

Polyandry

In human societies and the animal kingdom.



Msc literature report
January 2003

Author:
Margreet Brouwer

Supervisor:
Dr. J.M. Tinbergen

Animal ecology
Rijksuniversiteit Groningen
The Netherlands

Polyandry

In human societies and the animal kingdom.

Margreet Brouwer
Groningen, January 2003

MSc. Literature report
Department of animal ecology
Rijks *universiteit* Groningen

Rijksuniversiteit Groningen
Bibliotheek Biologisch Centrum
Kerklaan 30 — Postbus 14
9750 AA HAREN

Abstract

Polyandrous mating systems are found in both animals and humans. This paper focuses on the different hypotheses posed in literature as an explanation of polyandry. In this paper I aim to discover to which extent human polyandrous mating societies differ from polyandrous mating populations of other species in the animal kingdom. I emphasise evolutionary aspects.

Polyandry has, in literature, a wide range of definitions. In this report polyandry is classified in two groups, narrow sense and broad sense polyandry. In human (narrow sense) polyandrous societies one female marries several brothers. This system is thought to prevent landfragmentation, population growth and fragmentation of other properties needed in harsh ecological conditions. Striking are the similarities between the functions ascribed to human polyandry and other narrow sense polyandrous species in the animal kingdom, as for example the dunnock and chalcidids. In broad sense polyandry multiple mating by the female is central. In contrast to narrow sense polyandry a pair bond between partners is not required and males do not mate solely with one female.

Broad sense polyandry hypotheses are often based on genetic fitness benefits of multiple mating by females. Although no genetic fitness benefits of narrow sense polyandry are given in literature, I propose that for example the genetic diversity hypothesis might apply to narrow sense polyandrous species. The inbreeding avoidance hypothesis and sperm competition may possibly also give insight in why some species mate narrow sense polyandrously.

At last, factors affecting the stability of narrow sense polyandry are explored. These factors are, stability of environment, economic diversity, and number, age and relatedness of male partners.

Table of contents

Abstract

Table of contents

1. Mating systems	Page(s) 1 - 2
1.1 Human polyandry	
2. Narrow sense polyandry	Page(s) 3 - 5
2.1 Sex ratio	
2.2 Limiting population growth	
2.3 Landfragmentation	
2.4 Organize labour	
3. Parental care in narrow sense polyandry	Page(s) 6 - 8
3.1 Paternity	
3.2 Parental effort	
3.3 Male-only care	
4. Broad sense polyandry, genetic benefits	Page(s) 9 - 14
4.1 Promotion genetic diversity	
4.2 Prevent inbreeding, bet hedging	
4.3 Sperm competition	
4.4 Sperm storage	
4.5 Intragenomic conflict and genetic incompatibility	
5. Stability of narrow sense polyandry	Page(s) 15 - 18
5.1 Environmental and economic stability	
5.2 Social structure	
6. Discussion and conclusion	Page(s) 19 -21
References	Page(s) 22 - 24

1. Introduction: Mating systems

There are three main types of mating systems found in the animal kingdom and the human world, namely: monogamy, polygyny and polyandry. A mating system is a behaviour strategy to obtain mates. Polyandry is the subject of interest in this literature research. Polyandry is a broad term and used for the mating system in which one female mates with more than one male. Polyandry (narrow sense) in human societies mostly occurs between one female and several brothers. This female and her males have a pair bond in the form of a marriage. Explanations given for human polyandry mainly focuses on the control of resources and parental care as a result of a harsh environment. Economic, ecological and demographic variables play an important role in those explanations (Levine 1997). For some other polyandrous species of the animal kingdom those hypotheses do also apply. In the hypotheses explaining human polyandry hardly no attention is paid to possible genetic benefits of polyandry. Hypotheses explaining polyandry from a genetic point of view, so called broad sense polyandry, in which multiple mating by females is central are also discussed. They can provide alternative hypotheses for human narrow sense polyandry. The comparison of the hypotheses explaining narrow sense polyandry in human societies and other species of the animal kingdom is central in the study. In this literature review; polyandry, the existence and the stability of it will be discussed.

1.1 Polyandry

All human societies face certain problems for which kinship systems, marriage, and the creation of families offers solutions. Every society must regulate sexual access between males and females, must find satisfactory ways to organise labour between males and females, must assign responsibility for child care, and must provide a system to transfer property and social position between generations (Nanda 1998).

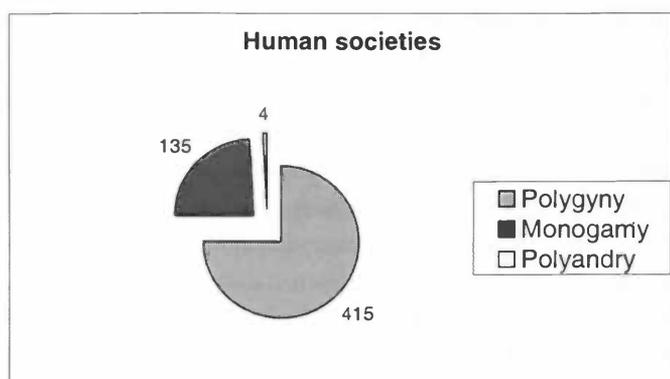


Figure 1: Mating systems in human societies

In a world sample of 554 societies, polygyny was favoured in 415, monogamy in 135 and polyandry only in 4 (Figure 1). About 70 percent of the world's societies prefer plural marriage (Nanda 1998). Polyandry is found primarily in parts of Tibet, Nepal and among the Toda and Pahari Hindus of India (Nanda 1998). It is not known whether these societies originated from one society or whether polyandry developed independently in those societies.

Also in other species of the animal kingdom polyandry is found. In birds monogamy is the dominant mating system, occurring in more than 90 percent of the species studied. True polyandry is extremely rare. Most documented cases are restricted to the avian orders Gruiformes and Charadriiformes (Emlen & Oring 1977). Also for insects

polyandrous mating is very rare. The overwhelming majority of species of social ants, bees, and wasps mate only once (Strassman 2001). The reverse appears to be true for mammals, less than 3 percent of the mammal's species having been reported as monogamous (Kleiman 1997). But strict polyandry also seems to be rare too for mammals.

Understanding polyandry challenges both traditional sociocultural and evolutionary understanding of marriage (Haddix 2001). For those interested in the evolution of behaviour, the existence of polyandry is difficult to explain. It appears to limit male productive success, defined as the number of surviving offspring produced. All human populations reproduce well below the theoretical maximum level of fertility, which considered to be more than 20 offspring per woman. The highest total fertility rate is found among Hutterites, an Anabaptist sect in North America (9.8 offspring per female, Wiley 1998). That total fertility rates as below 3.5 are found, requires explanation. Males that share access to a female are likely to leave less descendants than males that monopolise access to a female. Thus, the existence of polyandry may contradict the general prediction that evolution will favour the development of behaviours that increase the ability of individuals to survive and reproduce (Levine 1997). As in all behaviour, fitness advantages are used to give an evolutionary explanation for the existence of the behaviour. Fitness measures the reproductive success of an individual (or a genotype) relative to the reproductive success of other individuals (or genotypes) in the same or in other population (Emlen and Oring 1977). Human behavioural ecologists have used studies of marital strategies as one tool to understand human "mating" behaviour in general. These studies have identified some of the rules that people use in different cultural and environmental contexts as they make decisions about mate choice and reproduction (Haddix 2001). Thinking about why human females might have several sexual partners can give us some insight in why animal females do so. In this literature report two types of polyandry will be discussed, differing in broadness of its definition. The first type is the narrow sense polyandry. In the narrow sense polyandry one female mates with more than one male with which she has a pair bond. The males in this type of polyandry mate only with this one female. In this narrow sense polyandry females may trade sex for resources: money, food, a house, parental care or fertility. The second type is more broadly, and therefore called broad sense polyandry. In this broad type of polyandry the focus is on a female gaining extra matings, there is no pair bond required, nor do males mate only with one female. Females may engage in extra-pair copulations in order to improve the genetic quality of their offspring (Birkhead 2000). Because the main focus of narrow sense polyandry is on environmental and economic variables, attention will be paid to the broad sense polyandry to provide us with alternative, on genetic benefits based hypotheses for the narrow sense polyandry.

