biology,

Realfagbygget, N-7491 Trondheim, NORWAY

1. INTRODUCTION

Sterility and reduced fitness may be the consequences of breeding between different species (Ross et al., 1997). Inbreeding within a species may also reduce reproductive success of an individual. Westermarck (1891) suggested that genotypic similarity between mates might be advantageous, as long as the similarities were fairly moderate (Westermarck, 1891). A balance between inbreeding and outbreeding may be the most evolutionary profitable mating strategy (Lynch, 1991; Kruger et al., 2001). The frequency of altruistic behaviour will elevate if individuals interacting are related (Breden & Wade, 1991). On the other hand, inbreeding depression has been detected in many plant and animal species (Vantreuren et al., 1993). Inbreeding in human populations may differ due to environmental situations, migration, geographic factors, societal, cultural or economic factors (Hussain, 1999; Alper et al., 2004; Fuster & Colantonio, 2004; Hussain & Bittles, 1998; Fuster & Colantonio, 2003). Although fertility might be high in some consanguineous unions there are also reports describing hereditary disorders, congenital malformations, mental retardation and recessively transmitted diseases (Zlotogora, 2002; Sureender et al., 2003; Jaber et al., 2004; Koochmeshgi et al., 2002; Tuncbilek, 2001).

The aim of this study is to test if there is a tendency to avoid consanguinity between spouses when choosing a mate. We also test if the reproductive success of a marriage between spouses with a slight relationship is higher than both the reproductive success between mates of no relation and in a couple where mates are more closely related. The performed mate choice is predicted to adjust to these conditions in order to optimise the number of offspring in that mate choice should be influenced by the coefficient of relatedness. The variables recorded were number of children born to a woman, both boys and girls, and the number of children that reached adulthood.

2. MATERIAL AND METHODS

Data was collected from local history books describing a population in Soknedal, Central Norway (Haukdal, 1971). The books contain information about the families living in Soknedal during the period 1700-1900. The family histories (N = 3797) provide demographic data such as year of birth, marriage, number of children born, number of surviving children and death. High and low status groups are defined as in Røskaft et al. (1992). Data on marriages include 735 cases, and there were on average 4 marriages per year in the population as a whole, giving each woman 40 chances of getting married. This number is estimated from the age of marrying women, in that nearly all married before 30 years of age. This means that they had been available on the marriage market for about ten years. Therefore, a total of 40 marriages occurred during their mating period, and the same number of potential partners were consequently available.

Through generations, some genetic similarity in the population is expected because of geographical isolation. Marriages between persons who had ancestors in Soknedal for at least two generations were therefore given a coefficient of relatedness $r = 0.01$. Outbred couples, i.e. those who married a person from outside the parish, were given $r = 0.00$. Marriage between uncle and niece were given $r = 0.25$ ($N = 7$), cousins $r = 0.12$ ($N = 21$), second cousins $r = 0.03$ ($N = 34$) and marriage between a person and mother or father's cousin is given $r = 0.06$ ($N = 7$). Only first marriage of women were considered.

3. RESULTS

The estimate of how many men who were related to a woman closer than a third cousin in the population a girl could choose her husband from, gave a total of 15 relatives. Including third cousins this number is approaching 40 possible relatives available. For a high status girl in Soknedal the chance of getting married to a relative was therefore 27%. For a low status girl this probability was 17%. A random mating in the population would give a total of 24% marriages between relatives. The actual numbers for the high status group were 9 % and for the low status group under 6 % ($p < 0.001$). The hypothesis of inbreeding avoidance is therefore supported in this material.

Low status people were more often married to non-locals (43%), compared to the high status group (28%). The reason for this is probably that the low status group migrated more frequently than people with better outcome (Røskaft, submitted).

There were differences between birth numbers, survival rate, reproductive period and year of first birth, but none of them were statistically significant. There were no statistical difference between non-locally married, locally married or consanguineous women in numbers of children they gave birth to (ANOVA tests, n.s.: High status; local = 4.7 ± 3.0 ($N = 385$), non-local = 4.5 ± 3.0 ($N = 165$), consanguineous = 4.5 ± 3.0 ($N = 57$), low status; local = 3.5 ± 2.6 ($N = 65$) non-local = 3.8 ± 2.8 ($N = 56$), consanguineous = 3.4 ± 1.3 ($N = 7$).

There were no significant differences in the number of surviving offspring between the locally married and consanguineous married women (ANOVA tests, n.s.: High status, locally married = 4.1 ± 2.3, $N = 355$; high status, consanguineous married = 3.9 ± 2.3, $N = 53$). There was a small, but not significant lower number of surviving children among the consanguineous married women (ANOVA tests, n.s.: Low status, non-locally married = 3.3 ± 2.3, N = 51; low status, locally married = 3.2 ± 2.2, N = 55; low status, consanguineous married = 3.0 ± 1.4, N = 7). Differences in reproductive periods and age when giving birth for the first time results were neither statistically significant.

4. DISCUSSION

The inbreeding avoidance between related individuals in this parish is significant. However, the results show no statistically significant differences in fertility between the three groups called non-locally, consanguineous and locally married for either of the status groups.

In small communities like Soknedal, a probable assumption is that people would know the family relations between every individual, not only for mating decisions, but also for reciprocal deeds within families. It is therefore likely that mating decisions were taken on the basis of knowledge of kinship. Our prediction on inbreeding avoidance is therefore supported, despite the fact that we were unable to find any fitness effects of marriage between close relatives in Soknedal.

There is extensive evidence for assortative mating and homogamy in human mate choice (Pediaditakis, 1998). Both friends and spouses are chosen partly on the basis of genetic similarities, and random couples who were sexually interacting, but did not have children, were less similar to each other than couples who produced children (Rushton, 1989).

In all human cultures there are some prohibitions against marriages between parent-offspring and siblings (Jacquard, 1975). Prohibitions on marrying more distant relatives, as e.g. cousins, are also frequently found. The explanation for the incest taboos have so far been mostly speculative, and not considered to be part of a human universal behaviour (Diggs, 1997; Wilson & Daly, 1991). Marriages between uncle and niece or aunt and nephew may be common in some consanguineous unions, and strictly prohibited in others. One study reports different forms of consanguineous marriages of both close and distant relatives among the Hoti in Venezuela (Storrie, 2003). Some societies are practising cross-cousin marriages (Reddy & Modell, 1995; Yasmin et al., 1997; Storrie, 2003; Calderon et al., 1995). Some studies found a relatively higher fertility among consanguineous couples (Hann, 1985; Babu & Naidu, 1994; Reddy & Modell, 1995). Results also suggest that the higher number of conceptions may be a reproductive compensation for the higher post-natal mortality that exists among these women. Hann (1985) also reported lower primary sterility rates among consanguineously married women, but the net fertility were not overall significantly different between consanguineous and non-consanguineous partnerships.

To conclude, we found support for the prediction that relatives avoided mating with each other in Soknedal during 1700 – 1900 CE, but we did not find any support for a fitness benefit as a result of this behaviour.

References

Alper, O. M., Eregin, H., Manguoglu, A. E., Bilgen, T., Cetin, Z., Dedeoglu, N. & Luleci, G. 2004. Consanguineous marriages in the province of Antalya, Turkey. *Annales De Genetique*, **47,** 129-138.

Babu, B. V. & Naidu, J. M. 1994. Individual Fertility Rate among Minor Tribal Populations from Andhra-Pradesh, India. *Social Biology*, **41,** 274-277.

Breden, F. & Wade, M. J. 1991. Runaway Social Evolution - Reinforcing Selection for Inbreeding and Altruism. *Journal of Theoretical Biology*, **153,** 323-337.

Calderon, R., Morales, B., Pena, J. A. & Delgado, J. 1995. Sex-Linked Versus Autosomal Inbreeding Coefficient in Close Consanguineous Marriages in the Basque Country and Castile (Spain) - Genetic-Implications. *Journal of Biosocial Science*, **27,** 379-391.

Diggs, S. 1997. The plural taboo. *Journal of Analytical Psychology*, **42,** 459-479.

Fuster, V. & Colantonio, S. E. 2003. Inbreeding coefficients and degree of consanguineous marriages in Spain: A review. *American Journal of Human Biology*, **15,** 709-716.

Fuster, V. & Colantonio, S. E. 2004. Socioeconomic, demographic, and geographic variables affecting the diverse degrees of consanguineous marriages in Spain. *Human Biology*, **76,** 1-14.

Hann, K. L. 1985. Inbreeding and fertility in a South Indian population. *Annals of Human Biology*, **12,** 267-274.

Haukdal, J. 1971. *Busetnad og Folkeliv i Soknedal. Gard og grend. Bind 1-4*. Støren, Norway: Midtre Gauldal, (in Norwegian).

Hussain, R. 1999. Community perceptions of reasons for preference for consanguineous marriages in Pakistan. *Journal of Biosocial Science*, **31,** 449-461.

Hussain, R. & Bittles, A. H. 1998. The prevalence and demographic characteristics of consanguineous marriages in Pakistan. *Journal of Biosocial Science*, **30,** 261-275.

Jaber, L., Karim, I. A., Jawdat, A. M., Fausi, M. & Merlob, P. 2004. Awareness of folic acid for prevention of neural tube defects in a community with high prevalence of consanguineous marriages. *Annales De Genetique*, **47,** 69-75.

Jacquard, A. 1975. Inbreeding: One Word, Several Meanings. *Theoretical Population Biology*, **7,** 338-363.

Koochmeshgi, J., Bagheri, A. & Hosseini-Mazinani, S. M. 2002. Incidence of phenylketonuria in Iran estimated from consanguineous marriages. *Journal of Inherited Metabolic Disease*, **25,** 80-81.

Kruger, O., Lindstrom, J. & Amos, W. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution*, **55,** 1207-1214.

Lynch, M. 1991. The Genetic Interpretation of Inbreeding Depression and Outbreeding Depression. *Evolution*, **45,** 622-629.

Pediaditakis, N. 1998. Factors and their origins in mate selection and choice among humans: implications for individual psychotherapy and counseling. *Medical Hypotheses*, **51,** 359-366.

Reddy, P. H. & Modell, B. 1995. Consanguinity and Reproductive-Behavior in a Tribal Population the Baiga in Madhya-Pradesh, India. *Annals of Human Biology*, **22,** 235-246.

Ross, K. G., Krieger, M. J. B., Shoemaker, D. D., Vargo, E. L. & Keller, L. 1997. Hierarchical analysis of genetic structure in native fire ant populations: Results from three classes of molecular markers. *Genetics*, **147,** 643-655.

Rushton, J. P. 1989. Genetic Similarity Theory, Human Altruism, and Group Selection. *Behavioral and Brain Sciences*, **12,** 503-517.

Røskaft, E., Viken, Å., Bongard, T. 2005. Birth rank, family size, sex and life history; Data from a Norwegian human population during the period 1700-1900 CE. *Submitted to Behavioural Ecology*.

Røskaft, E., Wara, A. & Viken, Å. 1992. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, **13,** 443-461.

Storrie, R. 2003. Equivalence, personhood and relationality: Processes of relatedness among the Hoti of Venezuelan Guiana. *Journal of the Royal Anthropological Institute*, **9,** 407-428.

Sureender, S., Ramachandran, S., Subbiah, A. & Ravishankar, A. K. 2003. Consanguineous marriages and pregnancy wastage. *Indian Journal of Social Work*, **64,** 533-540.

Tuncbilek, E. 2001. Clinical outcomes of consanguineous marriages in Turkey. *Turkish Journal of Pediatrics*, **43,** 277-279.

Vantreuren, R., Bijlsma, R., Ouborg, N. J. & Vandelden, W. 1993. The Significance of Genetic Erosion in the Process of Extinction .4. Inbreeding Depression and Heterosis Effects Caused by Selfing and Outcrossing in Scabiosa-Columbaria. *Evolution*, **47,** 1669-1680.

Westermarck, E. 1891. *The History of Human Marriage*. London: Macmillan.

Wilson, M. & Daly, M. 1991. The Metaphorical Extension of Incest - a Human Universal. *Behavioral and Brain Sciences*, **14,** 280-280.

Yasmin, Naidu, J. M. & MascieTaylor, C. G. N. 1997. Consanguinity and its relationship to differential fertility and mortality in the Kotia: A tribal population of Andhra Pradesh, India. *Journal of Biosocial Science*, **29,** 171-180.

Zlotogora, J. 2002. What is the birth defect risk associated with consanguineous marriages? *American Journal of Medical Genetics*, **109,** 70-71.

Paper V

PAPER V

Do humans choose partners that physically resemble themselves?