2. Narrow sense polyandry

As discussed in the first chapter, marriage is a manner in which societies dictate sexual access between males and females. In narrow sense polyandry, the ecological background plays a very important role in explaining its existence. The ecological conditions, which favour polyandry in human societies is a harsh environment. A corollary of the view that polyandry is a response to specific environmental constraints is the idea that men who marry polyandrously actually may have greater reproductive fitness than those who marry monogamously or polygynously (Levine 1997). In this chapter benefits of the narrow sense polyandry found in human societies and other species of the animal kingdom will be discussed.

2.1 sex ratio

For sexual access between males and females the sex ratio plays an important role.

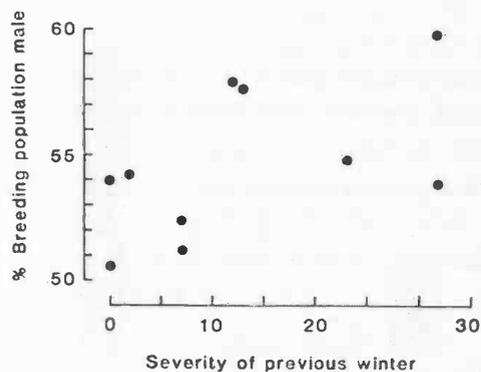


Figure 2: After Davies 1992. The sex ratio of the breeding population ($n = 10$ years) was more male-biased following a harsh winter.

Although no examples of a skewed sex ratio were discussed for human polyandry, it plays a role in narrow sense animal polyandry. The sex ratio can be affected by a harsh environment. In discussing the sex ratio, not the sex ratio of the overall population is important, but rather the ratio between fertilisable females to sexually active males. A skew in this ratio towards females promotes polyandry. This skew can occur as a result of several aspects. Davies, who studied dunnocks (*Prunella modularis*), found that harsh winters have a larger effect on the survival of

female dunnock than on the survival of male dunnocks. As a result of increased mortality among the females in harsher winters there was a greater male-bias in the sex ratio of the breeding population following a hard winter (Fig. 2). The severity of the winter and its effect on the sex ratio was partly responsible for the variation between years in the frequencies of the different mating systems (Davies 1992). Also for the native Tasmanian hen a skewed sex ratio was found. Trios are formed composed of two related males with one unrelated female. Both males appeared to mate with the female. Associated with this breeding structure, there

Non-breeders

In polyandrous populations or societies in which the ratio between fertilizable females and sexually active males is more or less one, females will be left over. In human societies these non-breeding individuals often provide care in other families or join a monastery.

These non-breeding individuals can be essential for the natal group. Saddleback tamarins (*Saguinus fuscicollis*) should mate in simple pairs only if they have older offspring living with them that could serve as helpers. In the absence of helpers, both males and females might benefit from conceiving and rearing young as polyandrous trios (Goldizen et al. 1996). Whether or not such nonbreeding auxiliaries will participate as helpers in the breeding activities of the group will depend upon costs and benefits of such aid giving, measured from the viewpoint of both breeder and helper (Emlen 1982). See also the text box "helpers at the nest" at page 5.

were more males than females among the young birds. But, the primary sex ratio was unknown. Maynard Smith (1972) assumes that polyandry evolved as an adaptation to the skewed sex ratio in the native Tasmanian hen. A skewed sex ratio was also found in the studied population of saddleback tamarins. Young females of saddleback tamarins (*Saguinus fuscicollis*) appear to wait in their natal groups for the first opportunity to fill a primary breeding position in their own or a neighbouring group. Variation in female lifetime reproductive success among saddleback tamarins is high. Half of the females studied from the time of birth never bred. The other half produced on average 3.5 young. In groups in which two females were present, the oldest female was the primary breeder, though breeding by secondary females did sometimes occur. A paucity of female breeding opportunities may explain high mortality of females between 2.5 and 4.5 years of age, resulting in a male-biased adult sex ratio (Goldizen 1996).

2.2 Limiting population growth

One manner to deal with a harsh environment is limiting the population growth. Polyandry has a role in limiting overall population growth while contributing to large labour forces within polyandrous households (Wiley 1998). This form of group selection can be seen as adaptive behaviour because the high-latitude Himalaya cannot support large and dense populations that would require large-scale, intensive agricultural production. At the same time, given the labour intensity and highly seasonal nature of agricultural production, individual households need large labour forces (Wiley 1998).

2.3 Landfragmentation

In human polyandrous societies, as a result of a harsh environment, several brothers marry one women to prevent landfragmentation. If one brother should marry monogamously or polygynously, there would not be enough food to support all these families. Polyandry benefits individuals and families by preserving large parcels of land (Levine 1997). Sri Lankan polyandry was a means of resolving social structure contradictions created when men and women both inherited substantial property and brothers maintained joint ownership of land. Under such circumstances, brothers found their interest divided by their wives' distinct property shares – a problem that could be avoided by polyandry (Levine 1997). The Toda of south India have the same reasons for marrying polyandrously (Nanda 1998). Also in the Indian Himalayas, where polyandry is commonly combined with polygyny, the beneficial consequences identified include less land fragmentation (Levine 1997). The importance of the environmental circumstances for the stability of polyandry is not only noticed for human societies. In other species of the animal kingdom a harsh environment can result in very low breeding opportunities for individuals. The hypotheses that polyandry has a function against the land fragmentation, and provides a surplus of male parental care, are not only found in human societies. In the animal kingdom so called helpers exists. The existence of helpers is often accredited to a shortage of land as well as to poor quality of available territories (see textbox “helpers at the nest”).

2.4 Organise labour

Polyandry in human societies regulates the labour that must be provided to successfully support a family. Under harsh environmental conditions more labour of parents may be needed to raise their offspring. In a society where men must be away from home for long periods of time, polyandry provides a woman with more than one

"Helpers at the nest"

The landfragmentation hypothesis as an explanation for polyandry has similarities with the benefits animals may have when they act as helpers. There are three possible circumstances under which males might act as helpers. Namely 1) as immatures that remain in their natal groups to act as helpers until they can acquire breeding territories of their own. The other two possible circumstances involve mature males. 2) When one male joins another on his territory in order to inherit the territory when the owner leaves or dies (satellite strategy) and 3) by forming a coalition with one or more males between whom the breeding (mating and helping) is shared (alliance strategy).

Satellite strategies in which the satellites own benefit comes from inheriting the territory occur widely throughout the animal kingdom (Dunbar 1995), though they do not normally involve parental care by the satellite. Alliance strategies are relatively rare. They occur under two conditions. 1) In groups of unrelated males when coalition size determines the duration of tenure or the success with which young are reared (dunnocks, Davies 1992). 2) By groups of related males where either the males share equally in mating opportunities (Tasmanian native hens, Ridpath & Maynard Smith 1972) or one male offsets a lower rate of mating by providing parental care for his brother's offspring (e.g. some human populations) (Dunbar 1995).

husband to take care of her and her children (Nanda 1998). Polyandry benefits individuals and families, supplementing inadequate male labour, and increasing the likelihood that one adult male would be at home while others are absent (Levine 1997). In the next chapter parental care provided in polyandrous populations will be discussed in more detail. Not only the amount of labour provided by males is important, but also the diversity of economic activities of males influence the stability of a polyandrous marriage.

Summarising, hypotheses given to explain narrow sense polyandry are mainly dealing with

ecological, economical and demographical variables which are influenced by harsh environmental conditions. The functional explanations of human polyandry proposed by sociocultural anthropologists are also proposed by evolutionary biologists. That means, those hypotheses are proposed for as well human polyandrous societies as other narrow sense polyandrous species of the animal kingdom. Explanations of narrow sense polyandry are subject to criticism – namely, that it is difficult to establish a consistent connection between specific economic, ecological, or demographic variables and the presence or absence of polyandry (Levine 1997).