Terje Bongard[1], Anne Kristiansen & Eivin Røskaft

[1]Corresponding author: Terje Bongard, Norwegian Institute for Nature Research, Tungasletta 2, 7485 Trondheim, Norway, Fax: +47 73801401, Phone: +47 73801544, E-mail: terje.bongard@nina.no

Abstract

The strategy of choosing a partner that is more similar to itself requires that the phenotype is reflecting the genotype. We tested assortative mating among a group of students in Trondheim, Norway and asked the following questions; 1) Do a person choose a partner that is more physically similar to itself than random? 2) Are other people able to pick out mated pairs from random groups? 101 test persons were presented a series of four photos, two males and two females and asked to pick out the pair. The pair was correctly picked out in 39.7 % (± 9.4) of the cases, which was higher than random (25 %). Altogether 89.5 percent of the test persons were able to pick out the pair more frequently than random. There was no significant difference between the two sexes in their ability to pick out the right pair from photos. There was a significant correlation between the age of a man and a woman and the height of the two individuals in a pair. However, none of the other correlations or cross-correlations between height, weight, hair colour or eye colour was statistically significant. Within a pair there was a highly significant positive correlation between the attractiveness of a man and a woman.

Introduction

Sexual selection theory states that the two sexes in monogamous species should be equally critical when choosing a partner (Davies, 1991; Trivers, 1972). Assortative mating implicates that certain phenotypes mate more frequently with each other than random (Partridge, 1983). There seems to be a strategic trade-off between ambitions and realism in human mate search. On one hand, trying to obtain a mate who is as attractive as possible and giving the best quality offspring, or on the other hand settle for the second or third best mate. This leads to the documented phenomenon of like attracts like, because the most stable and fitness-enhancing solution to the trade-off is to find a mate that is at about the same level of attraction (Buss & Schmitt, 1993; Fawcett & Johnstone, 2003). The ability to recognise other individuals by using different phenotypic traits was probably selected for at early stages in human evolutionary history, because of the strong selection pressure connected to the central evolutionary problem of mate choice and retention (Porter, 1987).

Research has shown that assortative mating is quite common among both insects and vertebrates (Burley, 1983; Buston & Emlen, 2003). Among plants, a preference for mating with the right form of polyploidy that enhance fitness is described (Husband & Sabara, 2004). There is some evidence that humans choose partners both resembling themselves morphologically as well as with similar cultural and educational background (Chambers et al., 1983; Sánchez-Andrés & Mesa, 1994; Hur, 2003; Thiessen & Gregg, 1980; Buston & Emlen, 2003). A passive component of human assortative mating which come from the fact that there are more likely to meet an individual resembling yourself in the same courtyard has often been used as an explanation for findings of assortative mating (Choudhury & Black, 1994; Lykken & Tellegen, 1993; Thiessen & Gregg, 1980; Vandenberg, 1972; Warren, 1966). The present study try to control for this factor by using strangers to assess whether individuals are a pair or not.

Given that the phenotype is reflecting the genotype, assortative mating will contribute to increased individual and inclusive fitness, and thereby also increase a potential for altruism towards a partner (Thiessen & Gregg, 1980; Sherman & Holmes, 1985). Assortative mating may, on the other hand, lead to costs such as inbreeding (Badaruddoza & Afzal, 1999). For this reason, assortative mating should be directed towards resembling phenotypes rather than towards close relatives (Halliday, 1983). This means that looks in itself is of higher information value than kinship knowledge when finding a mate.

Individuals tend to avoid mating with those they shared household with in order to avoid inbreeding (Erickson, 1993; Walter, 1997; Allardt, 2000; Bevc & Silverman, 2000; Walter & Buyske, 2003; Lieberman et al., 2003). Post-adoptive incest in humans indicate that sexual interest for close biological relatives may be present when relatives did not grow up together (Dewsbury, 1982; Greenberg & Littlewood, 1995). On the other hand, the potential to recognise relatives without having intermingled with them previously has been documented among several species and taxa (Brown & Brown, 1992; Quinn & Busack, 1985; Sherman & Holmes, 1985). A prediction suggested from this is that an optimum exists between inbreeding and outbreeding, and that appearance is a reliable cue for each mate seeker.

Fitness benefits from assortative mating consist of very different mechanisms. Partnership stability is important for bringing up children and to give them a head start. Divorced parents have children which are overrepresented in crime statistics and psychiatric diseases, and generally have lower education (Malone et al., 2004; Veijola et al., 2004; Quinlan, 2003; Boey et al., 2003; Weitoft et al., 2003; Agerbo et al., 2002). The choice of a partner both lower and higher in attractiveness increases the probability for divorce (Buss, 1994). Also on a genetic level there is support for the relevance of assortative mating, and the evaluation of appearance. Evidence suggests that there is a correlation between beauty, symmetry and developmental health in humans (Thornhill & Grammer, 1999). Disease and parasites are proposed to be one of the major ultimate driving forces on both natural and sexual selection. Indeed, the puzzling presence of sexual reproduction itself is attributed to the selective advantage of variance in the Major Histocompatibility Complex (MHC) and the subsequent effect of increased resistance against infections (Kurtz, 2003; Kurtz et al., 2004; Wedekind et al., 2004). It has been shown that human family members may recognise each other from phenotypic comparisons (odour, colour, behaviour etc). Scent, which are connected to the MHC phenotypic expressions, are genetically based and might be an important factor in assortative mating (Salter, 1996; Weisfeld et al., 2003; Wedekind, 1994; Schneider & Hendrix, 2000; Lykken et al., 1990). Evidence of assortative mating based on dissimilarities between mates in MHC in humans is extensive (Eggert et al., 1998;

Eklund et al., 2000; Bernatchez & Landry, 2003; Ober, 1999; Olsson et al., 2003; Thornhill et al., 2003; Wedekind et al., 1995); but see also (Hedrick & Black, 1997; Ihara et al., 2000).

The aim of this study was to test whether humans choose a partner that resembles herself physically, and to test if this is a human universal ability by using strangers to evaluate the pairs. If a stranger has the ability to evaluate other individuals as partners or not, he or she then presumably uses the same skills as when performing own mate choice. Finding this ability would be an interesting support for a domain-specific psychological mechanism evolved to deal with the challenge of mate choice (Barkow et al., 1992). Hypotheses tested in this study are:

1) There is assortative mating in body weight, body height, hair colour, eye colour and general attractiveness.
2) People are, independent of age and sex, able to identify members of a pair based on appearance on photos.

Material and Methods

One hundred student pairs were recruited for the study. They were either married or had lived together for at least two months. All pairs had been together for a maximum of three years. Both members of a pair were interviewed simultaneously. After being interviewed the students who accepted were photographed, and height and body weight were recorded. One person took the photographs in a standardised way by using the same setup, light and background. Eighty-six pairs accepted to participate in this part of the study.

The participants (N = 200) were between 20 and 34 years (women = 24.6 ± 2.6 years, N = 100, men = 25.6 ± 2.7 years, N = 100). In 65 % of the pairs both members were full time students. The pairs had stayed together for an average of 14 ± 9 months. Sixty-nine percent were cohabiting while 12 % were married and 19 % engaged and cohabiting. Only 6 % had children. Seventy-eight % stated that their intention were to stay together with the partner for the rest of their lives. Data was collected during April – November 1993.

Ten test persons, four women and six men, assessed the photos for general attractiveness. These 10 persons' age was between 22 and 37 years (women = 26.6 ± 2.9 years and men = 27.2 ± 5.3 years). The test persons ranked the physical attractiveness from the photos on a scale from 1 (lowest) to 10 (highest). It was underlined that their score should be objective and that they should have no connection with the person on the photos. A test person was not allowed to score a photo of a person he or she knew. Altogether, 172 photos (86 pairs) were ranked in accordance to the 1-10-scale. There was a highly significant repeatability between the different test person scores in all cases (Spearman rank correlations; 0. 322 < rho < 0.639, 45 tests, P < 0.001). The repeatability was also tested through a repeatability test (r = 0.305, d.f = 171, F = 4.955, P = 0.000) (Lessells & Boag, 1987).

The age of the test person did not affect the attractiveness score (Spearman rank correlation: rho = 0.20, n = 10, P = 0.629), neither when the sexes were tested separately (rho_{women} = 0.21, n = 4, P = 0.789; rho_{men} = 0.26, n = 6, P = 0.623). The two sexes thus seemed to agree about the relative degree of physical attractiveness of different persons, but they used the scale differently. These results are in accordance with a previous study (Kowner & Ogawa, 1995). The final attractiveness score was therefore averaged between the averages of the two sexes ($(X_{women} + X_{men})/2$).

Another group was given an envelope with four photos in order to pick out the couple. A total of 53 women and 52 men participated in this test. These test persons where either students or in permanent working positions. Their ages were 20 to 39 years (X_{women} = 25.8 ± 3.4 years; X_{men} = 27.8 ± 4.1 years). Of these 105 test persons, 83 were Norwegians and 22 were ”graduate” Euro American students at the University of California, Davis, USA.

Test persons were allowed to spend as much time they liked to pick out the couple they believed was going steady, but were not allowed to open the envelope again once they had finished. If they were familiar with one of the persons in an envelope they were not allowed to judge this envelope. Number of envelopes for each test person therefore varied between 25 and 38 (Mean = 33.6 ± 3.3). With this experimental set-up the test person was randomly expected to pick out the right pair in 25 % of the tests. The average test-score for one test person was defined as;

Number of right answers x 100 / number of envelopes.

Each mated pair (n =172) was thereafter scored as;

Number of times the pair was rightfully picked x 100 / Number of times the pair was tested.

Results

Body weight and height

The man in a pair was on average about one year older than the woman, and women being on average 24.6 ± 2.6 years while the men were 25.6 ± 2.7 years (paired sample t-test: t = -4.13, d.f. = 2, P = 0.000). However, there was a highly significant correlation between the age of a man and a woman within a pair (Spearman rank correlation; rho = 0.571, N = 100, P = 0.000). There was no significant correlation between the body weight of the two individuals in a pair (Pearson correlation; r = 0.150, N = 77, P = 0.191). However, there was a significant correlation between the height of the two individuals in a pair (Pearson correlation; r = 0.321, N = 80, P = 0.004). Forty-two % of the pairs reported similar hair colour while 36.7 % of the pairs reported similar eye colour. None of these relations were statistically significant, however (Pearson chi-square: χ^2 = 3.91, d.f. = 9, P = 0.917, respectively χ^2 = 9.78, d.f. = 16, P = 0.878).

Physical attractiveness

Women scored slightly above men in physical attractiveness (women = 4.7 ± 1.2, men = 4.5 ± 1.0), but the difference in score within a pair was not statistically significant (paired sample t-test: t = 1.93, d.f. = 77, P = 0.058). Within a pair there was a highly significant positive correlation between the attractiveness of a man and a woman (Pearson correlation; r = 0.551, N = 78, P < 0.001). Finally, there was a slightly negative correlation between physical attractiveness and age among men (Pearson correlation; r = -0.302, N = 78, P = 0.007), however, no such correlation between age and attractiveness was found among women (Pearson correlation; r = 0.060, N = 78, P = 0.598).

Ability to pick out a pair

There was no statistically significant difference between the test persons in their ability to pick out the pair (One-way-ANOVA; F = 2.90, d.f. = 102, P = 0.056). However, because the P-value was close to 0.05 we picked out 20 random test persons and tested that they systematically deviated from expected random scores, which is 25 % (paired t-tests; t = 5.82, N = 20, P < 0.001). The total variance among test persons showed no differences (Levenes test for homogeneity of variances; F = 0.006, d.f. = 102, P = 0.994).

There was no significant difference between the two sexes in their ability to pick out the right pair from the envelopes (women = 40. 7 ± 10.1 %; men 38.6 ± 8.6 %; t-test for independent groups: t = 1.18, d.f. = 103, P = 0.240; Levenes test for homogeneity of variance; F = 0.48, d.f. = 103, P = 0.491). There was no significant difference between the Norwegians (40.5 ± 9.3 %, N = 83) and North American students (36.5 ± 9.4 %, N = 22) in their ability to pick out the pair from an envelope (t-test for independent groups: t = 1.80, d.f. = 103, P = 0.075; Levenes test for homogeneity of variances: F = 0.05, d.f. = 103, P = 0.832). There was no relation between age and the ability to pick out the pair from the photos (Spearman rank correlations; rho = 0.123, N = 105, P = 0.226; women, rho = 0.150, N = 53, P = 0.275, men, rho = 0.091, N = 52, P = 0.549; Norwegians; rho = 0.081, N = 83, P = 0.493; North Americans; rho = 0.311, N = 22, P = 0.165). There was a near significant tendency to pick out the married, fiancées or cohabiting pairs more frequently (one-way-ANOVA; F = 3.09, d.f. = 69, P = 0.052; Levenes test of homogeneity of variances; F = 0.66, d.f. = 69, P = 0.521).

Because of these non-significant relations we pooled everything to a total sample (N = 105) in the further analyses. On average the pair was correctly picked out in 39.7 (± 9.4) % of the envelopes. Thus the correct pair was picked out almost 15 % more frequently than expected by random (t-test for paired groups: t = 15.9, N. = 105, P < 0.001). Altogether, 89.5 % (94/105) of the test persons were able to pick out the pair more frequently than random.