3. Parental care in narrow sense polyandry

One explanation why females copulate with different males is to trade sex for parental care (Soltis & McElreath 2001). But more can be said about parental care in

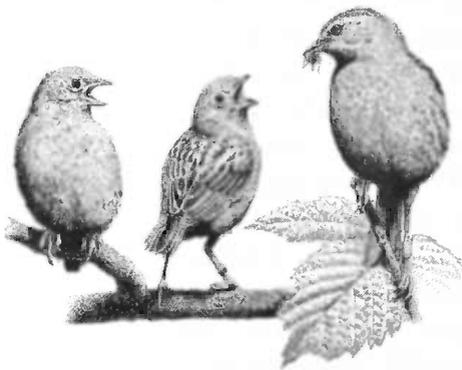


Figure 3: After Davies 1992. A dunnock male with two fledglings. Males help to feed the young only if they copulated with the mother earlier on in the mating period.

polyandrous mating species. The theoretical ideas in the papers by Maynard Smith (1972) and Emlen and Oring (1977) suggest that a detailed study of costs and benefits of parental care for males and females, together with a consideration of the potential to gain extra mates, might help to explain the variability (Davies 1992). It has been suggested that an important effect of parental care is its influence on the potential rate of reproduction of each sex. The sex with the highest potential rate of reproduction will be limited by the availability of the opposite sex. A strong selective advantage for male participation in parental care, such as guarding and defending offspring has been

suggested. Individuals will sometimes work harder if others do less and this raises the question whether it would pay to cheat by reducing parental effort and so relying on compensation responses by others (Davies 1992). If there is mating exclusivity, it is important that a male ensures that his offspring survives to reproductive age. Game theoretical analyses show that male investment in multiple females' offspring is favoured when male care increases offspring fitness, future-mating opportunity is limited, and group size is small. Under such circumstances, females may benefit from polyandry and receive parental investment from more than one male.

There are, however, several methods by which a male can contribute to the rearing of his offspring, and males of different species may exhibit any one of these paternal care patterns in varying degrees. The behavioural patterns are divided into direct and indirect forms of help. Indirect parental investment includes nest building and defence of the home range or nest, whereas direct interactions involve both proximity and responsiveness to the young (Kleiman 1977).

3.1 Paternity

In human polyandrous societies, when a wife becomes pregnant, determining the biological father is not considered necessary. Rather, a ceremony called "giving the bow" held in the seventh month of pregnancy, assigns the child a legal

Male incubation

In a very small percentage of species, males have assumed the full burden of incubation and brood rearing. Males should assume the bulk of parental care only when their individual fitness is increased through such an action. Bird species that exhibit male-only care tend to come from families that habitually nest at very low densities; usually less than one nest every hectare. In species belonging to lineages that are predisposed to offspring desertion but nest at low density, the male would gain very little from deserting because he is relatively unlikely to find another female in reproductive conditions (Owens 2002). Complete male parental care is most likely to develop in groups with slight to moderate parental care needs (precocial young). It should also be more prevalent among determinate than indeterminate egg layers (Emlen & Oring 1977). Male incubation preadapts a species for possible evolution towards polyandry (Emlen & Oring 1977).

or social father. This man makes a ceremonial bow and arrow from twigs and grass and presents these to the wife in front of his relatives. Usually the eldest brother performs the ceremony, and all subsequent children are considered his. After two or three children are born, another brother usually gives the bow. Occasionally a woman marries several men who are not biological brothers. When these men live in different villages, the wife lives in the village of each husband for a month. The men arrange among themselves who will give the bow when she becomes pregnant (Nanda 1998). Among the Karnali Tibetans, however, all paternity is attributed to the eldest brother and in fact, by villagers' report, younger brothers do in fact seem to have more limited opportunities to father children (Haddix 2001). For the amount of parental effort a dunnock male will provide, the change he fathers the offspring is important. The studied dunnock (*Prunella modularis*) showed that males feed nestlings more when they have higher change of paternity (Figure 3).

3.2 Parental effort

Among most animals, female parental effort greatly exceeds that of males. Consequently, most cases of polygamy involve male emancipation and the development of polygyny. However, a significant portion of species share parental care rather equally just as human polyandrous societies. Examples of such species are the dunnock (*Prunella modularis*), the native Tasmanian hen, the goldenlion tamarin (*Leontopithecus rosalia*) and the saddleback tamarin (*Saguinus fuscicollis*). In polyandrous groups of saddleback tamarins, two males share a female's copulations and co-operatively care for the young (Goldizen 1996). The same feature is observed for the golden lion tamarin, although paternity is more often monopolised by a single male.

3.3 Male-only care

When the future physical condition of the female is of direct importance to the male, a male increases his fitness through providing full parental care. When the female is no longer dependent on breeding conditions, she is able to produce

Deserting

As said, male-only care does not occur in mammals as a result of the internal gestation and lactation by the female. The care a male mammal provides, hinges on the benefits of deserting his female and young. The desertion of a male partly depends on how long it takes him to locate other females. Since the time taken to locate a second female is a function of the area the male has to search, the easiest way for a female to reduce the likelihood that the male gains by deserting her without incurring a serious cost for herself is to manipulate the probability that the male will locate another oestrous female. She can maximise the male's search cost most effectively by ensuring that other females remain as far away from her as possible (Dunbar 1995). But there are other options, prolonging the period that the male is forced to stay with the female in order to ensure fertilisation. One is to demand a high level of initial investment in pair bonding and/or a prolonged courtship from any prospective mate. The second is for females to conceal ovulation so as to force the male to mate with the female over a longer period in order to be sure of impregnating her (Dunbar 1988). The final option is for females to synchronise their reproductive cycles so as to make it difficult for a male to locate a second female who has not already been fertilised (Dunbar 1995). Factors that have been argued as promoting the occurrence of co-operative breeding and male care include the lack of opportunity to breed outside the group, increase in inclusive fitness, gain breeding experience, maintenance of group membership with the possibility of reproductive success in the future and in males the advantages of co-emigration with infants they helped to raise. In addition, infant carrying may be a courtship strategy of males (Rylands 1996).

additional or replacement clutches for the male. Lack of dependability can either result from great fluctuations in environmental suitability for breeding or from very low success rates of reproductive attempts (caused, for example, by high predation rates). From male's point of view, female emancipation can be viewed as an insurance strategy – when the failure rate is sufficient high, the cost involved in incubation may be less, on average, than the gain accrued by having a mate physiologically able to rapidly produce new clutches of eggs (Emlen & Oring 1977). From a female's viewpoint, the principle advantage of male incubation is a lessening of her metabolic burden, freeing her to devote increased time and energy to replenish nutrient and mineral reserves drained through egg production. Females also may experience large benefit from desertion, because they can mate with any male. Indeed, in some species there is evidence that deserting females store sperm from their first male and use this sperm to lay a second clutch of eggs that are then either incubated by the second male or even by the female herself. Desertion is, therefore, a safer option for females than males because females can always have at least one more reproductive opportunity, providing the breeding season is sufficiently long (Owens 2002) (see text box “deserting”). Emancipation allows the female opportunity to increase her fitness through continued production of multiple clutches. Female fitness can be increased only to the degree that males are sexually receptive and available to assume incubation of these additional clutches (Emlen & Oring 1977). For mammals as a result of internal gestation, the opportunity for a female to desert is lower than for birds. Since the female mammal has internal gestation and feeds developing offspring with products of her body, she is indispensable for the rearing of young. In mammals therefore, male only care does not exist (Kleiman 1977).

4. Broad sense polyandry, genetic benefits

In addition to the hypotheses discussed to explain narrow sense polyandry, in this chapter hypotheses from the broad sense polyandry will be discussed in order to deduct alternative (genetic) hypotheses for narrow sense polyandry. Darwin first discussed mating systems in a genetic context. Since then, major developments in genetic theory have allowed a better understanding of sex ratios, sexual dimorphism, and differential patterns in parental care (Emlen & Oring 1977). Hypotheses about the existence of polyandry dealing with genetic benefits are mainly found in articles about the animal kingdom. The idea that females have anything at all to gain by copulating with more than one male (broad sense polyandry) has had a rocky history (Birkhead 2000). Perhaps the solution to the mystery of multiple mating by females during their fertile period is contained in a related discovery that mate choice may yield genetic benefits. The importance of such findings for the theory of breeding systems is that genetic quality of mates supplements or supplants direct resources when animals shop for mates (Reynolds 1996). Females generally gain directly from remating in terms of increased reproductive fitness (Arnqvist & Nilsson 2000).

4.1 Promotion of genetic diversity

According to the genetic diversity hypothesis, females mate multiple to increase the genetic diversity of offspring produced in their lifetime. By having several sexual partners females might increase the genetic diversity of their offspring. In a rapidly changing world this might ensure that at least some female's offspring are adapted to prevailing environmental conditions and so will reproduce (Birkhead 2000). This hypothesis has been applied to social insects by Strassman (2001), and to the ruff by Lank (2002). Strassman found that multiple mating might occur among social insects because of the need for more sperm to fertilise the eggs, and the advantage of a genetically diverse brood. The workers remain together in close proximity, which could facilitate disease transmission among them, so a genetically diverse brood could be more resistant to diseases. Another advantage of a genetically diverse brood is that it could facilitate task specialisation (Strassman 2001). Also for bird species the genetic diversity hypothesis is mentioned. In pair-bonded species, certain

Two male morphs: the ruff

Why is polyandry unusually frequent in ruffs relative to other lekking species and to related shorebirds? Neither good genes, nor better genes, nor fertility insurance, nor inducing direct sperm competition and/or sperm selection by females predict the disproportionate crossmorph mating (Lank 2002). Active genetic diversification may apply with respect to the behavioural polymorphism in ruffs because of a Mendelian genetic basis for male behavioural morph determination and aspects of male – male co-operation and female choice (Lank 2002). One alternative hypothesis is that genetic diversification of offspring *per se* is favoured. Although genetic diversification is, according to Lank, a universal consequence of polyandry, it has widely been assumed to be inapplicable for birds in general (Lank 2002). Three common objections against its importance may be less applicable for the specific trait of male behavioural morph. First, females will substantially increase the genetic diversity of their offspring through multiple mating, at least with respect to male morph. Second, a theoretical decrease in parental fitness through increased sib competition in mixed broods is less applicable in a precocial species with small clutch size. Finally, because most ruffs do pursue polyandrous matings, rather than only those females whose partners are perceived as being of lower genetic quality, an adaptive role for diversification *per se* is plausible (Lank 2002).

females may attempt to improve the genetic benefits of their offspring through extrapair copulations, despite potential retaliation from their social mates (Birkhead & Moller 1993, Lank 2002). Lank (2002) used this hypothesis to explain polyandry for the lekking ruff (see text box “Two male morphs: the ruff”). Many published studies of birds documented non-random choice of extrapair mates, or second mates in non-pair-bonded species, which suggests choice for particular phenotypes potentially related to good genes (Lank 2002). This intriguing observation is consistent with the hypothesis that females actively diversify their offspring with respect to male morph (Lank 2002). The genetic diversity hypothesis might also apply to narrow sense polyandrous species. As discussed in previous chapters, for many narrow sense polyandrous species, a unstable environment lies on the basis of hypotheses explaining polyandry. Diversity of offspring might, especially in changing conditions, be favourable because it increases the chance that some of the children will become adults and reproduce. Furthermore, task specialisation is mentioned as benefit of offspring diversification. In human polyandrous societies a higher task specialisation increases the stability of a marriage. If diversity of the brood increases task specialisation, genetic diversity of offspring from polyandrous pair would have more stable pairbonds when they become adults and marry a female. Although the genetic diversity hypothesis seems to be sensible at first sight, population geneticists consider that the additional genetic variation a female would gain from being inseminated by more than one male would be trivial. The point can be most clearly seen by thinking of ourselves: we each have 23 chromosomes and, as a result of meiosis and recombination, a man can potentially produce 2^{23} different sperm types. It has therefore been assumed that by copulating with several partners females will do little to increase the genetic diversity of their offspring (Birkhead 2000). But for species as the ruff, with two different male morphs this hypothesis could apply.

4.2 Prevent inbreeding, Bet hedging

Stockley et al. (1993) proved in their study about the shrew (fig. 4) that the females did not avoid mating with relatives to prevent inbreeding. If females cannot always distinguish close kin, then they may copulate with several different males and so reduce the risk that all their offspring will be sired by a close relative (Stockley et al. 1993). Reduced fitness or inbreeding effects in offspring resulting from copulations between close relatives are well documented. If females are capable of sperm selection, they might therefore be expected to discriminate against the sperm of sibling males during sperm competition (Stockley 1999). In my opinion this hypothesis is important in species with small populations and very little dispersion from their natal groups: for example some narrow sense polyandrous chalcid species.



Figure 4: A shrew.
library.mcz.harvard.edu/spec_col/

4.3 Sperm competition

In many hypotheses about genetic benefits of multiple mating by females, sperm competition plays a role (see for example text box “intrinsic male quality”). The perspective of sperm competition has greatly increased our understanding of why males mate repeatedly with the same female, as well as male adaptations such as mate guarding, genital structure, testis size, ejaculate volume and sperm design (Reynolds

1996). But females provide opportunities for increased competition among sperm of different males, by increasing the length or complexity of their reproductive tracts (Keller & Reeve 1995). Lank found evidence for this in his study population of ruffs (*Philomachus Pugnax*). Females fertilised eggs using stored sperm, and the sperm size of the ruff support an evolutionary history of sperm competition and multiple

Intrinsic male quality

The quality of a male may be determined by sperm competition. Polyandry may enable sperm competition or female choice of sperm to increase the probability that eggs are fertilised by sperm from high-quality males; the so called intrinsic male quality hypothesis (Madsen 1992, Zeh & Zeh 1996). Under the intrinsic male quality hypothesis sperm competition plays an important role. The relationship found by Madsen (1992) between the number of matings of female adders and the mean viability of their offspring is consistent with a correlation between male quantity and fertilisation efficiency. The field studies of Madsen (1992) on Swedish adders provides evidence that multiple mate copulations, with different partners each time, increase offspring viability. Like all snakes, adders lack male parental care, and female co-operation is required for successful copulation. After mating, females store sperm in their reproductive tracts for months before ovulation. Female adders mate more than once per season, and usually with a different male each time. The female's reproductive success (litter size) is determined by the amount of energy she allocates to reproduction, so her reproductive output is not enhanced by additional matings: the number of copulations by a female was not significantly correlated with her litter size or with her fecundity relative to body size. Madsen argues, that a female adder benefits from multiple copulations through the genetic quality of her offspring. This advantage apparently results from more intense sperm competition in the female's reproductive tract, resulting in a higher proportion of her ova being fertilised by genetically superior males. Genetic factors may be particularly important in small isolated populations, because of the high potential for inbreeding depression. Females that mate more frequently are fertilised mostly by the sperm of 'better' males. The proportion of viable offspring increases with additional matings (Madsen 1992). In the article 'Snakes and female sexuality' Parker explores some doubts about the theory of Madsen. If rival ejaculates are similar in all but genes, the hypothesis of Madsen demands a correlation between sperm success and offspring viability. It is not immediately obvious why sperm carrying genes that increase offspring viability should outcompete rival sperm, unless the same deleterious mutations affect almost all aspects of phenotype, from gamete to adult. If this mechanism applies, proof is needed that stillborn offspring tend to come from males whose sperm fare badly under sperm competition (Parker 1992). Another question why females don't simply filter out 'poor quality' males by refusing to mate with them. Maybe females cannot discriminate between males, and rely on sperm competition as their only option (Parker 1992). At last. This hypothesis can not be applied to all polyandrous mating species. Only species which store sperm for longer periods can have sperm competition resulting in high quality offspring.