There was no relation between how often a pair was correctly picked out and the difference in height between the two individuals in a pair (Spearman rank correlation; rho = 0.161, N = 72, P = 0.176). Furthermore, difference in age (Spearman rank correlation; rho = -0.010, N = 72, P = 0.933), difference in physical attractiveness (Spearman rank correlation; rho = 0.053, N = 72, P = 0.658), mean age (Spearman rank correlation; rho = -0.020, N = 72, P = 0.897) or mean time they had been together (Spearman rank correlation; rho = -0.091, N = 71, P = 0.447), were not criteria for being picked out as a pair. However, difference in weight (Spearman rank correlation; rho = 0.249, N = 69, P

= 0.037) and mean physical attractiveness in a pair (Spearman rank correlation; rho = 0.253, N = 72, P = 0.036) were important criteria for being picked out rightfully.

Discussion

We found assortative mating in height, age and physical attractiveness, results that are in accordance with previous findings (Jakobi & Marquer, 1977; Hur, 2003; Sánchez-Andrés & Mesa, 1994; Susanne, 1997). It is not surprising that mated pairs are relatively similar with regard to many social and psychological traits, as age, civil status, religion, birthplace, socioeconomic status, education, ethnical background, race, intelligence, interests/hobbies, values, attitudes and personality. For a review, see Vandenberg (1972). However, if the benefits of assortative mating are increased inclusive fitness, this similarity is likely to be reflected in the genotype in order to inherit the tendency to perform assortative mating. In this study it was important that the studied pairs had not been mated too long in order to minimise the period of mutual influence (Burgess & Wallin, 1943; Griffiths & Kunz, 1973). The pairs were therefore limited to a maximum of three years together.

The test persons picked out the unknown pair in about 40 % of the envelopes, and almost 90 % of the persons picked out the right pair more frequently than random. This result indicate a domain-specific psychological mechanism selected to find suiting mates (Barkow et al., 1992). The results are in accordance with (Nesse et al., 1990) who found that more than 90 % of test persons had the ability to judge family resemblance. But what is the resemblance within a pair? It must be different from a normal family resemblance, but nevertheless represent an equivalent to a phenotypic resemblance that is found between relatives. The physical traits that were tested (eye colour, hair colour) were non-significantly assortative. However, general attractiveness was on the other hand, significantly assortative. Therefore, a person generally seems to fall in love with another person that phenotypically has matching traits more than a random person in the population. Our results are supported by others (Chambers et al., 1983; Griffiths & Kunz, 1973; Rushton, 1989). According to Holmes (1988): ”When traits used in phenotypic matching are genetically specified, an advantage of using a self template is that one’s own phenotype would usually provide an accurate kin referent, whereas a template based on the phenotypes of rearing associates might not if the associates were not all equally related”.

Although women tended to score the physical attractiveness of the portrayed persons higher than men (Kowner & Ogawa, 1995), the repeatability in this study was still very high. Thus we used the average scores as the value for each person that was tested. Normally men are older than women in relationships, frequently around 2-3 years (Buss, 1989; Røskaft et al., 1992). This condition reflects both male and female preferences. Men prefer younger mates with higher reproductive potential, while women prefer more status and accumulated wealth, and therefore often pick men who are older than themselves (Buss & Schmitt, 1993; Wiederman, 1993). We found that women were slightly but not significant more attractive than men, which is in support of the hypothesis that men are more happy with their mates if they are slightly more attractive than themselves (Weisfeld et al., 1992; Buss & Schmitt, 1993).

We found no gender difference in the ability to pick out the pairs from photos, however the variance among women was greater than among men which is supported by previous research (Nesse et al., 1990), and may be explained by the placing in the menstrual cycle. Nesse et al. (1990) found for instance that the ability to pick family resemblance was bimodal in women, i.e. an either-or ability. Similarly, Turkewitz & Ross-Kossak (1984) found that girls were bimodal in the ability to recognise faces and concluded that ”only individuals who would be most likely to use an advanced mode of processing facial information in fact exhibit a bimodal distribution of error scores”. This might be due to the fact that women suffer higher costs than men by doing the wrong choice (Irons, 1988; Trivers, 1972), and also that women are more often involved in the maintenance of relative-network (Dunbar & Spoors, 1995; Lykken et al., 1990).

Among test persons, we found no age effect or no difference between Norwegians and North American students in the ability to pick out the pair from the photo samples. Although this test was skewed with only 22 Americans compared to 83 Norwegians, we conclude that there is no effect of different nationalities or cultures in the ability to pick out pairs. This supports the findings of others concluding that the ability to consider phenotypes is a human universal independent of culture or nationality (Zebrowitz et al., 1993; Perrett et al., 1994; Jones & Hill, 1993). The general ability to compare and to judge the phenotypes of people from other cultures and races supports the presence of a human universal. Children start at an early age to choose whom they want to collaborate with and often are these criteria phenotypic similarity (Thiessen & Gregg, 1980). The interest for the opposite sex starts when children are 3-4 years and the first marriage often starts in the late teens (Buckle et al., 1996; Kurbatova & Pobedonostseva, 1991; Røskaft et al., 1992). The ability to associatively choose a partner is relying on the ability to see such traits at an early age. The ability to recognise similar traits is therefore independent of age and has a very low learning threshold (Nesse et al., 1990).

References

Agerbo, E., Nordentoft, M. & Mortensen, P. B. 2002. Familial, psychiatric, and socioeconomic risk factors for suicide in young people: nested case-control study. *British Medical Journal*, **325,** 74-77.

Allardt, E. 2000. Edward Westermarck: A sociologist relating nature and culture. *Acta Sociologica*, **43,** 299-306.

Badaruddoza, A. & Afzal, M. 1999. Genetical consequences of assortative mating in human population. *Man in India*, **79,** 69-76.

Barkow, J. H., L. Cosmides & Tooby, J. 1992. *The Adapted Mind*. New York: Oxford University Press.

Bernatchez, L. & Landry, C. 2003. MHC studies in nonmodel vertebrates: What have we learned about natural selection in 15 years? *Journal of Evolutionary Biology*, **16,** 363-377.

Bevc, I. & Silverman, I. 2000. Early separation and sibling incest: A test of the revised Westermarck theory. *Evolution and Human Behavior*, **21,** 151-161.

Boey, C. C. M., Omar, A. & Phillips, J. A. 2003. Correlation among academic performance, recurrent abdominal pain and other factors in Year-6 urban primary-school children in Malaysia. *Journal of Paediatrics and Child Health*, **39,** 352-357.

Brown, G. E. & Brown, J. A. 1992. Do rainbow troat and Atlantic salmon discriminate kin? *Canadian Journal of Zoology*, **70,** 1636-1640.

Buckle, L., Gallup, G. G. J. & Rodd, Z. A. 1996. Marriage as a reproductive contract: Patterns of marriage, divorce, and remarriage. *Ethology and Sociobiology*, **17,** 363-377.

Burgess, E. W. & Wallin, P. 1943. Homogamy in social characteristics. *The American Journal of Sociology*, **49,** 109-124.

Burley, N. 1983. The meaning of assortative mating. *Ethology and Sociobiology*, **4,** 191-203.

Buss, D. M. 1989. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, **12,** 1-49.

Buss, D. M. 1994. *The Evolution of Desire. Strategies of Human Mating*. New York, USA: Basic Books.

Buss, D. M. & Schmitt, D. P. 1993. Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, **100,** 204-232.

Buston, P. M. & Emlen, S. T. 2003. Cognitive processes underlying human mate choice: The relationship between self-perception and mate preference in Western society. *Proceedings of the National Academy of Sciences of the United States of America*, **100,** 8805-8810.

Chambers, V. J., Christiansen, J. R. & Kunz, P. R. 1983. Physiognomic homogamy: A test of physical similarity as a factor in the mate selection process. *Social Biology*, **330,** 151-157.

Choudhury, S. & Black, J. M. 1994. Barnacle geese preferentially pair with familiar associates from early life. *Animal Behaviour*, **48,** 81-88.

Davies, N. B. 1991. Mating systems. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by Krebs, J. R. & Davies, N. B.), pp. 263-294. Oxford: Oxford University Press.

Dewsbury, D. A. 1982. Avoidance of incestuous breeding between siblings in two species of Peromyscus mice. *Biology of Behaviour*, **7,** 157-159.

Dunbar, R. I. M. & Spoors, M. 1995. Social networks, support cliques, and kinship. *Human Nature*, **6,** 273-290.

Eggert, F., Muller-Ruchholtz, W. & Ferstl, R. 1998. Olfactory cues associated with the major histocompatibility complex. *Genetica*, **104,** 191-197.

Eklund, A. C., Belchak, M. M., Lapidos, K., Raha-Chowdhury, R. & Ober, C. 2000. Polymorphism in the HLA-linked olfactory receptor genes in the hutterites. *Human Immunology*, **61,** 711-717.

Erickson, M. T. 1993. Rethinking Oedipus: An evolutionary perspective of insect avoidance. *American Journal of Psychiatry*, **150,** 411-416.

Fawcett, T. W. & Johnstone, R. A. 2003. Mate choice in the face of costly competition. *Behavioral Ecology*, **14,** 771-779.

Greenberg, M. & Littlewood, R. 1995. Post-adoption incest and phenotypic matching: Experience, personal meanings and biosocial implications. *British Journal of Medical Psychology*, **68,** 29-44.

Griffiths, R. W. & Kunz, P. R. 1973. Assortative mating: A study of physiognomic homogamy. *Social Biology*, **20,** 448-453.

Halliday, T. R. 1983. Study of mate choice. In: *Mate Choice* (Ed. by Bateson, P.), pp. 3-32. Cambridge: Cambridge University Press.

Hedrick, P. W. & Black, F. L. 1997. HLA and mate selection. No evidence in South Amerindians. *American Journal of Human Genetics*, **61,** 505-511.

Holmes, W. G. 1988. Kinship and the development of social preferences. In: *Handbook of Behavioral Neurobiology* (Ed. by Blass, E. M.), pp. 389-413.

Hur, Y. M. 2003. Assortative mating for personality traits, educational level, religious affiliation, height, weight, and body mass index in parents of Korean twin sample. *Twin Research*, **6,** 467-470.

Husband, B. C. & Sabara, H. A. 2004. Reproductive isolation between autotetraploids and their diploid progenitors in fireweed, *Chamerion angustifolium* (Onagraceae). *New Phytologist*, **161,** 703-713.

Ihara, Y., Aoki, K., Tokunaga, K., Takahashi, K. & Juji, T. 2000. HLA and human mate choice: Tests on Japanese couples. *Anthropological Science*, **108,** 199-214.

Irons, W. 1988. Parental behavior in humans. In: *Human Reproductive Behaviour* (Ed. by Betzig, L. L., Borgerhoff Mulder, M. & Turke, P.), pp. 307-314. Cambridge: Cambridge University Press.

Jakobi, L. & Marquer, P. 1977. A study of the relationships between assortative mating and exogamy in two series of French married couples. *Journal of Human Evolution*, **6,** 115-122.

Jones, D. & Hill, K. 1993. Criteria of facial attractiveness in five populations. *Human Nature*, **4,** 271-296.

Kowner, R. & Ogawa, T. 1995. The role of raters sex, personality, and appearance in judgements of facial beauty. *Perceptual and Motor Skills*, **81,** 339-349.

Kurbatova, O. L. & Pobedonostseva, E. Y. 1991. Genetic demography of the Moscow population: migration, outbreeding and assortative mating. *Annals of Human Biology*, **18,** 31-46.

Kurtz, J. 2003. Sex, parasites and resistance; An evolutionary approach. *Journal of Zoology, London*, **106,** 327-339.

Kurtz, J., Kalbe, M., Aeschlimann, P. B., Haberli, M. A., Wegner, K. M., Reusch, T. B. H. & Milinsky, M. 2004. Major histocompatibility complex diversity influences parasite resistance and innate immunity in sticklebacks. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271,** 197-204.

Lessells, C. M. & Boag, P. T. 1987. Unrepeatable Repeatabilities - a Common Mistake. *Auk*, **104,** 116-121.

Lieberman, D., Tooby, J. & Cosmides, L. 2003. Does morality have a biological basis? An empirical test of the factors governing moral sentiments relating to incest. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270,** 819-826.

Lykken, D. T., Bouchard, T. J. J., McGue, M. & Tellegen, A. 1990. The Minnesota twin family registry: some initial findings. *Acta Genetical Medicine Gemelloly*, **39,** 35-70.

Lykken, D. T. & Tellegen, A. 1993. Is human mating adventitious or the result of lawful choice? A twin study of mate selection. *Personality and Social Psychology Bulletin*, **65,** 56-68.

Malone, P. S., Lansford, J. E., Castellino, D. R., Berlin, L. J., Dodge, K. A., Bates, J. E. & Pettit, G. S. 2004. Divorce and child behavior problems: Applying latent change score models to life event data. *Structural Equation Modeling-a Multidisciplinary Journal*, **11,** 401-423.

Nesse, R., Silverman, A. & Bortz, A. 1990. Sex differences in ability to recognize family resemblance. *Ethology and Sociobiology*, **11,** 11-21.

Ober, C. 1999. Studies of HLA, fertility and mate choice in a human isolate. *Human Reproduction Update*, **5,** 103-107.

Olsson, M., Madsen, T., Nordby, J., Wapstra, E., Ujvari, B. & Wittsell, H. 2003. Major histocompability complex and mate choice in sand lizards. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270,** 254-256.

Partridge, L. 1983. Non-random mating and offspring fitness. In: *Mate Choice* (Ed. by Bateson, P.), pp. 227-255. Cambridge: Cambridge University Press.

Perrett, D. I., May, K. A. & Yoshikawa, S. 1994. Facial shape and judgements of female attractiveness. *Nature, London*, **368,** 239-242.

Porter, R. H. 1987. Kin recognition: functions and mediating mechanisms. In: *Sociobiology and Psychology: Ideas, Issues and Applications*, pp. 175-203.

Quinlan, R. J. 2003. Father absence, parental care, and female reproductive development. *Evolution and Human Behavior*, **24,** 376-390.

Quinn, T. P. & Busack, C. A. 1985. Chemosensory recognintion of siblings in juvernile coho salmon (*Oncorhynchus kisutch*). *Animal Behaviour*, **33,** 51-56.

Rushton, J. P. 1989. Genetic simiarity, human altruism, and group selection. *Behavioral and Brain Sciences*, **12,** 503-559.

Røskaft, E., Wara, A. & Viken, Å. 1992. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, **13,** 443-461.

Salter, F. 1996. Carrier females and sender males: An evolutionary hypothesis linking female attractiveness, family resemblance, and paternity confidence. *Ethology and Sociobiology*, **17,** 211-220.

Sánchez-Andrés, A. & Mesa, M. S. 1994. Assortative mating in a Spanish population: Effects of social factors and cohabitation time. *Journal of Biosocial Science*, **26,** 441-450.

Schneider, M. A. & Hendrix, L. 2000. Olfactory sexual inhibition and the Westermarck effect. *Human Nature*, **11,** 65-91.

Sherman, P. W. & Holmes, W. G. 1985. Kin recognition: issues and evidence. In: *Experimental Behavioral Ecology and Sociobiology* (Ed. by Holldobler, B. & Lindauer, M.), pp. 437-460. Massachusetts: Sunderland.

Susanne, C. 1997. Heritability of anthropological characters. *Human Biology*, **49,** 573-580.

Thiessen, D. & Gregg, B. 1980. Human assortative mating and genetic equilibrium: An evolutionary perspective. *Ethology and Sociobiology*, **1,** 111-140.

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCollough, J. K. & Franklin, M. 2003. Major histocompability complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology*, **14,** 668-678.

Thornhill, R. & Grammer, K. 1999. The body and face of women: One ornament that signals quality? *Evolution and Human Behavior*, **20,** 105-120.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man1871-1971* (Ed. by Campbell, B. G.), pp. 136-179. Chicago: Aldine Publishing Co.

Turkewitz, G. & Ross-Kossak, P. 1984. Multiple modes of right-hemisphere information processing: Age and sex differences in facial recognition. *Developmental Psychology*, **20,** 95-103.

Vandenberg, S. G. 1972. Assortative mating, or who marries whom? *Behaviour Genetics*, **2,** 127-157.

Veijola, J., Maki, P., Joukamaa, M., Laara, E., Hakko, H. & Isohanni, M. 2004. Parental separation at birth and depression in adulthood: a long-term follow-up of the Finnish Christmas Seal Home Children. *Psychological Medicine*, **34,** 357-362.

Walter, A. 1997. The evolutionary psychology of mate selection in Morocco: A multivariate analysis. *Human Nature*, **8,** 113-137.

Walter, A. & Buyske, S. 2003. The Westermarck Effect and early childhood co-socialization: Sex differences in inbreeding-avoidance. *British Journal of Developmental Psychology*, **21,** 353-365.

Warren, B. L. 1966. A multiple variable approach to the assortative mating phenomenon. *Eugenics Quarterly*, **13,** 285-290.

Wedekind, C. 1994. Handicaps not obligatory in sexual selection for resistance genes. *Journal of theoretical Biology*, **170,** 57-62.

Wedekind, C., Seebeck, T., Bettens, F. & Paepke, A. J. 1995. MHC-dependent mate preferences in humans. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **260,** 245-249.

Wedekind, C., Walker, M., Portmann, J., Cenni, B., Muller, R. & Binz, T. 2004. MHC-linked susceptibility to a bacterial infection, but no MHC-linked cryptic female choice in whitefish. *Journal of Evolutionary Biology*, **17,** 11-18.

Weisfeld, G. E., Russell, R. J. H., Phillips, K. A., Gall, J. A. & Lichtman, C. M. 2003. Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *Journal of Experimental Child Psychology*, **85,** 279-295.

Weisfeld, G. E., Russell, R. J. H., Weisfeld, C. C. & Wells, P. A. 1992. Correlates of satisfaction in British marriages. *Ethology and Sociobiology*, **13,** 125-145.

Weitoft, G. R., Hjern, A., Haglund, B. & Rosen, M. 2003. Mortality, severe morbidity, and injury in children living with single parents in Sweden: a population-based study. *Lancet*, **361,** 289-295.

Wiederman, M. W. 1993. Evolved gender differences in mate preferences: Evidence from personal advertisements. *Ethology and Sociobiology*, **14,** 331-352.

Zebrowitz, L. E., Montepare, J. M. & Lee, H. K. 1993. They don't all look alike: Individuated impressions of other racial groups. *Journal of Personality and Social Psychology*, **65,** 85-101.

Paper VI

PAPER VI

Factors affecting the length of a relationship; A female perspective

Bongard, Terje[1,2]*, Rosenqvist, Gunilla.*[2]*, Røskaft, Eivin.*[2]

[1] Norwegian Institute of Nature Research (NINA), Tungasletta 2, 7485 Trondheim, Norway. Email: terje.bongard@nina.no

[2] Norwegian University of Science and Technology, Department of Biology.
7491 Trondheim, Norway. Email: roskaft@nt.ntnu.no

Abstract

This paper presents results concerning female view of the male commitment into a relationship, his economic status variables and his ambition levels. We tested predictions derived from evolutionary biology concerning female mate choice through a questionnaire given to 22 000 female subscribers of a Norwegian magazine. The expectations of a stable economic wealth prior to engagement affected positively the length of relationships. The partner's economic stability, the respondent's perceived economic satisfaction and the partner’s investment in children from previous relationships were significantly higher in an ongoing than in a broken relationship.

Key words: divorce, mate choice, female perspective, evolutionary biology

1. Introduction

Human cognitive mechanisms can be viewed as unconscious drivers, evolved to make the most optimal decision in our evolutionary past. Men and women have a comprehensive understanding of own marital value and is weighting this up against the value of possible partners, also those who are not within physical reach. These values and preferences seem to be universal and cross-cultural (Barkow, Cosmides, & Tooby, 1992; Buss, 1989, 2000; Buunk, Angleitner, Oubaid, & Buss, 1996). The consequences of these decisions might often be divorce. Divorce is a common strategy in most species and is hypothesised to optimise the trade-off between mating effort and parental effort (Fisher, 1989; McNamara, Forslund, & Lang, 1999). The decision to leave may involve costs in several ways, one being the loss of reproductive time. Cultural differences among human populations constitute problems concerning the research on mate choice and divorce. Humans are nevertheless in many cases a well suitable species to investigate, because of the possibilities for thorough and detailed scrutiny of relationships (Choudhury, 1995; Weisfeld, Russell, Weisfeld, & Wells, 1992).

Sexual competition in humans is expected to be high because of the high investment in the offspring by both fathers and mothers, and thereby quests for a high quality partner. The human male is adapted to commit himself to an unusual high degree of paternal effort compared to mammal species in general, although their investment is exceeded several folds by the females (Low, 2000).

The aim of this paper is to study divorce using humans as a model by examining some factors concerning resources and mate retention. We test the hypothesis that females will appreciate male stability, ambitions and willingness to invest. The following predictions are tested:

- Perceived high commitment in the form of economic confidence, satisfaction and predictability are factors preventing divorce.

One aspect of this is how the spouses trust each other by having shared their economy. High confidence in each other was assumed to be a sign of a stable partnership.

- A high level of male ambition in relation to his career will prevent divorce.
- An increase in a man’s socioeconomic status from the day they met will prevent divorce.

- A perception of a fair outcome of who gets the last word in disputes will prevent divorce.

Debates and quarrels are strategies to win small fights over resources in daily lives, and solving them in a just way is crucial in well-functioning partnerships.

- A woman's perception of high investment in her previous children will prevent divorce.

It is proposed that investing in a woman's children from previous relationships can be seen as a mating tactic for a stepfather, implying enhanced prospects of future reproduction with the children's genetic mother (Sarah Blaffer Hrdy, 1999; Low, 2000; Rohwer, Herron, & Daly, 1999). Analogous to this, nuptial gifts are well documented in biology (Engqvist & Sauer, 2002; Fedorka & Mousseau, 2002), and symbols of commitment presented to women by men can be very powerful in provoking content and thereby stabilise relationships. This mechanism was probably important, and still is in all known cultures including Western societies where the economical value of the gift may be of no importance for a woman's prosperity (Rapoport, 2000).

2. Material and methods

The Norwegian female weekly magazine "KK", (short for "Women's clothing" in Norwegian) financed the printing of a questionnaire which was sent to their subscribers (N = 22 000) as an enclosure in the 25th issue in the year 2000. The response was 15 %, or about 3800 cases. About 400 replies are removed from any further analyses due to risks of misinterpretations, including five male respondents. The file contains a total of 3441 female cases: 1044 cases of single women with broken relationships, and 2397 with ongoing relationships. However, the latter group also responded for partners in previous relationships.

According to a social profile of the subscribers made by Norwegian Micromosaic LTD on a project grant, the people reading KK are overrepresented in the age groups between 31 and 55 years. There is also an overweight of white-collar persons living in detached houses in urban areas, having medium to high income and education (unpubl.).

The whole questionnaire consisted of 65 questions concerning age, physical data, relationship status, ethnicity, occupation, income and economy, diseases, number of children, parental status and other family matters. The full spreadsheet matrix has a total of 419 variables. The female respondent was asked to answer questions both for herself, her present partner, and previous partner from her longest relationship.

To test the predictions outlined the following questions were presented:

A: “How pleased are/were you regarding your partner’s general investment and commitment in the partnership?”

B: “Who get/got the last word in disputes?”

C: “When you entered the relationship, did you expect the economy to be satisfactory?”

D: “Was/is the economy actually satisfactory?”

E: “How stable and predictable is/was your partner in economic matters?”

F: “To which degree did you share the income?”

G: “Is/was your partner ambitious regarding his career and job status?”

H: “If you have children from previous relationships, how pleased are/were you with your partner’s investment in this/these child/children?”

The answers were categorised on a scale from one to five, for example:

“To what degree did you have shared economy?” Options were “All shared” (= 1), “Mostly shared” (= 2), “Half separated/shared” (= 3), “Mostly separated” (= 4), and “All separated” (= 5).

In addition, a series of questions constructed to reveal changes in the man’s socio-economic status during the relationship were presented. We have coded the different occupations on a status scale from 0 to 12 according to the standard used by The Norwegian Statistical Agency (Anon, 1984).

The women are not categorised in age groups or education level. The prediction from evolutionary biology is that the tested attitudes are human universals, regardless of differences in cultural or environmental factors, and should be significantly present in all age cohorts and educational groups (Barkow et al., 1992; Buss, 1994). Exceptions are expected to be statistically rare (S. B. Hrdy, 2004).

Respondents were asked to answer separate questions for their ongoing and longest previous relationships. Only relationships that lasted for more than six months were included in the study. In the further analyses, both divorced and other types of broken relationships are called “broken”, and for married, cohabiting and other types of ongoing relationships the word “together” is used. All statistical analyses are non-parametric and two-tailed.

3. Results

The five predictions outlined were all supported by the results. All differences are highly significant ($p = 0.0001$). Among the broken relationships 42.7 % of the women had been dissatisfied with her partner’s general effort and commitment, while only 7.4 % of the women were dissatisfied in their present relationship (Table 1A). The stability of a relationship was significantly higher when a woman felt an equal outcome of a dispute (62.1 % in the ongoing relationships) than when she reported an unequal outcome of a dispute, regardless of which of the two spouses dominated (40.0 % in the broken relationships; Table 1B). Twice as many women from broken relationships reported that they dominated discussions (8.1 % compared to 4.1 %; Table 1B).

Women from both broken and ongoing relationships expected economic stability when the relationship started, but respondents from ongoing relationships had significantly higher confidence in that this would be the case (Table 1C). When entering into a relationship, 6.7 % of the broken compared to 2.9 % for the ongoing relationships had little confidence in the economic stability (Table 1C). 31.7 % of the respondents from broken relationships reported an unsatisfactory economy, while 52.1 % were satisfied. In ongoing relationships 7.4 % reported to have an unsatisfactory economy while 82.1 % reported a satisfactory economy (Table 1D). Male predictability in economic matters also hinders divorce. Less than 10 % of the ongoing couples included unpredictable males compared to 31.5 % of the broken relationships (Table 1E). The degree of joint economy did also significantly influence divorce rate, 69.8 % of ongoing relationships shared the economy, compared to 57.1 % among broken ones (Table 1F).