paternity. In passerine birds and shorebirds, sperm size increases with higher rates of multiple paternity, and ruffs have the longest sperm of any shorebird yet measured (Lank 2002). The anti-sperm response of females provides an other manner in which sperm competition may take place. Keller & Reeve (1995) (see text box "sexual

selected sperm hypothesis”) pointed out that there are several means by which females may increase the probability that their eggs will be fertilised by a male with high fertilisation efficiency, including the following: providing a challenging genital environment. Two selective forces may work in species in which males are able to displace sperm. First, the probability that a male with relatively ‘vigorous’ sperm will fertilise eggs is higher when females acquire similar amounts of sperm than when they acquire uneven amounts of sperm from different males. Second, females should also want their eggs to be fertilised by males that are efficient in displacing the sperm of other males. The outcome is that females should let the second male try to displace sperm, but make it so difficult that only ‘good’ males can achieve this feat and they should resist a males attempt to remating (Keller & Reeve 1995). If sperm of different males differ in their success in fertilising an egg, females may increase this variability by producing a challenging genital environment in which only the most ‘vigorous’ sperm could reach and fertilise an egg. Evidence suggest that this may be true in mammals and birds. There can be important immune responses against sperm, with high concentrations of antisperm antibodies occurring in the cervical mucus of a number of species, including humans (Keller & Reeve 1995). In species with internal fertilisation males typically inseminate very large numbers of sperm of which only a tiny proportion ever reach the vicinity of the ova (Birkhead 1993). In terms of its structure, chemical composition and immune response, the female reproductive tract of mammals and birds is particularly hostile to sperm (Birkhead 1993). Birkhead (1993) considered a number of explanations for why female anti-sperm responses have evolved in birds and mammals (Birkhead 1993). The barriers to sperm are diverse: physical barriers, chemical composition of the cervical mucus differs markedly from what is apparently optimal for sperm, phagocytosis, immune responses (high concentrations of anti-sperm antibodies occur in the cervical mucus of a number of mammals, including humans) (Birkhead 1993). Birkhead (2000) explains the female anti-sperm responses in the following way. A non-functional, proximate explanation for high sperm mortality is that it is merely a consequence of females making conditions in their reproductive tract hostile to any foreign bodies, including bacterial infections, parasites and other pathogens. On consequence of this hostile environment is that most sperm die. During reproduction the increase in sex hormone results in the female’s immune system being depressed at this time. The relatively long generation time of sperm compared to the generation time of bacteria and other pathogens, prevents males from never overcoming these female anti-sperm responses (Birkhead 1993). Birkhead (1993) also proposed that female anti-sperm responses provide mechanisms by which females ensure that their eggs are ‘fertilised’ by the fittest sperm, or minimise the risk of being fertilised by the ‘worst’ sperm in the population. Whereas their hypothesis posits female choice based on inherent male genetic quality, the genetic incompatibility hypothesis asserts that sperm quality is a relative characteristic which depends, at least in part, on the genetic of the female herself (Zeh & Zeh 1997).

4.4 Sperm storage

In discussing the anti-sperm response there is one important difference between birds and mammals, namely the ability of storing sperm. In bird species, during copulation the male deposits sperm in the female’s vagina: some sperm subsequently move into storage tubules located at the utero-vaginal junction. Sperm are then released over days, or weeks, from these tubules and carried up the oviduct to the infundibulum where fertilisation takes place. The more frequent a female recopulates, the more

likely it is that sperm competition will occur, depending of course, on when remating takes place relative to how many sperm the female has in her sperm store. If a female waits to remate until her sperm stores are empty, then sperm competition will be non-existent. But if, as occur in nature, she remates as soon as she's less than half full, sperm competition will be intense (Birkhead 2000). However, few of the sperm inseminated ever reach the sperm storage tubules and fewer still reach the infundibulum. Many sperm are ejected from the female's cloaca within 30 to 60 minutes of insemination. In birds the utero-vaginal junction serves, among other things, as a barrier to sperm. It was originally thought that the sperm storage tubules were responsible for the selection of sperm, but it now appears that selection, on basis of spermatozoan surface properties, takes place in the vagina (Birkhead 1993). Processes of sperm selection similar to those described for birds also occur in mammals, although most mammals do not store sperm for as long as birds. Only a small proportion of the sperm inseminated reach the distal parts of the female reproductive tract. As in birds, some female mammals actively eject sperm (rats, pigs, sheep, humans etc.). But despite the apparent similarity between polyandrous marriage in humans and polyandrous mating system in birds, the potential for sperm competition among humans is probably rather limited (Birkhead 2000). Sperm competition as a cause of polyandry is discussed for humans. But the discussion is far more detailed for animals. One study suggesting that sperm competition may be one of the benefits of polyandry in human societies is that of Thornhill about female orgasm. Thornhill (1995) hypothesises that because the female orgasm is not necessary for conception it seems reasonable that it is an adaptation for manipulating the outcome of sperm competition and promote conception with males of high quality, resulting from facultative polyandry.

4.5 Intragenomic conflict and genetic incompatibility

Females might base their choice of partner on genetic complementarity. At first no one bothered to follow up this ideas because no one could imagine how, on the basis of a male's appearance, a female could assess whether his genotype would match her own. Later, when it was clear that females routinely copulated with several males and that some females at least had the ability to discriminate between the sperm of different males, did the idea of post-insemination choice based on compatibility seem feasible. Zeh and Zeh (1996, 1997) have championed the view that females copulate with different males to minimise their chances of being fertilised by incompatible male. They point out that there is abundant evidence for genetic incompatibility – inbreeding depression being the most obvious example. They also draw attention to a recently discovered cause of incompatibility – the existence of genetic conflicts within and between the nucleus and cytoplasm. Such intragenomic conflicts results in genomes being dynamic and evolving entities. The state of genomic flux will of course increase the likelihood that your genes will not be compatible with those of your partner (Birkhead 2000). Genetic incompatibility is well known in humans, as evidenced by spontaneous abortion of very early embryos when both parents are of the same HLA haplotype; that is, have the same human leukocyte antigen sperm – part of the human version of the MHC (Birkhead 2000). In response to the previous hypotheses, Zeh & Zeh (1996) present the genetic incompatibility hypothesis. Zeh & Zeh proposed that accumulation of sperm from several males shifts the arena of sexual selection from the external environment to the female reproductive tract, where interactions at the molecular and cellular level can provide females with direct mechanisms for assessing genetic incompatibility (Zeh & Zeh 1997). The genetic

incompatibility hypothesis differs fundamentally from other genetic benefit models of polyandry in that the fitness consequences of intragenomic conflict depend on an interaction between maternal and paternal haplotypes and are thus non-additive. This undermines the notion of female choice based exclusively on inherent in 'good genes' models of sexual selection, explaining the persistence of additive genetic variance in fitness (Zeh & Zeh 1996). Females mate with more than one male as a hedge against incompatibility arising as a secondary consequence of various agents of intragenomic conflict and other forces acting at suborganismal level (Zeh & Zeh 1996). Fundamental to this hypothesis is the premise that post-copulatory mechanisms are available to polyandrous females which enables them to safeguard their reproductive investment against the threat of genetic incompatibility. Where this is not the case, a polyandrous female would, on average, suffer the same reproductive cost of incompatibility as a female randomly mated to a single male. Zeh & Zeh suggest that, if intragenomic conflict is the driving force favouring polyandry as a means of discrimination against genetically incompatible genotypes, polyandry itself may restrain the spread of selfish genetic elements (Zeh & Zeh 1996). It is clear that selfish genetic elements have the potential to have severe impact on female fitness and that the extent to which they do so in any given female depends on how her nuclear and cytoplasmic genotypes interact with the nuclear genes of her mate (Zeh & Zeh 1996). Compatibility between maternal and paternal genomes is likely to be particularly critical for species in which both fertilisation and embryonic development occur within the female.

5. Stability of narrow sense polyandry

In the previous chapters explanations for the existence of polyandry are discussed. In the narrow sense polyandry the harsh environment plays an important role. Narrow sense polyandry in a harsh environment, prevents landfragmentation, provides sufficient amount of male labour to support the family and it limits populations growth. It is logically therefor that in discussing the stability the environment and its consequences for the social structure is central. In this chapter the stability of factors influencing narrow sense polyandry will be discussed. In discussing the stability of a polyandrous mating system fitness, costs en benefits are keywords.

5.1 Environmental and economical stability

Under harsh conditions in human polyandrous societies several brothers marry one female to prevent the fragmentation of property. In most human societies, women's access to property is through men. The polyandrous female often has an economic motive for trying to maintain harmony and unity, and keeping the marriage polyandrous. The polyandrous woman who divorces her husbands usually gets nothing except her own dowry (Schuler 1987). Univariate analyses of wealth, diversity of economic investments, and number of brothers within a marriage show that wealth is an important predictor for the stability of the marriage. Not only the amount of wealth is important but also a high diversity of property (figure 5). Permutations unique to the resources base of these villagers play an important role, and that is why diversification as well as amount of wealth is important. Recent studies of indigenous ethnic Tibetan communities in India and Nepal have described a sharp decline in polyandry following economic changes and fuller incorporation into the modern world economy. In Limi, for example, men began leaving their polyandrous marriages after the community shifted from dependence on agriculture to major involvement in long-

distance trade and an expansion of herding (Levine 1997). This subscribes the importance of the environment for the existence of polyandry. The importance of the environmental circumstances for the stability of polyandry is not only noticed for human societies. Changes in the ecological conditions may result in a shift to an other type of breeding system. If the productivity or the spatial or temporal distribution of a critical recourse changes from year to year or from area to area, corresponding changes are expected in the environmental potential for polyandry (Emlen & Oring 1977). Ecological parameters impose limits on the range of types of social organisation that will be adaptive. With differences in the dispersion of a critical

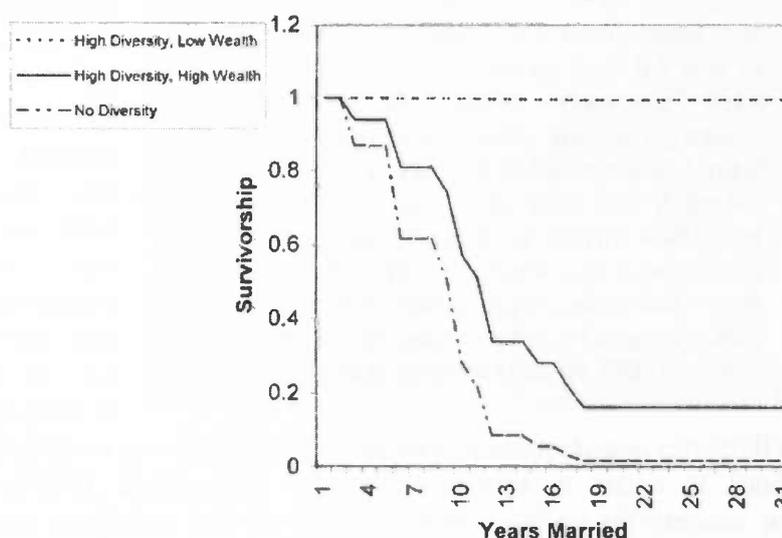


Figure 5. After Haddix 2001. Estimated survival curves for polyandrous marriages with differing amounts of wealth, among the Tibetan communities of northwestern Nepal.

distance trade and an expansion of herding (Levine 1997). This subscribes the importance of the environment for the existence of polyandry. The importance of the environmental circumstances for the stability of polyandry is not only noticed for human societies. Changes in the ecological conditions may result in a shift to an other type of breeding system. If the productivity or the spatial or temporal distribution of a critical recourse changes from year to year or from area to area, corresponding changes are expected in the environmental potential for polyandry (Emlen & Oring 1977). Ecological parameters impose limits on the range of types of social organisation that will be adaptive. With differences in the dispersion of a critical

resource, the availability of mates, or other factors, optimal social strategies shift, resulting in a fine tuning of social organisation to these ecological constraints (Emlen & Oring 1977). For example the opportunity for a male to desert rests partly on the environmental conditions (see text box “deserting” page 7).

Davies (1992) study on dunnocks (*Prunella modularis*) reported that the mating system of dunnocks varied in relation to their resources base: when food was scarce, polyandrous associations predominated, whereas when food was abundant, monogamy was more common. It is intriguing to see that in the dunnock species, although polyandry is a rare mating system, it is most likely to occur in harsh environment where hard work is needed to maintain an estate (see text box “the dunnock”). The stability of polyandry depends on the stability of the environment. (Davies 1992). Also in the chalcitrichids the quality and quantity of the habitat is important for the stability of a mating system. The quality of successional habitats occupied by marmosets and tamarins will depend on food resources; distribution and abundance (spatial and temporal) of small animal prey, fruits, and gum sources; as well as the availability of dense vegetation as

The dunnock

Observations and experiments showed that dunnock mating combinations were formed by females first settling in relation to food and nest sites, and males then competing to monopolise the female territories. The change in female territory size between years was correlated with their change in mating system. Females whose territory increased had more males defending them while females whose territory decreased in size had fewer males (Davies 1992). The picture that emerges is one of females settling to form a mosaic of female territories, with males then competing to monopolise parts of this mosaic by themselves setting up territories overlapping the female distribution. The variable mating system reflects different degrees of female defence by males, with all different mating systems (Davies 1992). The larger territories occurred in poorer habitats. A female territory size is influenced by food distribution, and the size of her territory then determines the mating system through her ease of monopolisation by males (Davies 1992). Differences between polyandry and polygyny arise largely as a result of differences in female territory size; the average territory size defended by two males is the same in polygyny and polyandry, but female territory size is markedly larger in polyandry than polygyny, and within polygyny it is smaller in three-female systems than in two-female systems (Davies 1992).

a refuge from predators, predation pressure, and the number of competitors, especially other primates (Rylands 1996). Differences between localities in terms of food resources, competition, and predation are the key to understanding differences in demographics and home range size between populations of the same or congeneric species. Only through an understanding of the variation in habitats, along with comparative studies in feeding ecology, will it be possible to obtain a clearer view of the overall adaptive trends selecting for the social, reproductive, and demographic traits of these animals (Rylands 1996). As a limiting resource to marmosets and tamarins, the availability, dispersion, successional stage, and “quality” of these patches will determine population densities, group size and home ranges, and predictably group stability and dispersal patterns (Rylands 1996).

5.2 Social structure

In human polyandrous societies several brothers marry one female. The number and the relatedness of those brothers influence the stability of those polyandrous marriages. Both, the number and the relatedness of the brothers influence the chance

that the males have to father the children produced in a marriage. Also the age differences of the males are important. The larger the age disparity, the lower the chance is for the youngest brother(s) to father the children produced in the marriage. All the factors influencing the stability of polyandry are closely correlated (Levine 1997). Some insight about factors that influence the stability of polyandrous marriages comes from polyandrous people themselves. When asked what undermines and leads to the dissolution of a polyandrous marriages, the Nyinba mention the size of the sibling group, the closeness of kinship among co-husbands, the extent of landholdings or the ease of excess to reclaimable land, the success of the relationship with the common wife, and the presence or absence of “own children” within the marriage (Levine 1988). In human societies, polyandrous marital units are nearly always composed of brother marrying one female. The males often have the same

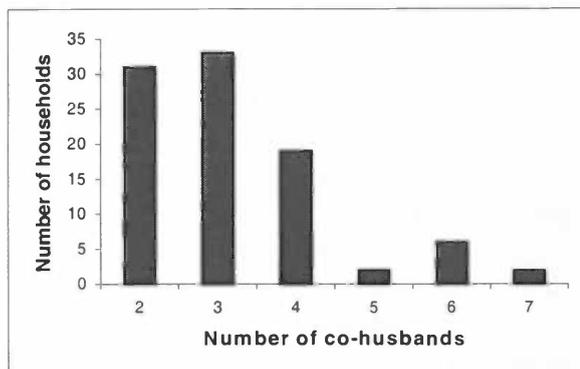


Figure 6: After Levine 1997. Number of co-husbands per household. The average polyandrous household initially contained 3.5 co-husbands; the Nyinba consider 3 the optimal number.

mother and are therefore related to each other. But among the Nyinba some polyandrous marriages between unrelated males and a female exist. Levine (1997) has suggested that co-husbands who have different parents are less tolerant of inequities than co-husbands who have the same parents. In Nyinba community, all brothers jointly marry a single woman, so the number of co-husbands initially depend upon the size of the fraternal sibling group. The most frequent is 3 co-husbands

(Figure 6). The largest sibling groups were the least stable in the Nyinba community (Levine 1997).