Ambitious men were significantly overrepresented among ongoing relationships, 46.5 %, compared to 35 % among broken ones. Nevertheless, this is only true up to a certain level. Very ambitious men were over-represented in broken relationships (22.1 %) compared to ongoing ones (16 %, Table 1G and Figure 1).

Women who were dissatisfied with their partner's effort and commitment to children from previous relationships were significantly more likely to break their relationships (Table 1H). In the broken relationships 35.3 % were dissatisfied with the investment from their partner while only 9.0 % were dissatisfied in the ongoing ones (Table 1H).

The socio-economic status (SES) is measured and categorised by occupation. Although men in both broken and ongoing relationships increased in SES, men in ongoing relationships increased their SES significantly more (Table 2). There were also significantly fewer men in the lowest socio-economic categories among the ongoing pairs compared to the broken ones (Table 2).

4. Discussion

Humans, just like any other sexual species, are selected to react upon the environment in a way that is logical when considering the evolutionary past. This is also true for human mating behaviour. Appreciation of commitment, resources and industriousness are qualities assumed to have boosted fitness in the past. Women who preferred a partner who invested and committed himself to her and their relationship left more female ancestors with the same male preference (Buss, 1994; Buss & Schmitt, 1993; Cherlin, 1992). A woman selecting a careless partner was, according to this scenario, evolutionary ousted.

Conflicts may be present in all forms of relationships in all kinds of organisms, including humans, and can be seen as conventionalised fights over resources in the grey area between egoism and reciprocity (Ali, 2003; Dale & Slagsvold, 1995; Kurzynski, 1998; McElreath, 2003; Nie, 2003; Nugent, 2002; Peters, 2002; Rettig, Leichtentritt, & Stanton, 1999; Tsang, Shaner, & Vidulich, 1995). It is crucial for pairs to cope with disagreements. Quarrels can be seen as a form of unconscious evaluation of mismatch, and that biting each other and blaming the partner make it easier to break up (Buss, 1994; Buss & Schmitt, 1993). Escalation of quarrels may also give the individual a relief and confirmation of having done the right thing when finally divorce arrives. The respondents reporting equal outcome of who gets the last word in disputes are having lower divorce rates. They quarrel all right, but they nevertheless have the feeling of justice that seems to stabilise the relationship. A tilting of this balance either way increases the probability of divorce.

Resources are of less value if they are uncertain and unpredictable. Thus, the thrust that a chosen partner is able to provide and cope with the economy is an important expectation when entering and holding on to a relationship. Female reproductive success is normally not limited by access to males, but by access to resources (Andersson, 1994; Sarah Blaffer Hrdy, 1999; Low, 2000; Røskaft, Wara, & Viken, 1992; Trivers, 1972).

The frequency of stepchildren in new relationships are increasing in western societies where divorce rates are up to 50 % (Fisher, 1989; K. L. White & Booth, 1985). A woman could use this situation to evaluate a partner's willingness to invest and thereby measure the rate of commitment. Men's investment may in these kinds of circumstances be seen as a way of getting a woman's benevolence (Daly & Wilson, 1988). Our results support the presence of cognitive mechanisms that make a man reluctant in raising another man's child. This factor destabilises a relationship (Billy, Landale, & McLaughlin, 1986; Daly & Wilson, 1988).

The interesting result that over-ambitious men have higher risks of loosing their partner may have several explanations. These men are perhaps either failing to commit themselves to the relationship because of their time consuming work, or they are becoming increasingly attractive because of their higher status. A consequence of this may be a destabilisation of the relationship. It is probably an optimum for a man to act somewhere between ambition, investment and increasing attraction that will fulfil his partner's need for an ambitious spouse without her loosing him altogether.

Jalovaara (2003) found similar results from an investigation in Finland. She found that for couples in which both partners were at the lowest educational level, the risk of divorce was lower than could be expected on the basis of the previously documented overall inverse association between each spouse's education and the risk of divorce. Such an association is expected to diminish for the lowest educational group. Low education will normally stabilise a partnership because of the perceived lower attractiveness of her spouse. Such women are perhaps making the best of a bad job by staying with the one they have. Further results from this study revealed that women who were employed or were homemakers, and who had employed husbands, were engaged in comparatively stable marriages; couples in which the husband, the wife, or both partners were unemployed had an elevated risk of divorce. In this situation she gets the feeling that she could have made a better choice, which destabilises the relationship. A husband with a high income reduced the risk of divorce, and a wife with a high income increased the divorce risk. She was at a very high risk particularly when the wife's income exceeded that of the husband (Jalovaara, 2003). The highest educated couples experienced that there are relatively few potential mates that could match the already chosen spouse. Therefore there was apparently little to gain by trying to do better, and consequently the divorce rate in this group was relatively low. The most stable marriages were those with a homemaking wife and an employed husband. In this situation, the wife is economically dependent of her husband and he provides all the incoming resources, fulfilling the wife's demands for a providing male.

Jalovaara's (op cit) findings are consistent with predictions from evolutionary biology, although she did not interpret her results in this context. Unemployment and low income increased the divorce risk. These factors are clues that trigger a woman's feeling of insecurity, and subsequently tear off the bonds to an inferior male that might have reduced her fitness. The resource situation in Western societies today is probably causing an increase in divorce rates, because women leaving their husbands do not run the same risks of being without support and resources as they did only a few decades ago. This may lower the threshold for leaving a partner from a woman's point of view (Buss, 1994). Science is in need of developing new theoretical framework to explain divorce rates between 40 and 50 % in the Western societies (Cherlin, 1992; Teachman, 1986; L. K. White, 1990). In Norway,

47.8 % of all ongoing marriages are predicted to break up (Statistics Norway 2003, unpublished, see: http://www.ssb.no/english/subjects/02/02/30/skilsmisse_en/).
Increase in social status and ambitions to acquire better jobs and positions are attractive male traits from a female perspective (Buss, 1994). Ambitious husbands are trying to be ahead of their fellow men, and are thereby signalling ability and drive to seek resources. The same qualities are assumed to have increased reproductive success in our evolutionary past (Røskaft et al., 1992). Eagerness to increase status, getting a better position in the group and increase the resource accumulation would have out-competed contentment and laziness. The striving to "keep up with the Joneses" is an aspect of this behavioral trait. Modern evolutionary theory predicts a conflict source in the disparity between the innate need for a woman to collect resources, commitment and investment from a man, and the Western wealth and excess of these resources. Today's resource situation might trigger a discontent that is difficult to satisfy (Low, 2000). Not fulfilling these needs might lead to increasing divorce rates. A woman of today is expecting the same satisfaction as her ancestors, who on the other hand did not have the world's rich and successful people to compare her life situation with (Buss, 2000).

The majority of scientific studies suffer from the uncertainty of how general the results are, and questionnaires are no exception in the respect of their validity for the whole population. Nevertheless, the strength of evolutionary biology theory is that the hypotheses and predictions derived from it is expected to be generally valid for all groups and case selections, provided there are enough cases to overcome stochastic noise. The proximate behavior mechanisms are predicted to be homologous for all cultures and populations.

A factor of uncertainty in all questionnaire studies is the retrospective nature of the answers, in that the respondents were asked questions about the past. On one hand respondents could probably remember their previous partnerships more problematic and negative than they really were. But, on the other hand, problems and conflicts tend to faint away during time. It is difficult to decide which of these mechanisms that will dominate. Regardless of this the results will reflect each woman's personal perception, and consequently reflect her own pros and cons of the matter in question.

Acknowledgments

We thank “KK” for their kind support, and Kyrre Svarva, Norwegian University of Science and Technology, for his help in preparing data files.

References

ALI, S. H. (2003). Environmental planning and cooperative behavior - Catalyzing sustainable consensus. Journal of Planning Education and Research, 23(2), 165-176.

ANDERSSON, M. (1994). Sexual Selection. Princeton, N.J.: Princeton University Press.

ANON. (1984). Standard for Classification of Socioeconomic Status. Statistics Norway. (Standard for inndeling etter sosioøkonomisk status). Oslo: Statistisk Sentralbyrå, Statistics Norway.

BARKOW, J. H., COSMIDES, & TOOBY, J. (1992). The Adapted Mind. New York: Oxford University Press.

BILLY, J., LANDALE, N., & MCLAUGHLIN, S. (1986). The effect of marital status at first birth on marital dissolution among adolescent mothers. Demography, 233, 29-349.

BUSS, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behavioral and Brain Sciences, 12, 1-49.

BUSS, D. M. (1994). The Evolution of Desire. Strategies of Human Mating. New York, USA: Basic Books.

BUSS, D. M. (2000). The evolution of happiness. American Psychologist, 55(1), 15-23.

BUSS, D. M., & SCHMITT, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. Psychological Review, 100, 204-232.

BUUNK, B. P., ANGLEITNER, A., OUBAID, V., & BUSS, D. M. (1996). Sex differences in jealousy in evolutionary and cultural perspective: Tests from the Netherlands, Germany, and the United States. Psychological Science, 7(6), 359-363.

CHERLIN, A. J. (1992). Marriage, divorce, remarriage (Rev. and enl. ed.). Cambridge, Mass.: Harvard University Press.

CHOUDHURY, S. (1995). Divorce in Birds - a Review of the Hypotheses. Animal Behaviour, 50, 413-429.

DALE, S., & SLAGSVOLD, T. (1995). Female Contests for Nest Sites and Mates in the Pied Flycatcher Ficedula-Hypoleuca. Ethology, 99(3), 209-222.

DALY, M., & WILSON, M. (1988). Homicide. New York: Aldine de Gruyter.

ENGQVIST, L., & SAUER, K. P. (2002). Amorous scorpionflies: causes and consequences of the long pairing prelude of Panorpa cognata. Animal Behaviour, 63, 667-675.

FEDORKA, K. M., & MOUSSEAU, T. A. (2002). Material and genetic benefits of female multiple mating and polyandry. Animal Behaviour, 64, 361-367.

FISHER, H. E. (1989). Evolution of Human Serial Pairbonding. American Journal of Physical Anthropology, 78(3), 331-354.

HRDY, S. B. (1999). Mother nature : a history of mothers, infants, and natural selection. New York: Pantheon Books.

HRDY, S. B. (2004). Evolution's rainbow: Diversity, gender and sexuality in nature and people. Nature, 429(6987), 19-21.

JALOVAARA, M. (2003). The joint effects of marriage partners' socioeconomic positions on the risk of divorce. Demography, 40(1), 67-81.

KURZYNSKI, M. J. (1998). The virtue of forgiveness as a human resource management strategy. Journal of Business Ethics, 17(1), 77-85.

LOW, B. S. (2000). Why Sex Matters: A Darwinian Look at Human Behavior. Princeton: Princeton University Press.

MCELREATH, R. (2003). Reputation and the evolution of conflict. Journal of Theoretical Biology, 220(3), 345-357.

MCNAMARA, J. M., FORSLUND, P., & LANG, A. (1999). An ESS model for divorce strategies in birds. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 354(1380), 223-236.

NIE, M. (2003). Drivers of natural resource-based political conflict. Policy Sciences, 36(3-4), 307-341.

NUGENT, P. S. (2002). Managing conflict: Third-party interventions for managers. Academy of Management Executive, 16(1), 139-154.

PETERS, S. (2002). Courting future resource conflict: The shortcomings of western response strategies to new energy vulnerabilities. Energy Exploration & Exploitation, 20-1(6-1), 29-60.

RAPOPORT, Y. (2000). Matrimonial gifts in early Islamic Egypt. Islamic Law and Society, 7, 1-36.

RETTIG, K. D., LEICHTENTRITT, R. D., & STANTON, L. M. (1999). Understanding noncustodial fathers' family and life satisfaction from resource theory perspective. Journal of Family Issues, 20(4), 507-538.

ROHWER, S., HERRON, J. C., & DALY, M. (1999). Stepparental behaviour as mating effort in birds and other animals. Evolution and Human Behaviour, 20, 367-390.

RØSKAFT, E., WARA, A., & VIKEN, Å. (1992). Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. Ethology and Sociobiology, 13(5-6), 443-461.

TEACHMAN, J. D. (1986). First and second marital dissolution: A decomposition exercise for whites and blacks. Sociological Quarterly, 27, 571-590.

TRIVERS, R. L. (1972). Parental investment and sexual selection. In B. G. Campbell (Ed.), Sexual Selection and the Descent of Man1871-1971 (pp. 136-179). Chicago: Aldine Publishing Co.

TSANG, P. S., SHANER, T. L., & VIDULICH, M. A. (1995). Resource Scarcity and Outcome Conflict in Time-Sharing Performance. Perception & Psychophysics, 57(3), 365-378.

WEISFELD, G. E., Russell, R. J. H., Weisfeld, C. C., & Wells, P. A. (1992). Correlates of satisfaction in British marriages. Ethology and Sociobiology, 13, 125-145.