The Nyinba believe that trifraternal polyandry is highly desirable and that larger marital unions are problematic because they are prone to discord. Figure 7 shows that the largest sibling groups were the least stable. Following evolutionary biological predictions, larger sibling groups might be undesirable because they

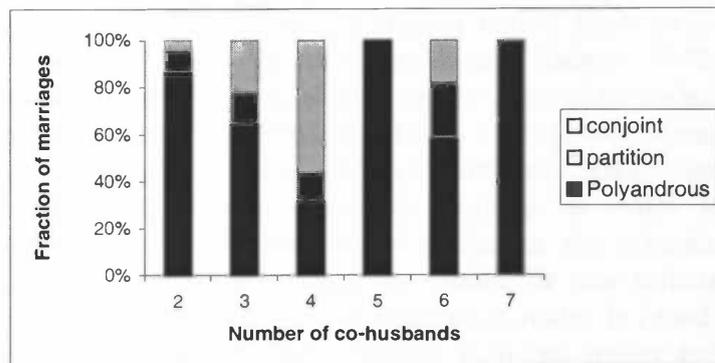


Figure 7: After Levine 1997. Number of co-husbands by type of household.

impose greater limits upon men’s reproductive opportunities. The number of brothers and the birth order are correlated with magnitude of age differences among husband and wives. When brothers marry, their common wife is typically somewhat younger than the oldest brother but older than the other brothers. In evolutionary analyses, men’s contentment with their marriages is expected to be linked to the reproductive consequences of polyandry. The theory of kin selection predicts that unreciprocal altruism will be restricted to kin. Altruism is defined as an act that reduces the genetic fitness of the donor and increases the genetic fitness of the recipient. Kinship provides

a mechanism for the evolution of altruistic interactions because relatives are descendents from a common ancestor and are therefore likely to share some fraction of their genetic material (Hamilton 1964, Levine 1997). The reproductive success of a male depends on the relatedness between the males, but also on the chance each man has to father the children from his female. Thus, in human societies and in some animal species, especially the species with a long maturation age, disparity in age among males and female is expected to be an important source of dissatisfaction because men remain fertile longer than women. Cross-cultural data suggest that evolution has shaped human psychology and created strong preferences among men for wives who are younger than themselves (Levine 1997). A man who is much younger than his wife may be concerned about her ability to produce children in the future. This may be a particular concern for men of high birth order, since marriages are likely to be contracted by or for first-born brothers (Levine 1997). In Nyinba landholding families the youngest brothers were the ones who most often left their wife to find a younger wife (Levine 1997). Levine (1997) conjectured that Nyinba men's decision to leave their marriages are mainly influenced by their disadvantages within the sibling group and their relationship with much older wives, which reduces their chances of reproducing successfully within the polyandrous marriage. The importance of these factors is underscored by the fact that when men remarry, they remedy these circumstances by marrying women younger than their first wives and by siring more children than they had in their first marriages (Levine 1997). Contrary to the prediction that the number of children produced in a marriage will tend to bind husbands to their shared wife, the number of children produced in polyandrous marriages did not appear to be associated with the probability that a partitioning will occur (Haddix 2001).

The degree of relatedness between the males, the number of males and their age disparities are often the key to understanding the evolution of co-operation in animal societies (Hamilton 1964, Davies 1992). In some species of birds, closely related individuals share mates. For example, polyandry in Tasmanian native hens arises sometimes when two brothers share a female (Maynard Smith and Ridpath 1972, Davies 1992). Polyandry involved both unrelated and related males in the chalcid population studied by Goldizen (Goldizen et al. 1996). But Baker et al (1993) found evidence that golden lion tamarin duos composed of siblings were more stable than those composed of unrelated males. In primates, also the number of males is important. Dunbar (1995) reported that as the number of males in the alliance increases, their combined effectiveness at either holding the female or rear infants must increase proportionally. For the dunnock an optimal number of males is found: dunnock females with two mates were better off than a female with one male and much better than a female with three males, because the parental investment of the male correspond with his chance to father the offspring (Birkhead 2000).

6. Discussion and conclusion

Polyandry in literature, has a wide range of definitions. One of the emphases of this report was to make a comparison between human and animal polyandry, therefore the main focus has been on narrow sense polyandry. In many respects, the similarities between human polyandrous societies and some polyandrous species as the dunnock and callitrichids are particularly interesting (Dunbar 1995).

6.1 Broad sense integrated in narrow sense hypotheses

The main emphasis of investigating hypotheses used to declare benefits of multiple mating by females was to find out whether these hypotheses can also be applied to narrow sense polyandrous populations. Explanations given to this type of polyandry in which multiple mating by the female is central, often have a genetic background. Inbreeding avoidance and genetic diversity of offspring are examples of those broad sense hypotheses.

The inbreeding avoidance hypothesis argues that multiple mating by females decreases inbreeding. I am intended to believe that this hypothesis can not be applied to human polyandry because humans have, on general, insight in their own and their partner(s) kinship history. Nevertheless, for other narrow sense polyandrous species this inbreeding avoidance hypothesis might apply, and depends on their ability to distinguish relatives from unrelated individuals.

In applying the genetic diversity hypotheses on human polyandry and other narrow sense polyandrous species a new dilemma arises, namely diversity of offspring versus the relatedness between the males and their combined offspring. Genetic diversity in offspring, and the accompanying diversity in fitness of the offspring, is higher if the offspring is fathered by unrelated males than by brothers. A polyandrous female should therefore try to mate with males that are not related to each other. On the other hand, males are more related to their borthers' offspring than they are to offspring of unrelated males. A male in a polyandrous pairbond will therefore be more inclined to invest in parental care for a mixed group of offspring, if the co-fathers of this set are closely related. Although genetic diversity of offspring is higher if unrelated fathers have children with a female, the genetic diversity hypothesis does not have to be rejected. Genetic diversity of offspring is higher when a female has children of related brothers, than when she has offspring with only one male. It might be that although the relatedness of males towards their combined offspring, which is important for their parental effort, is of more importance than the diversity in fitness of the offspring it is this diversity of the offspring that makes is beneficial for a female to be polyandrous. Diverse fitness in offspring as well as parental care is, especially in a unstable environment, important for the fitness of the parents.

Sperm competition also is a keyword in explaining multiple mating by females. In discussing sperm competition as an explanation for multiple mating several morpho-physiological factors play a role and therefore influence the benefits of it. Differences per polyandrous population are in the number of young produced per litter, the duration of the gestation, the length of the fertile period and the period over which a female can store sperm. I am intended to believe that sperm competition as one of the benefits of multiple mating is of little or no importance for human polyandry. In contrast to birds, human females do not store sperm for long periods. The storage of

sperm in human females would be rather worthless because the survival of sperm in the human female body is merely three days.

At present, the intragenomic conflict hypothesis, proposed by Zeh & Zeh, is acknowledged to be important for explanations declaring the existence of multiple mating. This hypothesis might be of importance for human polyandry because it is based on genetic complementarity between males and females. According to Birkhead (2000) genetic incompatibility is well known in humans. This enlarges the probability for a polyandrous female to produce offspring, because the chance that all males in a polyandrous marriage are genetic incompatible to her is lower than the chance that one male in a monogamous marriage is genetic incompatible to her. Of course a remark about the relatedness of the males in a polyandrous marriage must be made. I assume that brothers have a higher probability to be genetic incompatible to a female than unrelated males. Because brothers born in a polyandrous marriage are less related to each other than brothers in a monogamous marriage, mating with several brothers is according to this hypothesis still favourable above mating monogamously.

At last, one hypothesis about why populations might mate polyandrously has not been discussed. The phylogentic background of polyandrous species has not been investigated in this report. In my opinion phylogeny is subordinate. In many polyandrous species the mating system is very flexible. Under harsh conditions polyandry is promoted, but under other circumstances the mating system shifts to monogamy, polygyny or even polygynandry. I am intended to believe that phylogeny plays a role in the tendency of species to mate polyandrous, but does not dictate it.

Summarising, there seem to be hypotheses explaining multiple mating from a genetic point of view which might also be applied to narrow sense polyandry. Therefore, I recommend that future hypotheses explaining narrow sense polyandry must not only investigate the environment and behaviour of polyandrous populations but must pay in addition attention to the morphofysiology of polyandrous species and the possible genetic fitness benefits of polyandry.