WHITE, K. L., & Booth, A. (1985). The quality and stability of remarriages: The role of stepchildren. American Sociological Review, 50, 689-698.

WHITE, L. K. (1990). Determinants of divorce: A review of research in the eighties. Journal of Marriage and the Family, 52, 904-912.

Table 1. Frequencies on how the responding women perceived their partner in ongoing and broken relationships (Chi-square tests; Chi-square values always >76).

A: The respondent’s perception of the partners general investment and commitment

Pairbond	Very unsatisfied	Unsatisfied	No opinion	Satisfied	Very satisfied	P= (N=)
Broken	11.3	31.4	21.5	26.8	9.1	
Together	1.0	6.4	10.7	46.1	35.8	.0001 (3422)

B: The respondent’s evaluation of “Who had the last word in disputes”

	Almost always ego	More often ego	Equally ego and partner	More often partner	Almost always partner	
Broken	8.1	17.7	40.0	25.5	8.7	
Together	4.1	22.8	62.1	10.0	1.0	.0001 (3396)

C: The respondent’s confidence in expected economic stability

	Very little confidence	Little confidence	No opinion	High confidence	Very high confidence	
Broken	1.7	5.0	45.5	34.8	13.0	
Together	0.9	2.0	37.4	40.1	19.6	.0001 (3414)

Table 1 cont.

D: The respondent's perception of the economic satisfaction in the relationship

Pairbond	Very unsatisfied	Unsatisfied	No opinion	Satisfied	Very satisfied	P= (N=)
Broken	12.3	19.4	16.2	40.8	11.3	
Together	2.4	5.0	10.5	54.2	27.9	.0001 (3412)

E: The partner's predictability in economic matters

	Very unpredictable	Unpredictable	No opinion	Predictable	Very predictable	
Broken	13.9	17.6	14.3	31.7	22.4	
Together	2.4	7.4	9.6	41.2	39.4	.0001 (3417)

F: The degree of shared economy

	Nothing shared	Almost no shared	No opinion	Mostly shared	All shared	
Broken	13.8	21.3	7.8	32.5	24.6	
Together	10.9	14.9	4.4	40.1	29.7	.0001 (3417)

Table 1 cont.

G: The partner's ambitions in status increase

	Very unambitious	Unambitious	No opinion	Ambitious	Very ambitious	P= (N=)
Broken	7.6	15.0	20.3	35.0	22.1	
Together	3.2	11.2	23.2	46.5	16.0	.0001 (3416)

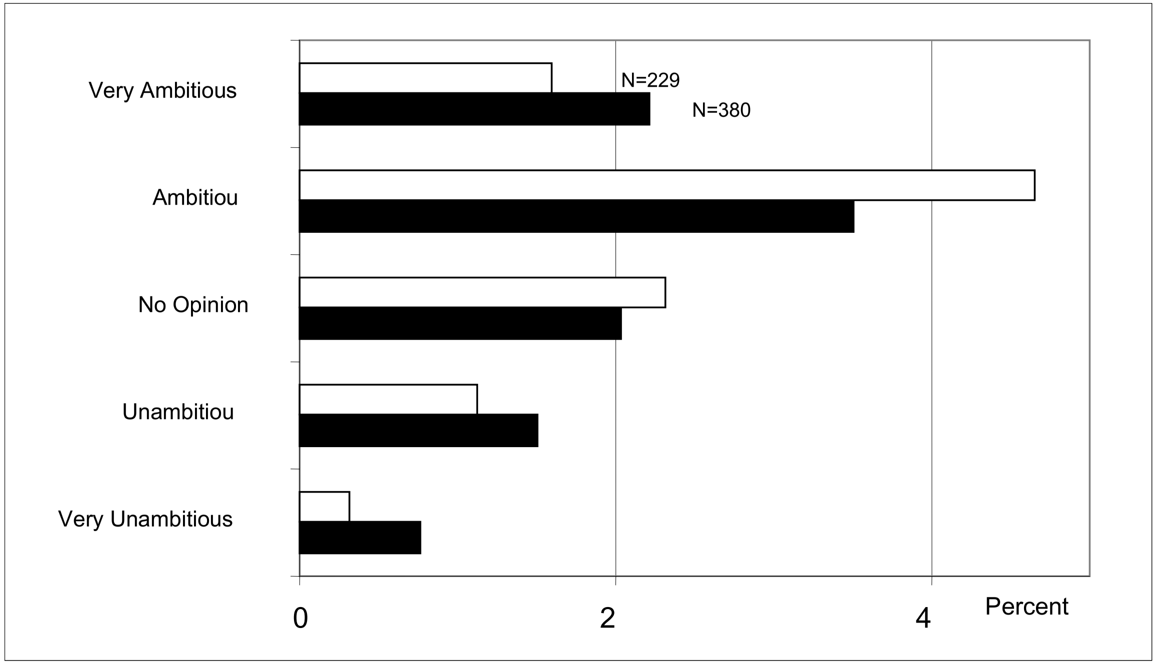
H: The respondent's satisfaction with her partner's investment in her children from previous relationships

Pairbond	Very unsatisfied	Unsatisfied	No opinion	Satisfied	Very satisfied	
Broken	15.6	19.7	27.9	22.1	14.8	
Together	2.7	6.3	16.8	37.3	36.9	.0001 (599)

Table 2. The frequency of broken and remaining relationships in relations to change in socio-economic status

Time	Pairbond	Low	Lower middle	Upper middle	High	Chi-square	P= (N =)
Respondent	Broken	17.5	33.4	18.5	30.5		
at start-up	together	22.9	38.1	16.2	22.8	33.1	.005 (3360)
Respondent	Broken	11.2	23.8	17.8	47.2		
now	Together	10.7	19.1	17.4	52.8	10.7	.005 (3208)
Partner	Broken	28.4	27.8	12.5	31.4		
at start-up	Together	28.9	33.1	10.5	27.6	9.97	.005 (3310)
Partner	Broken	19.4	17.2	15.3	48.1		
now	Together	14.0	14.2	13.2	58.6	44.8	.005 (3116)

Figure 1. Partner ambition's influence on divorce rate. Black bars are divorced couples, white bars are married or cohabiting ($p < 0.0001$, total $N = 3416$).


Very Ambitious
Ambitiou
No Opinion
Unambitiou
Very Unambitious
N=229
N=380
0
2
4
Percent

Paper VII

PAPER VII

Parents experience higher conflict levels with their offspring in daily-life situations than do nursery school teachers

EIVIN RØSKAFT[1], TERJE BONGARD AND LISE MUNKEBY

Department of Biology, Norwegian University of Science and Technology, Realfagbygget N-7491
Trondheim, NORWAY

[1] Corresponding author; roskaft@nt.ntnu.no

Abstract

Phenotypic levels of daily-life parental-offspring conflicts in two different social contexts were studied; 1) between biological parents and their offspring at home, and 2) between the adults and the same children in the nursery school. Parents and nursery school teachers were asked how the children acted in conflicting situations that frequently occur during a day. Parents reported a higher level of conflict with their children than did teachers from nursery schools. Parents did not experience differences in conflict level between boys and girls, while nursery school teachers did experience such differences.

INTRODUCTION

Conflicts in general might be seen as the results of fights over the allocation of resources which in one way or another are considered important in an evolutionary perspective. These resources might be as diverse as parental attention and care, access to fertile females, security and violence, occupation of land or struggle for religious power. This observation holds for individual as well as societal conflicts of both serious and more insignificant kind (Don-Yehiya, 1998; Perezagote, 1986; Schudlich, Shamir, & Cummings, 2004; Summerfield, 1998). For humans, exceptions include persons with diseases or psychiatric disorders who typically have irrational and evolutionary improper behaviour. Even random violence may be interpreted as a result of a selection for being dominant (Linstead, 1997; Thornhill & Palmer, 2000). These generalisations fit an evolutionary model by focusing on the problems ancestors were to deal with. Selection to cope with conflicts has provided humans with domain-specific psychological mechanisms constructed for optimising the personal outcome of competing for resources (Barkow, L. Cosmides, & Tooby, 1992).

During evolution, resources have not been ad libitum and strategies to claim for limited resources within family groups (e.g. begging, breast-feeding disagreement) have been demonstrated in several species (Burford, Friedrich, & Yasukawa, 1998; Davies, Kilner, & Noble, 1998; Ottoson, Bäckman, & Smith, 1997; Geoffrey A Parker, Royle, & Hartley, 2002; Wright, 1998). Contemporary surplus of food and shelter among modern humans will not alter children strategies for craving more, a well-known fact for all parents. Parent-offspring conflicts may vary from offspring manipulation of parental investment (G.A. Parker, 1985; G A Parker & MacNair, 1978; Trivers, 1974) to complete parental control (G.A. Parker, 1985; G A Parker & MacNair, 1979). However, offspring might also be honest in their needs or demands (Godfray, 1991, 1995b), but see (Johnstone, 1999).

A prediction derived from parent-offspring theory is that children are selected to demand more resources and attention from their biological parents than from other adult persons they interact with. Biological parents will consequently also be selected to invest more than other adults.

In this paper we use humans as models by assuming that children demands will be expressed as a level of conflict with the provider, consequently that expectations of higher investment will manifest itself in a higher conflict level with the parents than with other adult persons. We measure how parents and adults experience different conflict levels in analogous social contexts in the children's daily lives. A difference will suggest the presence of parent-offspring conflict.

We assume that parent-offspring conflict has a genetic basis (Kölliker & Richner, 2001). Because of the inherited nature of the need for attention and care, cravings will therefore be expressed even if offspring receive more resources than needed, and even among modern humans (Buijzen & Valkenburg, 2003).

The study of parent-offspring conflict is important for many reasons (Godfray, 1995a); 1) Interactions between parents and their offspring is the basic and most common social behavior. 2) Parent-offspring conflict can be regarded as social evolution from a genetically point of view (Dawkins, 1989; Kölliker & Richner, 2001). 3) There has been a growing interest in studies of parent-offspring conflicts in humans, and there is a need for a better knowledge of these aspects in order to understand human social behavior and social conflicts. More insight and understanding can be valuable in clinical treatment of personal and family problems.

Of all known species, the human being *Homo sapiens* has the longest and most energy demanding parental care. Due to its large brain, human babies are born at a very premature stage, making parental care necessary for many years. Partly because of this, humans have offspring that overlap in time, and there is no interval to recover between each offspring (Low, 2000). This setting gives a substantial leeway for parent-offspring conflicts to arise.

MATERIAL AND METHODS

We studied the level of conflict in two different social contexts; 1) between parents and their offspring at home, and 2) between adults and the same children in the nursery school. Teachers and nursery schools are new in an evolutionary context and may be regarded as experimental control situations. The level of conflict was assessed from the grown-up person's point of view. Offspring solicitation is what they do in daily life and parental response is their assessment of offspring solicitation. Offspring crying is for instance a viable behavior and is adaptive in human infants (Lummaa, Vuorisalo, Barr, & Lehtonen, 1998).

We developed a questionnaire that was distributed to 13 different nursery schools owned by the Trondheim municipality, Central Norway. The questionnaires were distributed during the period February - May 2001. The first edition of the questionnaire was used as a pilot test in one nursery school, and led to several minor changes of the questionnaire. The pilot nursery school was not used in the final test. A letter to be given permission to submit the questionnaire was originally sent to 21 nursery schools, of which thirteen gave a positive reply. The leaders of the approving nursery schools sent the questionnaire home with each child. Six hundred and fifty families received the questionnaire, of which 271 parents answered (42 % response). We did not send reminders. Children with special needs or a diagnosis of any kind were excluded. A similar questionnaire was presented to the nursery school teacher who had the best knowledge of the same child. Two-hundred-and-sixty-eight teachers answered the same questionnaire for 268 pupils.

The parents provided standard information about the child's age, number of siblings, family status and their own level of education. We furthermore asked how much time the parents spent together with their child on a standard day. The children were in the nursery schools for at least six hours every day, about the same awake time as the biological parents were having with the children.

We asked the parents and nursery school teachers how a child behaved in conflicting situations that occur frequently during a day, presented as statements to be agreed or disagreed on;
1) during *meals*: “I never experience that the child is making a scene in connection with: Dinner, lunch, serving of sweets or cakes”.
2) when the child was going to *rest*: “I never experience that the child is reluctant to go to rest”.
3) during *toilet* visits: “I never experience that the child is making a scene in connection with changing of baby’s napkin or toilet visits”.
4) when the child was going to *dress* or *undress*: “I never experience that the child is making a scene when dressing: Outdoor clothes, indoor clothes”.

5) when the child was going to be washed (*hygiene*): “I never experience that the child is making a scene when washing: Hands, face”.

6) general *indoor*: “I never experience that the child is making a scene when told to: Sit quietly, tidy its own mess”.

7) *outdoor* activities: “I always experience that the child is cooperating when: Visiting a library, visiting a cinema or a theatre, going shopping”.

8) reactions from the child when he/she was told to *behave* in a particular way: “I never experience that the child is making a scene when disciplined”.

The alternative answers were; totally agree = 1, partly agree = 2, partly disagree = 3, totally disagree = 4.

There was no guidance to the respondents on which of the parent that should respond to the questionnaire, therefore 213 answers (78%) were from their biological mothers, 53 (20%) from their biological father and 5 (2%) from adoptive mothers. One hundred and thirty-four of the respondents had a higher education level (University/ College) while 123 had a lower education level. Seventy-seven were women and seven were men among the nursery school respondents. The parents responded for 144 (53%) girls and 127 (47%) boys, distributed among age groups from one year up to six years. After removing stepparents, children with special needs and some unclear answers, the total number of respondents were 248 parents and 236 teachers. The number of children was quite similar among the three highest age groups while among the three lower age groups there were a declining number of children in each age group. The sex ratio was not statistically significant skewed from 1:1 for any age group.

RESULTS

Figure 1 sum up the difference in conflict levels between the parents and the teachers. The reported conflict levels within all contexts correlated highly significant both within the parents (Spearman rank tests; $0.164<\text{rho}<0.477$, $N=248$, $P<0.001$) and teachers groups (Spearman rank tests; $0.187<\text{rho}<0.633$, $N=236$, $P<0.001$). There was a statistically significant correlated difference between the reported level of conflict between parents and teachers in all eight context categories, parents always reporting a higher level of conflict (Wilcoxon signed rank tests, N=236, P<0.05 in all cases; Fig 1). However, the variation in level of conflict for each context was similar for parents and teachers (Spearman rank test, rho=0.886, N=8, P=0.003; Fig. 1). In the further analyses we therefore average the eight reported conflict contexts and call it "conflict level". Thus parents reported a mean conflict level of 2.3 (±SD=0.5, N=248) while the mean reported conflict level for the teachers was 1.9 (SD±0.7, N=236, Wilcoxon signed rank test, Z=-8.10, P<0.001). For each child, there was a statistically significant correlation between the reported conflict level of the parents and that of the teacher (Spearman rank test, rho=0.149, N=236, P=0.019).

There was no difference between the reported conflict level in relation to the sex of the child among parents (Kendall's tau- b=-0.064, N=245, P=0.219). However, among the teachers a statistically significant higher level of conflict with boys than with girls was reported (Kendall's tau-b=-0.12, N=232, P=0.017). Mothers (N=199) and fathers (N=49) did not report any significant difference in the level of conflict with their child (Kendall's tau-b=0.054, N=248, P=0.329). Among the teachers, on the other hand, the female (N=208) respondents reported a significantly higher level of conflict than the male (N=28) respondents (Kendall's tau-b=0.120, N=236, P=0.017). Single parents (N=38) reported a similar level of conflict as did two parents (N=210; Kendall's tau b=-0.037, N=248, P=0.438). We found no age related level of reported conflicts among mothers (Kendall's tau-b=-0.018, N=196, P=0.697). There was a negative correlation between reported conflict level and age of the child (parents; Kendall's tau-b=-0.140, N=248, P=0.003; teachers; Kendall's tau-b=-0.097,N=248, P=0.042).

A General Lineal Model (GLM) analysis in which conflict level was the dependent variable show that neither the sex of the parents nor the sex of the child had a significant influence of the conflict level (GLM corrected model, F=1.71, df=3, P=0.166). Among the teachers however, the sex of both the child and the adult contributed significantly to the conflict level (GLM corrected model, F=5.57, df=3, P=0.001; sex of teacher, F=6.63, df=1, P=0.011; sex of child, F=5.35, df=1, P=0.022). A confounding finding is that the teacher as a person also has a significant effect. Some teachers reported higher levels of conflict with their children than others (F=4.99, df=1, P=0.027).

DISCUSSION

Studies on humans are extremely easy to criticise because of the individual complexity and the many explanations that can be offered. Typically, there are as many views on matters as there are people involved. The present study is no exception, but we fail to find substantial and holding competing hypotheses for why there are such significant differences in conflict levels as described. Generally, conflict levels between parents and offspring can be viewed as a measure of differences in demands and cravings a child and its parents are upholding (Daly & Wilson, 1990). A child which is being discontent increases the level of conflict towards the providers, which during evolutionary time usually have been its biological parents (Buijzen & Valkenburg, 2003).

Social sciences use the questionnaire method quite extensively, and analyses of methodological difficulties are many and thorough (Schaeffer & Presser, 2003). One of the main problems of asking people is that one cannot be sure of whether the respondents remember correct, responds to the current mood he or she is in at the moment, twists the answer in a more acceptable direction, simply lies in the self-report or directly to an interviewer. These problems are usually met with an evaluation of in which direction it is likely that the answers will turn (Fowler, 1993). In our study we will argue that it is more probable that the parents have underreported the conflict levels than opposite in order to curb embarrassing quarrel levels with their children. Any possible skewed symmetry in the nursery teachers' answers is not so obvious. Teachers might underreport conflict levels to make it look as if they have better control and a better rapport with their kids, but the opposite may also be the case. Questionnaires of this kind might be interpreted by the teachers as a tool for getting more employees. There is generally a notorious lack of teachers in kindergartens, and reporting high conflict levels to the management might relieve the situation.

In questionnaire censuses there are two important factors; 1) the selection of respondents and 2) how the questions are raised (Fowler, 1993). In this research we considered both issues.

We spread our questionnaires to different nursery schools in different districts of Trondheim, and the questions were selected as statements, with the least probable as the first option. We also selected contexts that can be experienced both at home as well as in the nursery school, and at the same time are situations of investment and need for attention and care. There are no valid arguments that can be raised against the assumption that the contexts are comparable in how they are perceived by the children. A difference in environmental factors like the presence of nursery teachers instead of parents are precisely the factors we wanted to control for, and predicted different conflict levels from. The chosen contexts are in themselves situations well known leading to conflicts.

This study is based on a questionnaire, and not direct observations, because the individual persons' feeling of conflict level is the variable we wanted to address in order to test the hypothesis. Systematic errors like the possibility that nursery teachers might have a different perception of a conflict than parents seem highly unlikely, because the level of conflict reported by the adult person correlate between the different settings. The reported variation was similar for parents and school teachers being relatively high during meals, what was called typical indoor situations and when the adult person was correcting the behavior of the child. The lowest conflict levels were reported from both groups during toilet visits and the outdoor situations.

A clear pattern emerged in that the parent reported a higher level of conflict than the nursery school teacher in all eight social contexts. In general thus, the parent's perception is that the children during their daily life are more difficult to handle than the nursery school colleagues perceive it to be. We claim that the observed difference in conflict levels are a measure of higher demands for attention and care from the children at home than in similar contexts in the nursery school. The results give support for the hypothesis that children have an innate and selected mechanism that guides them in different social contexts, and that they easily assess differences important for the level of care and attention they can expect to get. Children expect a higher investment from their parents than from their teachers, and therefore solicit more in the parent-offspring context. Such contextual related behavior in the children will optimise their own social status and benefits in the form of resources and attention, and is the conceptual background for parent-offspring conflict (Barkow et al., 1992; Low, 2000; Ridley, 1994).

Studies of parent-offspring conflicts on a phenotypic level have increased in recent years (Kilner &

Johnstone, 1997; Kölliker, Richner, Werner, & Heeb, 1998, 1999; Mock & Parker, 1997). Particularly nestling birds may modify their solicitation behavior according to the strategy of their parents (Budden & Wright, 2001; Kedar, Rodriguez-Girones, Yedvab, Winkler, & Lotem, 2000; Kilner & Johnstone, 1997; Kölliker et al., 1998; Slagsvold, 1997). Increased level of soliciting by an offspring may lead to a higher effort by the parents which under natural conditions may be more costly for them in terms of fitness loss. For instance in birds, parents frequently respond to increased begging call activity by increasing their feeding effort (Burford et al., 1998; Davies et al., 1998; Ottoson et al., 1997; Wright, 1998). Variation in soliciting activity is measured by the rate of peeping or begging in chicken (Kölliker, Brinkhof, Heeb, Fitze, & Richner, 2000; Webster & Hurnik, 1987). Similar results have been found among rodents (Brunelli, Vinocur, Soo-Hoo, & Hofer, 1997; Graham & Letz, 1979). The crying of human babies induces physiological stress responses in their parents (Wiesenfeld & Zander Malatesta, 1983), and elicits caring behavior (Lummaa et al., 1998). Intensity of crying of human neonates differ significantly between individuals (Barr, 1999; Furlow, 1997; Korner, 1974), a variation that may be triggered by individual differences in genetic variation, physiology and individual life history (Kölliker & Richner, 2001).

Extensive work has been done to describe conflicts between family members without considering the evolutionary background for human behavior (e.g. (Demo & Cox, 2000; Lollis, van Engen, Burns, & Nowack, 1999). Giving one sibling more food, gifts or attention than the other has a tendency to evoke indignation, independent of whether either of them is in need of more or not (Mock & Parker, 1997). The reaction may be both loud and visible, or more subtle. This is an experience all parents have. More research is needed to test the hypothesis that the feeling of unfairness is generally more evident among siblings than among unrelated children, an analogous hypothesis to the one tested in the present study.

Our results of reported conflict level from the experimental situation (nursery schools) and at home were positively correlated, which might indicate a genetic component in the soliciting level in each of the individual children.

An interesting cultural deviance is described from China. In this country, parent-offspring conflict is culturally skewed towards the parents' benefit, because the children are taught filial piety and respect from not only the parents, but from all social institutions in the society. It is considered to be a shame not to be obedient (Yeh & Bedford, 2004). This is an example of how human universal behavior can be altered and adjusted with the help of culture. The conflict is nevertheless not removed, only muted down to a certain level, and is constantly being exposed to change back. The normal development of an adolescent into an attractive partner includes a necessary component of self-consciousness founded on the selected need to "stand on one's own feet", which typically includes opposing the parents (Low, 2000; Ridley, 1994; Steinberg, 2001).

Male offspring are more demanding, visible and risk-prone in their behavior, which could be an adaptation that works both to claim more resources and attention from their parents (Boomsma, Keller, & Nielsen, 1995; Clutton-Brock, Albon, & Guinness, 1984; Slagsvold, Røskaft, & Engen, 1986; Strohm & Linsenmair, 1999), and being competitive among peers, giving the boy a head start in the competition for status and position (Low, 2000; Ridley, 1994). In general, boys and girls behave differently almost from birth. Boys are more aggressive and play more rough and tumble (Boulton, 1996; Geary, 1998; Scott & Panksepp, 2003). Girls, on the other hand, are more into communications and making alliances (Leaper, Tenenbaum, & Shaffer, 1999; Low, 2000). The behavior of boys is often more loud and confrontational. Thus the behavior of the boys demands higher adult attention and investment. Our results support the idea that adults other than parents may consider these sex differences more troublesome and problematic. The parents are less considerate towards these differences, because it is "their child". The Trivers-Willard hypothesis suggests that it is more expensive to produce high quality boys with a high competitive edge, and the parents will be adapted to invest more as the boys are adapted to demand more resources and attention than girls (Trivers & Willard, 1973). This hypothesis is supported in numerous species (Bradshaw, Harcourt, & Davis, 2003; Janota, Soukup, & Thompson, 2002). For humans, the results are nevertheless inconclusive and obscured by factors difficult to control for (Keller, Nesse, & Hofferth, 2001; Koziel & Ulijaszek, 2001). The nursery school teachers functioned as a control group in our study, and the results indicate a higher investment in boys. Adults other than the parents will invest equal in children of both sexes, and because boys are more demanding, the level of conflict is expected to be higher between non-biological persons and boys.

(Fisher, 1930) argued that parents should invest equally in the two sexes, so if one of the sexes cost more to produce, this sex will die at a higher rate (Røskaft & Slagsvold, 1985; Slagsvold et al., 1986). Normally do boys die at higher rates than girls, and that might be a result of higher costs of producing boys (Røskaft & Slagsvold, 1985). However, parents might invest more in boys if this is evolutionary beneficial. Consequently, if parents report a similar level of conflict between boys and girls, our conclusion is that this may reflect a higher level of tolerance towards boys.

For the average parent, the benefit of investing more in boys than in girls may be higher in societies where competition between males are low, which implies a higher chance for the investment to be evolutionary profitable (Trivers & Willard, 1973). Already as new born, boys are bigger than girls and have spent longer time in the mothers' uterus (Low, 2000).

We found no difference between the sex of the parent and their reported level of conflict. If the children expect less from their father they will not escalate conflicts up to the same level as they would towards the mother. Therefore the parents may report similar levels of conflict even though the demand level with the father may be lower. Another constraint with this kind of data is a possible skewness in the responding fathers group (15 % of the respondents). Fathers responding to this questionnaire might generally be more willing to invest than those who did not respond. The education level of the responding fathers was also much higher than the average education level of Norwegian men, indicating that the father sample was skewed.

Environmental variability may lead to the maintenance of genetic variation in soliciting and providing behaviour because no single strategy does best under all environmental conditions (G A Parker & MacNair, 1978). Selection may favour phenotypically plastic strategies, which would allow individuals to cope optimally with changing environments (Kölliker & Richner, 2001). This is probably more important in humans than in other species.