6.2 Future of narrow sense polyandry

Now we know that human polyandry is comparable to some other narrow sense polyandrous species of the animal kingdom, knowledge about human as well as animal polyandry can give an opening to thoughts about the stability of human and animal polyandry in the future. The stability of polyandry is partly determined by ecological factors. For the stability of polyandry in human societies, wealth, the number and relatedness of brothers in a marriage, as well as age disparities are important. Those factors also play an important role in some animal species. In those narrow sense polyandrous species changes in the environment can induce changes in the type of mating system. For the future of human polyandry several scenarios can be discussed. It might be that polyandry among human societies will perish. As the contact between human societies is becoming more and more intense, people will move to other, more fertile parts of the world and integrate with other people. Transfer of property as in trade, tourism etc. will make that polyandrous mating societies will be no longer only dependent on their own land. as a result of the industrialisation on the same quantity of land, more people can survive. A harsh environment might become of less importance for the type of human mating structure.

This can already be seen in some of the human polyandrous societies (Levine 1997). On the contrary, in an other scenario human polyandry might increase. If the human population keeps on growing, a situation of overpopulation can arise. As said in the second chapter polyandry may have a function in limiting population growth. In an overpopulated world polyandry might be the preferable mating system.

For the animal kingdom the following scenario can be discussed. Harsh environmental conditions stimulate polyandry. The human world claims more and more of the available land. The quantity and quality of land for animal species will diminish. It may be that some species, especially those with a phylogentic tendency for variability of their mating system, become polyandrous.

Furthermore Kleiman (1977) makes an other remark about the future of human polyandrous societies. 'In species exhibiting long-term pair bonding, for example man, there is often a reduction in the degree of sexual dimorphism, both behavioural and morphological'. The question that must be addressed is whether and to what degree humans must be biologically consistent with a breeding system that is apparently culturally determined. For example, two of the current demands of the women's liberation movement in West, namely a reduction in the sexual dimorphism of behaviour through equal wages and job opportunities, and a higher paternal investment in child rearing, are biologically more compatible with monogamy than with polyandry (Kleiman 1977). If these cultural developments will continue, the occurrence of not only polyandry, but of polygamy in general may decline in human societies.

References

- Arnqvist G. & Nilsson T. (2000). The evolution of polyandry: multiple mating and female fitness in insects. *Animal behaviour*. Volume 60. Pp. 145-164.
- Baker A.J., Dietz J.M., Kleiman D.G. (1993). Behavioural evidence for monopolisation of paternity in multiple-male groups of golden lion tamarin (*Leontopithecus rosalia*s). *Animal behaviour*. Volume 46. Pp. 1091-1103.
- Bentzen P., Olson J.B., McLean J.E., Seamons T.R. & Quinn T.P. (2001). Kinship analysis of Pacific Salmon: Insight into mating, homing, and timing of reproduction. *The journal of heredity*. Volume 92. Pp. 127-136.
- Birkhead T. R., Moller A.P. & Sutherland W.J. (1993). Why do females make it so difficult for males to fertilise their eggs. *Journal of theoretical biology*. Volume 161. Pp. 51-60.
- Birkhead T.R. & Moller A.P. (1995). Extra-pair copulation and extra-pair paternity in birds. *Animal behaviour*. Volume 49. Pp. 843-848.
- Birkhead T. 2000. Promiscuity. An evolutionary history of sperm competition and sexual conflict. Faber and Faber. Pp. 195-233.
- Borgerhoff Mulder M. (2001). Using phylogenetically based comparative methods in Anthropology: More questions than answers. *Evolutionary Anthropology*, volume 10, Pp. 99-111.
- Davies N.B. (1992). *Dunnock behaviour and social evolution*. Oxford series in ecology and evolution. Oxford University press.
- Dunbar R.I.M. (1995). The mating system of callitrichid primates: I. Conditions for the co-evolution of pair bonding and twinning. *Animal behaviour*. Volume 50. Pp. 1057-1070.
- Dunbar R.I.M. (1995). The mating system of callitrichid primates: II. The impact of helpers. *Animal behaviour*. Volume 50. Pp. 1071-1089.
- Emlen S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*. Volume 197. Pp. 215-223.
- Emlen S.T. (1982). The evolution of helping. An ecological constraints model. *The American naturalist*. Volume 119. Pp. 29-39.
- Goldizen A. W., Mendelson J. Van Vaardingen M. & Terborgh J. (1996). Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: evidence from thirteen-year study of a marked population. *American journal of primatology*. Volume 38. Pp. 57-83
- Haddix K. A. (2001). Leaving your wife and brothers: when polyandrous marriages fall apart. *Evolution and human behaviour*. Volume 22, issue 1, Pp. 47-60.
- Hamilton W.D. (1964). The genetic evolution of social behaviour. I. *Journal of theoretical biology*. Volume 7. Pp. 1-16.

- Hamilton W.D. (1964). The genetic evolution of social behaviour. II. *Journal of theoretical biology*. Volume 7. Pp. 17-52.
- Houston A.I. (1995). Parental effort and paternity. *Animal behaviour*. Volume 50. Pp. 1635-1644.
- Keller L. & Reeve H.K. (1995). Why do females mate with multiple males? The sexually selected sperm hypothesis. *Advances in the study of behaviour*. Volume 24. Pp. 291-315.
- Kleiman D.G. (1977). Monogamy in mammals. *The quarterly review of biology*. Volume 52. Pp. 39-69.
- Lank D.B. (2002). High frequency of polyandry in a lek mating system. *Behavioural ecology*. Volume 13. Number 2. Pp. 209-215.
- Levine N. E. & Silk J. B. (1997). Why polyandry fails: Sources of instability in polyandrous marriages. *Current anthropology*. Volume 38. Number 3. Pp. 375- 398.
- Madsen T., Shine R., Loman J. & Hakansson T. (1992). Why do female adders copulate so frequently. *Nature*. volume 355. Pp. 440-441.
- Maynard Smith J. & Ridpath M.G. (1972). Wife sharing in the Tasmanian native hen *Tribonyx mortierii*: A case of kin selection. *The American Naturalist*. Volume 106. Pp. 447-452.
- Nanda S. & Warms R. (1998). *Cultural anthropology, sixth edition*. Wadsworth Publishing Company.
- Owens I. P. F. (2002). Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities. *The royal society*. Volume 357. Pp. 283-293.
- Parker G.A. (1992). Snakes and female sexuality. *Nature*. Volume 355. Pp. 395-396.
- Reynolds J.D. (1996). Animal breeding systems. *Trends in ecology and evolution*. Volume 11. Number 2. Pp. 68- 72.
- Rylands A. B. (1996). Habitat and the evolution of social and reproductive behaviour in Callitrichidae. *American journal of primatology*. Volume 38. Pp. 5-18.
- Schuler S.R. (1987). The other side of polyandry. Property, stratification, and nonmarriage in the Nepal Himalayas. Women in cross-cultural perspective series. Westview Press. Boulder and London.
- Soltis J. & McElreath R. (2001). Can females gain extra parental investment by mating with multiple mates? A game theory approach. *The American naturalist*. Volume 158, no 5. Pp. 519-529.
- Stockley P., Searle J.B., MacDonald D.W. & Jones C.S. (1993). Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. *Proceedings of the royal soc. of London*. Volume 254. Pp. 173-179.

Strassman J. (2001). The rarity of multiple mating by females in the social Hymenoptera. *Insectes Sociaux*. Volume 48. Pp. 1-13.

Thornhill R., Gangestad S.W., & Comer R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal behaviour*. Volume 50. Pp. 1601-1615.

Wiley A.S. (1998). The ecology of low natural fertility in Ladakh. *Journal of biosocial science*. Volume 30. Pages 457-480.

Zeh J.A. & Zeh D.W. (1996). The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Biological sciences*. Volume 263. Pp. 1711-1717.

Zeh J.A. & Zeh D.W. (1997). The evolution of polyandry II: post-copulatory defences against genetic incompatibility. *The Royal Society*. Volume 264. Pp. 69-75.

On the frontpage:

1. Nyinba bride:

<http://www.occ.cccd.edu/online/gholland/meet11/index.cfm#polyandry>

2. Golden lion tamarind:

<http://natzoo.si.edu/gltprogram/>

3. Tasmanian native hen:

<http://www.dailystarnews.com/magazine/2002/08/05/wildlife.htm>