We tested the sample for pseudo-replications among the nursery school teachers and found that there were individual differences in how they reported conflicts. Because nursery schools are typical female workplaces the male sample became insufficient. However, despite these differences, female teachers did report a higher level of conflict with the children than did men. The same explanation for this might be that children's demands are generally higher for women than for men.

Problems in foster families might be better understood in the light of the emotional differences between biological parents and foster parents. The two different settings might alter the expectations both adults and children have (Orme & Buehler, 2001).

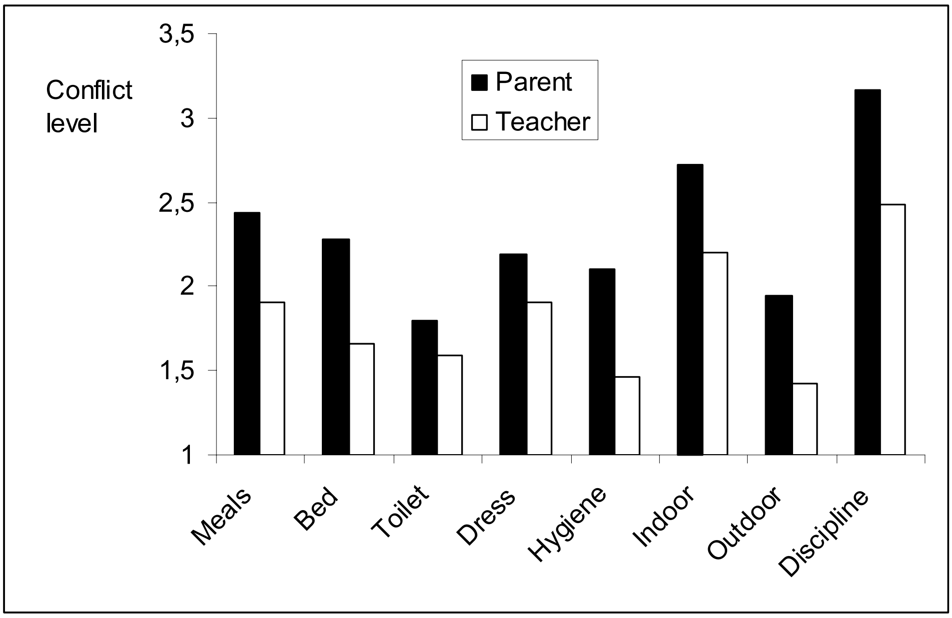


Fig. 1. Mean level of conflict between parents and offspring, and nursery school teachers and the same children, in eight different contexts.

References

Barkow, J. H., L. Cosmides, & Tooby, J. (1992). *The Adapted Mind*. New York: Oxford University Press.

Barr, R. G. (1999). Infant crying behavior and colic: an interpretation in evolutionary perspective. In W. R. Trevathan, E. O. Smith & J. J. McKenna (Eds.), *Evolutionary Medicine* (pp. 27-51). New York: Oxford University Press.

Boomsma, J. J., Keller, L. F., & Nielsen, M. G. (1995). A comparative analysis of sex-ratio investment parameters in ants. *Functional Ecology, 9*(5), 743-753.

Boulton, M. J. (1996). A comparison of 8- and 11-year-old girls' and boys' participation in specific types of rough-and-tumble play. *Aggressive Behavior, 22*(4), 271-287.

Bradshaw, C. J. A., Harcourt, R. G., & Davis, L. S. (2003). Male-biased sex ratios in New Zealand fur seal pups relative to environmental variation. *Behavioural Ecology and Sociobiology, 53*(5), 297-307.

Brunelli, S. A., Vinocur, D. D., Soo-Hoo, D., & Hofer, M. A. (1997). Five generations of selective breeding for ultrasonic vocalization (USV) responses in N:N IH strain rats. *Developmental Psychobiology, 31*, 255-265.

Budden, A. J., & Wright, J. (2001). Begging in nestling birds. *Current Ornithology, 16*, 83-118.

Buijzen, M., & Valkenburg, P. M. (2003). The effects of television advertising on materialism, parent-child conflict, and unhappiness: A review of research. *Applied developmental psychology, 24*, 437-456.

Burford, J. E., Friedrich, T. J., & Yasukawa, K. (1998). Responses to playback of nestling begging in the red-winged blackbird, *Agelaius phoeniceus*. *Animal Behaviour, 56*, 555-561.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1984). Maternal dominance, breeding success and birth sex ratios in red deer. *Nature, London, 308*(22 March), 358-360.

Daly, M., & Wilson, M. (1990). Is parent-offspring conflict sex-linked - Freudian and Darwinian models. *Journal of Personality, 58*(1), 163-189.

Davies, N. B., Kilner, R. M., & Noble, D. G. (1998). Nestling cuckoos, Cuculus canorus, exploit hosts with begging calls that mimic a brood. *Proceedings of the Royal Society of London Series B-Biological Sciences, 265*(1397), 673-678.

Dawkins, R. (1989). *The Selfish Gene* (2nd ed.). Oxford: Oxford University Press.

Demo, D. H., & Cox, M. J. (2000). Families with young children: A review of research in the 1990s. *Journal of Marriage and the Family, 62*, 876-895.

Don-Yehiya, E. (1998). Rituals of conflict: Religion, politics and public policy in Israel. *American Political Science Review, 92*(2), 492-493.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Fowler, F. J. (1993). *Survey Research Methods* (2nd ed.): Sage Publications.

Furlow, F. B. (1997). Human neonatal cry quality as an honest signal of fitness. *Evolution and Human Behavior, 18*, 175-193.

Geary, D. (1998). *Male, Female: The Evolution of Human Sex Differences.*

Godfray, H. C. J. (1991). Signalling of need by offspring to their parents. *Nature, London, 352*, 328-330.

Godfray, H. C. J. (1995a). Evolutionary theory of parent-offspring conflict. *Nature, London, 376*, 133-138.

Godfray, H. C. J. (1995b). Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. *American Naturalist, 146*, 1-24.

Graham, M., & Letz, R. (1979). Within-species variation in the development of ultrasonic signaling of preweaning vrats. *Developmental Psychobiology, 12*, 129-136.

Janota, S. M., Soukup, S. S., & Thompson, C. (2002). Male-biased offspring sex ratio in the house wren. *Condor, 104*(4), 881- 885.

Johnstone, R. A. (1999). Signaling of need, sibling competition, and the cost of honesty. *Proceedings of the National Academy of Science of the United States of America, 96*(22), 12644-12649.

Kedar, H., Rodriguez-Girones, M. A., Yedvab, S., Winkler, D. W., & Lotem, A. (2000). Experimental evidence for offspring learning in parent-offspring communication. *Proceedings of the Royal Society of London, Series B, 267*, 1723-1727.

Keller, M. C., Nesse, R. M., & Hofferth, S. (2001). The Trivers-Willard hypothesis of parental investment - No effect in the contemporary United States. *Evolution and Human Behavior, 22*(5), 343- 360.

Kilner, R., & Johnstone, R. A. (1997). Begging the question; are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution, 12*, 11-15.

Korner, S. F. (1974). The effect of the Infant's state, level of arousal, sex, and ontogenetic stage on the caregiver. In M. Lewis & L. A. Rosenblum (Eds.), *The Effect of the Infant on its Caregiver* (pp. 105-121). New York: J. Wiley.

Koziel, S., & Ulijaszek, S. J. (2001). Waiting for Trivers and Willard: Do the rich really favor sons? *American Journal of Physical Anthropology, 115*(1), 71-79.

Kölliker, M., Brinkhof, M. W. G., Heeb, P., Fitze, P. S., & Richner, H. (2000). The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proceedings of the Royal Society of London, Series B, 267*, 2127-2132.

Kölliker, M., & Richner, H. (2001). Parent-offspring conflict and the genetics of offspring solicitation and parental response. *Animal Behaviour, 62*, 395-407.

Kölliker, M., Richner, H., Werner, I., & Heeb, P. (1998). Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour, 55*, 215-222.

Kölliker, M., Richner, H., Werner, I., & Heeb, P. (1999). Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour, 55*, 215-222.

Leaper, C., Tenenbaum, H. R., & Shaffer, T. G. (1999). Communication patterns of African American girls and boys from low-income, urban backgrounds. *Child Development, 70*(6), 1489-1503.

Linstead, S. (1997). Abjection and organization: Men, violence, and management. *Human Relations, 50*(9), 1115-1145.

Lollis, S., van Engen, G., Burns, L., & Nowack, K. (1999). Sibling Socialisation of Moral Orientation: "Share with me!" "No, it's mine!" *Journal of Moral Education, 28*(3), 339-357.

Low, B. S. (2000). *Why Sex Matters: A Darwinian Look at Human Behavior*. Princeton: Princeton University Press.

Lummaa, V., Vuorisalo, T., Barr, R. G., & Lehtonen, L. (1998). Why cry? Adaptive significance of intensive crying in human infants. *Evolution and Human Behavior, 19*(3), 193-202.

Mock, D. W., & Parker, G. A. (1997). *The Evolution of Sibling Rivalry*. Oxford, New York, Tokyo: Oxford University Press.

Orme, J. G., & Buehler, C. (2001). Foster family characteristics and behavioral and emotional problems of foster children: A narrative review. *Family Relations, 50*(1), 3-15.

Ottoson, U., Bäckman, J., & Smith, H. G. (1997). Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca*. *Behavioural Ecology and Sociobiology, 41*, 381-384.

Parker, G. A. (1985). Models of Parent-Offspring Conflict. V. Effects of the Behaviour of the Two Parents. *Animal Behaviour, 33*, 519-533.

Parker, G. A., & MacNair, M. R. (1978). Models of parent-offspring conflict. I. Monogamy. *Animal Behaviour, 26*, 97-110.

Parker, G. A., & MacNair, M. R. (1979). Models of patrent-offspring conflict. IV: Supression: evolutionary retaliation by the parent. *Animal Behaviour, 27*, 1210-1235.

Parker, G. A., Royle, N. J., & Hartley, I. R. (2002). Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society of London B, 357*, 297-307.

Perezagote, A. (1986). The Role of Religion in the Definition of a Symbolic Conflict - Religion and the Basque Problem. *Social Compass, 33*(4), 419-435.

Ridley, M. (1994). *The Red Queen: Sex and the evolution of human nature*: Penguin books.

Røskaft, E., & Slagsvold, T. (1985). Differential mortality of male and female offspring in experimentally manipulated broods of the rook. *Journal of Animal Ecology, 54*, 261-266.

Schaeffer, N. C., & Presser, S. (2003). The science of asking questions. *Annual review of sociology, 29*, 65-88.

Schudlich, T. D. D. R., Shamir, H., & Cummings, E. M. (2004). Marital conflict, children's representations of family relationships, and children's dispositions towards peer conflict strategies. *Social Development, 13*(2), 171-192.

Scott, E., & Panksepp, J. (2003). Rough-and-tumble play in human children. *Aggressive Behavior, 29*(6), 539-551.

Slagsvold, T. (1997). Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Animal Behaviour, 54*, 1357-1368.

Slagsvold, T., Røskaft, E., & Engen, S. (1986). Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scandinavica, 17*, 117-125.

Steinberg, L. (2001). We know some things: Parent-adolescent relationships in retrospect and prospect. *Journal of research on adolescence, 11*(1), 1-19.

Strohm, E., & Linsenmair, K. E. (1999). Measurement of parental investment and sex allocation in the European beewolf *Philanthus triangulum* F. (Hymenoptera: Sphecidae). *Behavioural Ecology and Sociobiology, 47*(1-2), 76-88.

Summerfield, D. (1998). Protecting children from armed conflict - Children affected by war must not be stigmatised as permanently damaged. *British Medical Journal, 317*(7167), 1249-1249.

Thornhill, R., & Palmer, C. T. (2000). Why men rape - Prevention efforts will founder until they are based on the understanding that rape evolved as a form of male reproductive behavior. *Sciences-New York, 40*(1), 30-36.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist, 1*, 249-264.

Trivers, R. L., & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science, 179*, 90-92.

Webster, A. B., & Hurnik, J. F. (1987). Heritability of the peep vocalization in white leghorn-type chicks. *Applied Animal Behaviour Sciences, 19*, 157-168.

Wiesenfeld, A. R., & Zander Malatesta, C. (1983). Assessing caregiver sensitivity to infants. In L. A. Rosenblum & H. Moltz (Eds.), *Symbiosis in Parent-Offspring Interaction* (pp. 173-188). New York: Plenum.

Wright, J. (1998). Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from the play-backs of chick begging. *Behavioural Ecology and Sociobiology, 42*, 423-429.

Yeh, K.-H., & Bedford, O. (2004). Filial belief and parent-child conflict. *International journal of psychology, 39*(2), 132-144.

Doctoral theses in Biology
Norwegian University of Science and Technology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.

1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).

1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.

1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.

1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply

1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.

1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models

1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)

1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)

1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Salvesen, Ingrid	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Hilmo, Olga	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)

2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronical constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears

2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment

2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms