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# Do Bateman's principles extend to human societies?

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Bachelor thesis

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## Summary

Bateman's work on fruit flies contributed strongly to the understanding of sexual selection mechanisms, as first mentioned by Charles Darwin. Bateman concluded from his experiments that males show a higher variance in reproductive success than females (Principle I), that males show a higher variance in mating success than females (Principle II) and that the relationship between reproductive success and mating success is stronger in males than in females (Principle III). Consequently, sexual selection pressure on traits that increase the probability of getting multiple mating partners will be higher in males than in females. The aim of this thesis is to investigate if Bateman's principles extend to human societies as well. A distinction is made between populations with different mating systems (e.g. polygamous, or monogamous). Bateman's principles were observed in several human populations, including modern Western populations. Nevertheless, Bateman's first principle seems present to a greater extent in polygynous populations and, although little was known about variances in mating success and the relationship between reproductive success and mating success, this is also expected for the second and third principle. These findings highlight the opportunity for sexual selection mechanisms to work in human societies. However, several limitations, such as the fact that most databases about reproductive success and mating success are biased, should be taken into account when interpreting evidence found for Bateman's principles in humans. Further research, for example with the addition of data about population density or sex ratio, is necessary to determine the differences in mating and reproductive behavior between the sexes and to see if these differences are to the same extent present in different human populations.

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## Introduction

Charles Darwin tried to solve the question why in most species males have certain traits that decrease survival (Darwin, 1871). For instance, male guppies have a conspicuous color pattern, which increases the probability of getting caught by predators (Godin & McDonough, 2003). Darwin came up with the idea of sexual selection: selection pressures that arise out competition between animals to obtain mating partners (Darwin, 1871). However, it remained unclear why this sexual selection, in most species, is more prominent in males than it is in females. Bateman (1948) provided an explanation by using the results of his experiments on fruit flies (Andersson & Iwasa, 1996).

In 1948 Bateman conducted experiments on adult fruit flies (*Drosophila melanogaster*) to determine their reproductive and mating behavior. He introduced five male fruit flies to five female fruit flies, so that each female could choose from five males and each male had to compete for the females with four other males (Bateman, 1948). In total, six series of experiments were conducted. These series differed in factors such as time of the experiment and age of the flies (Bateman, 1948; Tang-Martinez & Ryder, 2005). Bateman assumed that having particular marker combinations would not influence the offspring survival. Under this assumption the offspring will divide into four different genotypes with a frequency of 25%, according to the principles of Mendelian inheritance. Bateman calculated the number of offspring and the number of sexual partners for both male and female fruit flies. The results were analyzed for the six different series and comparable series were combined to draw conclusions (Bateman, 1948). From his experiments Bateman concluded several things. First, he noted that the male/female ratio of variance in number of offspring, the so-called reproductive success, varied between 1.63 and 8.14 for the different series and concluded that males compared to females show greater variance in number of offspring (Principle I). Second, he stated that males show greater variance in number of sexual partners, the so-called mating success, in comparison to females (Principle II). Third, he concluded that the relationship between number of offspring and number of sexual partners is stronger in males than in females (Principle III) (Arnold, 1994; Brown et al., 2009; Jokela et al., 2010). Figure 1 illustrates the latter principle.

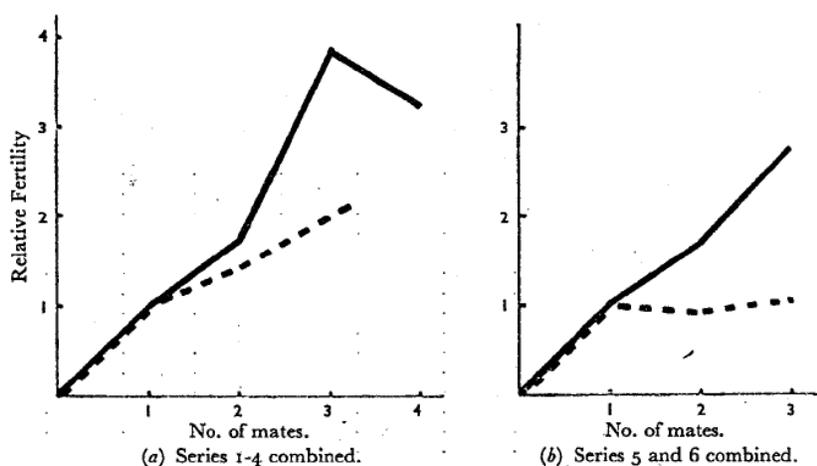


Figure 1: The relationship between number of sexual partners and fertility relative to the fertility with one sexual partner. Comparable series were combined to draw conclusions. The closed lines represent the data for males and the broken lines represent the data for females (Bateman, 1948).

The relationship between reproductive success and mating success is known as the Bateman gradient or the sexual selection gradient (Brown et al., 2009). Bateman stated that in most species the sex with the strongest relationship between mating success and reproductive success is the male (Bateman, 1948). The sex of an individual is based on the size of the gametes: an individual with small gametes is defined as male. Males have a large amount of small sperms, while females have a limited amount of big eggs. Bateman thought that the differences in gamete size between the sexes are the reason for the differences in strength of the Bateman gradient (Bateman, 1948). For females their reproductive success is limited by the number of eggs, while for males their reproductive success is limited by the number of sexual partners (Trivers, 1972). Therefore, males have to compete with other males to obtain multiple mating partners, to increase their reproductive success, while females have to choose their sexual partners carefully. Consequently, in males there will be stronger sexual selection pressure on features that help in obtaining sexual partners (Andersson & Iwasa, 1996; Jones et al., 2002; Brown et al., 2009; Jokela et al., 2010). Thus, Bateman's third principle is predominantly important for sexual selection and evolution (Jokela et al., 2010). Because in most species the Bateman gradient is strongest in males, I will assume in this thesis that males are the sex with the strongest relationship between mating success and reproductive success.

Trivers (1972) added the aspect of paternal investment to the findings of Bateman. He thought that differences in strength of sexual selection between the sexes depend strongly on the amount of parental investment. Investing in particular offspring lowers the opportunity to invest in other offspring. The total number of offspring produced by one sex has to be equal to the total number of offspring of the other sex, according to the biological principles of sexual reproduction. Therefore, the greatest investing sex will be the limited sex. Individuals of the less investing sex, usually the males, will compete with other individuals of that sex to obtain individuals from the limited sex. This is because for the less investing sex, reproductive success will increase with mating success and therefore it is beneficial to have multiple mating partners. For the most investing sex, the costs of being promiscuous (spending energy on obtaining mating partners) are higher than the benefits (producing offspring), therefore this sex has to be the choosy one (Trivers, 1972; Jokela et al., 2010). So, differences in parental investment between the sexes are a key determinant for the Bateman gradient (Andrade & Kasumovic, 2005).

Emlen & Oring (1977) claimed that the operational sex ratio also should be taken into account to explain the differences in strength of sexual selection between the sexes. The operational sex ratio comprises the ratio of sexually active males to sexually active females. When the operational sex ratio becomes biased towards one sex, sexual selection pressure will be stronger in that sex because of the increased competition (Emlen & Oring, 1977; Weir et al., 2011). When males invest less in offspring compared to females, the ratio of sexually active males to sexually active females becomes male-biased and therefore the sexual selection pressure will be greater in males. In this condition, it is expected that the variance in reproductive success (Bateman's first principle) will be higher in males (Trivers, 1972; Emlen & Oring, 1977).

According to Bateman, the previously described sex differences in the strength of sexual selection are equal across the animal kingdom (Bateman, 1948, Trivers, 1972). In contrast, Arnold (1994) hypothesized that there are variations in the relationship between reproductive success and mating success across different mating systems. From his point of view, there are four different types of relationships between reproductive success and mating success. The male fruit flies in the original

Bateman experiment showed a linear relationship. Another relationship is that of intermediate optimum, meaning the number of offspring is largest at a certain point in the middle of mating success. Another possibility is that mating with multiple partners would not lead to an increase in reproductive success, the so-called single-mate saturation relationship. The last relationship is that of diminishing returns, meaning that mating with multiple partners leads progressively to less reproductive success (Arnold, 1994). Arnold argued that the sexual selection gradient is the most important factor in understanding the structure of a mating system and other related aspects, such as parental investment and sex ratio (Arnold, 1994).

The most common mating systems are monogamy, polygyny and polyandry. A monogamous mating system comprises both females and males with one spouse. In a polygynous system, it is possible for males to have two or more females at the same time. A polyandrous system comprises females with two or more males at the same time (Borgerhoff Mulder, 2009). Sexual selection is relatively weak in monogamous systems compared to polygynous systems, because the sex differences in variance in mating success tend to be small in monogamous systems (Emlen & Oring, 1977). In humans, there is huge variation in mating system structure, with polygyny as the most common mating system (83%). In addition, 16% and 1% of the human societies are respectively monogamous and polyandrous (Murdock, 1967). Monogamy is, however, the most common mating system in the Western world. Questions can be raised to what extent there is opportunity for sexual selection in such monogamous societies. Because, as the sex differences in variance in reproductive success and mating success are small, it is unlikely to find a stronger relationship between reproductive success and mating success in males than in females (Käär et al., 1998). However, the modern Western society allows the opportunity to remarry and have multiple sexual partners during a lifetime, so-called serial monogamy (Borgerhoff Mulder, 2009). Whether classical sexual selection is still present in current human society is a frequently debated topic among scientists (Courtiol et al., 2012). The aim of thesis is to investigate if Bateman's principles extend to human societies. Furthermore, a distinction between populations with different mating systems is made. The focus will mainly be on modern Western human societies, because theory (Käär et al., 1998) predicts the strength of sexual selection pressure to be very small among these kinds of societies.

## Does Bateman's first principle extend to human societies?

Bateman showed in his experiments that male fruit flies have a higher variance in number of offspring (reproductive success) compared to female fruit flies (Bateman, 1948). Whether there is also a higher variance in reproductive success among human males than among females is investigated in this chapter.

### General findings

Brown et al. (2009) collected data from several human populations and compared the variance in reproductive success in males with the variance in reproductive success in females. They found that, when averaging the data of all the populations, males have a higher variance in reproductive success than females (the ratio of variance in male reproductive success to female reproductive success is above 1). However, this variance differed largely between the different populations, which was probably due to the differences in mating systems between the populations. In polygynous populations the sex differences in variance in reproductive success were, in general, bigger than those in monogamous populations. In serial monogamous populations these sex differences were close to those of polygynous populations (Brown et al., 2009). This is shown in table 1 and figure 2. In addition, Betzig (2012) compared data of reproductive success from different populations. There seem to be differences in mean and variance in reproductive success between different types of populations (hunters and gatherers/herders and gardeners/ full time farmers). Hunters and gatherers have a smaller range and variance in reproductive success than the others types of populations. But, the sex differences in range and variance were small in these populations. In contrast, in the herders and gardeners populations the variance and range in reproductive success did differ between the sexes, as it was greater among males (Betzig, 2012). The findings of Betzig and Brown et al. illustrate that, as there are large differences between the different human populations, it is unlikely to find a universal pattern in sex differences in variances in reproductive success. Therefore, it is useful to distinguish between the different mating systems and different populations when investigating the variance in reproductive success.

### Serial monogamous populations

In modern Western societies, serial monogamy is the most common mating system, meaning it is possible to remarry and have multiple mating partners during a lifetime. There are several studies done in serial monogamous populations, in both Western and non-Western societies. In three studies variance in reproductive success was significantly higher among males than among females, shown in table 1. For instance, Marlowe (2000) collected data in the Hadza population in Tanzania and found that in this population, the variance in reproductive success was significantly higher among males (Marlowe, 2000). Additionally, Jokela et al. (2010) found that in modern United States the variance in number of offspring was significantly greater in males than in females. A distinction between different ethnic groups was made, but there were no differences in variance in number of offspring between the different ethnic groups (Jokela et al., 2010). These results are shown in figure 3.

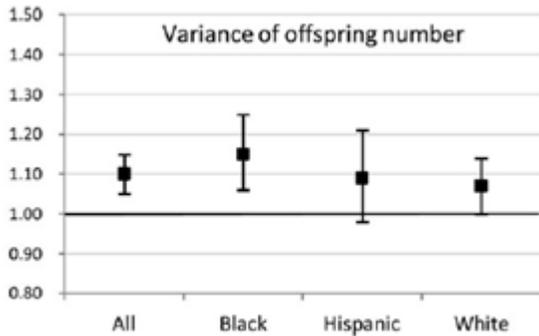


Figure 3: The male/female variance ratio of reproductive success for the different ethnic groups (Jokela et al., 2010).

Contrasting, in two studies no significant sex difference in variance in reproductive success was found. Borgerhoff Mulder (2009) investigated the consequences of serial monogamy in a population in Tanzania (Pimbwe) and showed that there were no significant differences in variance in reproductive success between the sexes (Borgerhoff Mulder, 2009). A recent study of Barthold et al. (2012) in modern Europe confirmed that there was no significant difference in variance in number of offspring between the sexes (Barthold et al., 2012). Figure 2 displays that, when taking all the data of Brown et al. together and make a distinction in mating system, the male/female ratio of variance in reproductive success in serial monogamous populations is close to that of polygynous populations.

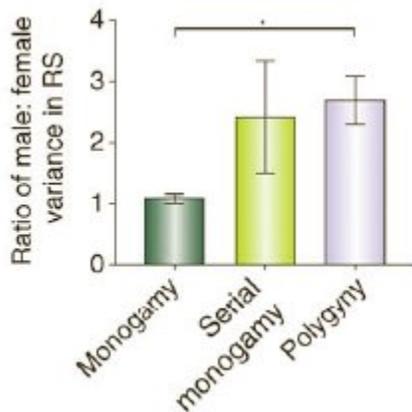


Figure 2: The male/female ratio of variance in reproductive success for the different mating systems (Brown et al., 2009).

### Monogamous populations

A strictly monogamous mating system comprises both females and males with one spouse during a lifespan, whereas in serial monogamous systems it is possible to remarry and have multiple mating partners in series. It is expected that in monogamous societies the sex differences in variance in number of offspring are small. Several studies are done to determine the differences in variance in reproductive success between the sexes in a monogamous population, shown in table 1 (Low, 1991; Pettay et al., 2005; Quinlan & Flinn, 2005; Weeden et al., 2006; Brown et al., 2009). Two studies show a significant greater variance in reproductive success among males than among females. Weeden et al. (2006) collected data from a sample in the United States and established that in males there is a significant

higher variance in reproductive success than in females (Weeden et al., 2006). In addition, Low (1991) showed that also in monogamous Swedish populations in the nineteenth century males had a significant greater variance in reproductive success compared to females (Low, 1991). In contrast, four studies showed no significant sex difference in variance in reproductive success. For instance, Pettay et al. (2005) collected data from four generations of a preindustrial Finnish population with a monogamous mating system. For males and females the mean number of offspring was 3.39 and 3.47 respectively. The variance in reproductive success was 6.0 and 7.6 respectively. This sex difference in variance in reproductive success was non-significant (Pettay et al., 2005). Quinlan & Flinn (2005) confirmed this with results from a non-Western monogamous population in Dominica (Quinlan & Flinn, 2005). Thus, some of the previous described studies demonstrate that males show a higher variance in reproductive success than females in monogamous populations as well. However, Brown et al. demonstrated that these differences in variance in reproductive success between the sexes are smaller differences than those in polygynous societies (Brown et al., 2009). When taking all the data from the monogamous populations together, shown in figure 2, Brown et al. established that there is no significant difference in variance in reproductive success between males and females (Brown et al., 2009).

### Polygynous populations

In polygynous societies males are allowed to have multiple females at the same time, therefore it is expected that it is most likely to find evidence for Bateman's first principle in populations with a polygynous mating system. Indeed, in 7, out of 9, investigated populations, there is a significant greater variance in number of offspring in males in comparison to females, shown in table 1. For instance, Salzano et al. (1967) established data from a polygynous Brazilian population (Xavante) and found that males and females in the Xavante population produced, on average, 3.6 offspring, but the variance in number of children for females was 3.9 whereas this was much higher for males, namely 12.1. The male/female ratio was 3.10 (Salzano et al., 1967). In contrast, two studies found no significant differences in variance in reproductive success between the sexes. For instance, Hewlett (1988) found that among the Aka population in central Africa, the variance in reproductive success for males and females is respectively 8.6 and 5.2 (ratio of 1.66) and this sex difference is non-significant (Hewlett, 1988; Brown et al., 2009). Brown et al. showed that, in general, polygynous populations have a higher variance in reproductive success for both males and females. Furthermore, the male/female ratio of variance in reproductive success is higher in polygynous societies compared to monogamous societies. This ratio is in polygynous societies significant above 1, meaning males show a significant greater variance in reproductive success than females (Brown et al., 2009). This is displayed in figure 2.

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Table 1: Mean and variance in number of offspring for the different sexes.

Population	$N_m$	Mean <sub>m</sub>	Var <sub>m</sub>	$N_f$	Mean <sub>f</sub>	Var <sub>f</sub>	Var <sub>m</sub> :Var <sub>f</sub>	Mating system	P-value* mean	P-value** variance	Ref.
Finland 1745-1900	125	3.4	6	138	3.5	7.6	0.79	monogamy	0.76	0.91	Pettay et al. 2005
Modern Europe	17233	2.0	1.9	21707	2.1	1.9	0.97	serial monogamy	<0.0001	0.68	Barthold et al. 2012
Norway 1700-1900	955	4.7	8.5	991	4.5	8.3	1.02	monogamy	0.13	0.38	***
Pitcairn Island genealogical data	145	4.6	23.6	127	4.7	23.2	1.02	monogamy	0.87	0.46	***
Modern USA	3700	x	2.25	4010	x	2.04	1.10	serial monogamy	x	0.07****	Jokela et al. 2010
Iran Yomut Turkmen	267	5.1	8.1	216	3.9	7.1	1.14	polygyny	<0.0001	0.16	***
Sweden 1825-1896	1201	2.1	11.5	1050	2.4	9.7	1.18	monogamy	0.03	0.004	Low 1991
Dominica	130	4.4	14.3	124	5	11.6	1.23	monogamy	0.19	0.12	Quinlan & Flinn 2005
Tanzania Pimbwe	138	6.0	9	154	6.1	7.3	1.24	serial monogamy	0.76	0.098	Borgerhoff Mulder 2009
Modern USA	1099	2.0	2.3	1344	2.0	1.8	1.27	monogamy	1.0	<0.0001	Weeden et al. 2006
Central Africa Aka	29	6.3	8.6	34	6.2	5.2	1.66	polygyny	0.88	0.08	Hewlett 1988
Botswana Dobe !Kung	35	5.1	8.6	62	4.7	4.9	1.77	serial monogamy	0.45	0.03	***
Tanzania Hadza	54	4.3	9.8	44	3.6	5.1	1.93	polygyny	0.22	0.01	***
Venezuela	279	3.7	10.1	380	3.4	4.4	2.30	polygyny	0.15	<0.0001	***

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Yanomamo											
Chad Dazagada	44	8.6	15.0	33	6.4	6.5	2.31	polygyny	0.006	0.008	***
Chad Arabs	23	10.3	14.4	22	8.3	5.1	2.82	polygyny	0.04	0.01	***
Brazil Xavante	62	3.6	12.1	44	3.6	3.9	3.10	polygyny	1.0	<0.0001	Salzano et al. 1967
Kenya Kipsigis	82	10.9	24.4	260	6.6	5.9	4.18	polygyny	<0.0001	<0.0001	***
Paraguay Ache	48	6.4	15.1	25	7.8	3.6	4.22	serial monogamy	0.09	0.0002	***
Mali Dogon	44	6.1	10.7	48	3.2	2.3	4.75	polygyny	<0.0001	<0.0001	***

\*P-value for the difference in the mean number of children for the sexes, derived from an independent samples t-test

\*\* P-value for the difference in the variance in number of children for the sexes, derived from an F-test of equality of variances

\*\*\*Refers to the study of Brown et al. in 2009

\*\*\*\*According to Jokela et al. there was a significant difference in variance in offspring between the sexes. However, in this thesis an F-test is used to determine equality of variances and this test revealed there were no significant differences in variance in offspring between the sexes

## Does Bateman's second principle extend to human societies?

Bateman's second principle states that males show, compared to females, a higher variance in mating success. It is expected that this principle extends to polygynous populations, because polygyny will lead to some males with multiple females, while other males do not have any female (Brown et al., 2009). If Bateman's second principle extends to monogamous populations is doubtful, because monogamy means that individuals only have one mating partner. In this situation, males do not have to compete with other males to obtain multiple females. One way in which individuals could increase mating success in monogamous societies is to remarry. It is possible that there are differences in remarriage success between the sexes.

### (Serial) monogamous and polygynous populations

Indeed, Käär et al. (1998) demonstrated that males remarry more often in comparison with females in preindustrial monogamous populations in Finland (Käär et al., 1998). Buckle et al. (1996) confirmed that also in a modern Western society, remarrying is more common in males than in females, probably because males have a longer reproductive period compared to females (Buckle et al., 1996). Complementary, studies done in serial monogamous societies show a significant higher variance in mating success in males than in females (Schmitt, 2005; Borgerhoff Mulder, 2009; Jokela et al., 2010). Jokela et al. (2010) investigated the differences in variance in mating success between the sexes in the United States and found that the variance in number of mating partners was greater in males than in females. This variance was significantly greater for Black males (Jokela et al., 2010). These results are shown in figure 4.

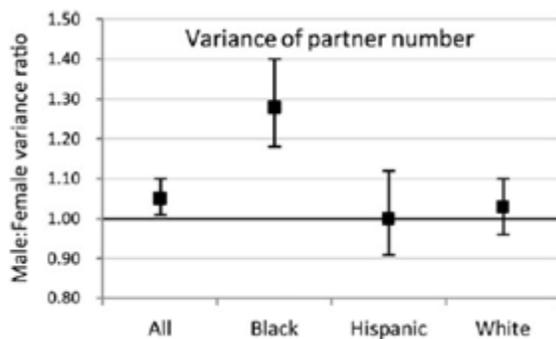


Figure 4: The male/female variance ratio of mating success for the different ethnic groups (Jokela et al., 2010).

In the non-Western Pimbwe population a higher percentage of males were never married than females (respectively 2.2% and 1.3%) and there was also a higher percentage of males with three or more spouses in comparison to females (respectively 15.2% and 13%) (Borgerhoff Mulder, 2009). Additionally, Schmitt (2005) calculated the sociosexuality score for several modern populations, both Western and non-Western, around the world. The sociosexuality score was calculated from answers given in a questionnaire about sexual behavior. Individuals with a higher sociosexuality score for instance had sex with more partners in the previous year, thought they will have sex with more partners in the next five years and had more one-night stands than individuals with a lower sociosexuality score. The variance in

sociosexuality was significantly greater among males than among females in 47, out of 48, investigated populations. The sex differences were smaller in populations with more equality between males and females (Schmitt, 2005). Unfortunately, little is known about mating success in polygynous populations (Brown et al., 2009). Nevertheless, it is expected that in polygynous populations sex differences in variance in mating success are highest.

### IPUMS international database

In addition to the previous described studies, data about marital status and number of marriages was collected from the database of IPUMS international (Minnesota Population Center, 2011). IPUMS international collects and distributes data from numerous societies. When analyzing the obtained data, only the head of the household or spouse with an age of/above 45 were included. A sample from Argentina showed that males were significantly more often single/never married than females. Additionally, in both a sample from the United States in 1960 and in 1980 males had significantly more often more than one marriage compared to females. Contrasting, in both an Austrian sample and two samples from the United States females were significantly more often single/never married in comparison to males. Thus, some evidence for Bateman's second principle in humans was found in this database. A detailed version of these findings is shown in table 2.

Table 2: Results derived from the IPUMS international database.

Country	Year	N <sub>m</sub>	single/never married <sub>m</sub> (%)	>1 marriage <sub>m</sub> (%)	N <sub>f</sub>	single/never married <sub>f</sub> (%)	>1 marriage <sub>f</sub> (%)	P-value*	P-value**
Argentina	2001	41 67 57	12.47	12.47	46 95 64	11.36	7.59	<0.0001	χ***
Austria	2001	13 16 61	6.46	x	15 61 88	6.92	x	<0.0001	x
United States	1960	22 06 95	3.84	17.85	22 64 69	4.12	16.79	<0.0001	<0.0001
United States	1980	14 51 00 9	3.47	19.21	17 10 25 7	3.55	18.60	0.0002	<0.0001

\*P-value for the sex differences in percentage single/never married, derived from a Chi square test

\*\*P-value for the sex differences in percentage more than one marriage, derived from a Chi square test

\*\*\* Only for currently married individuals, the number of marriages was known, therefore doing a Chi square test would lead to incorrect results

## Does Bateman's third principle extend to human societies?

Bateman's third principle comprises the relationship between reproductive success and mating success. This relationship is, according to Bateman, stronger in males than in females (Bateman, 1948). As mentioned before, Arnold (1994) hypothesized that there are four possible types of relationships between reproductive success and mating success and that this relationship is most important in understanding the structure of a mating system. The relationship between reproductive success and mating success will be non-linear if paternal investment is high, because in this way it is costly to have multiple mating partners. In this way, other types of relationships are likely, such as diminishing returns (Geary, 2000). A relationship with diminishing returns means that mating with multiple partners leads progressively to less reproductive success (Arnold, 1994). Males tend to invest less in offspring in polygynous societies (Geary, 2000), therefore it is expected that in such societies there will be a linear Bateman gradient in males. According to Bateman, in females the relationship between reproductive success and mating success tend to be less strong than in males, because reproductive success is limited by the number of eggs and not by the number of mating partners (Bateman, 1948). However, Hrdy (1996) discussed the possible benefits for females to mate with multiple sexual partners. It could be possible that mating with multiple sexual partners leads to access to particular resources, such as meat. Another possibility is that having multiple mating partners lowers the risk of infanticide (the killing of offspring). From this point of view, mating with multiple sexual partners might result in higher reproductive success in females (Hrdy, 1996). In this chapter the relationship between number of offspring and number of mating partners for the different sexes is investigated. Again a distinction is made between populations with different mating systems.

### Serial monogamous populations

Several studies, done in modern Western serial monogamous populations, show that there is a positive association between mating success and reproductive success in males, but not in females (Forsberg & Tullberg, 1995; Jokela et al., 2010). For instance, a cohort study of Forsberg & Tullberg in 1995 showed that in modern serial monogamous Sweden remating leads to an increase in the number of offspring for males. For females, increasing number of mating partners did not lead to increased reproductive success (Forsberg & Tullberg, 1995). More evidence for Bateman's third principle in serial monogamous populations comes from a study done by Jokela et al. (2010) in the United States. Sex differences in the relation between number of offspring and mating success were found, in males there was a positive association between number of offspring and mating success. However, this association was not significant for White males, when dividing the males in different ethnic groups. The studies done by Forsberg & Tullberg and Jokela et al. indicate that having multiple mating partners in modern serial monogamous societies will increase the number of offspring for males, but not necessarily for females (Forsberg & Tullberg, 1995; Jokela et al., 2010). However, Borgerhoff Mulder (2009) found a negative association between mating success (number of spouses) and reproductive success (surviving offspring) in males in the Pimbwe population in Tanzania, a non-Western serial monogamous population. In addition, when the number of spouses increases, the fertility decreases in males. Contradictory, for females it seems to be beneficial to have three or more spouses. Figure 5 illustrates these results.

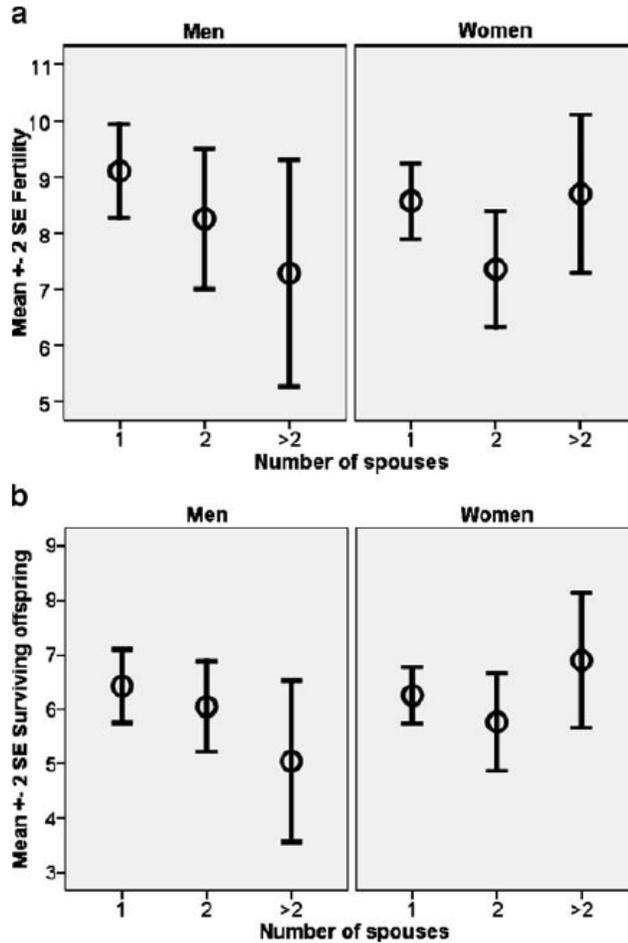


Figure 5: The relationship between number of spouses and (a) fertility and (b) surviving offspring (Borgerhoff Mulder, 2009).

According to Borgerhoff Mulder (2009), it is possible that the negative association between reproductive success and mating success in males is due to the fact males with multiple mating partners tend to drink more alcohol and work less hard than males with one mating partner. This could result in a lower probability to mate with pre-menopausal females, reducing the chance of producing offspring. Contrasting, females with three or more spouses are more likely to work hard than females with one spouse. Borgerhoff Mulder (2009) argued that Trivers original thoughts about paternal investment and sexual selection are too simplistic, because in the Pimbwe population, females mate with multiple partners and at the same show high levels of investment in offspring. This could be because there are several potential benefits for females to having multiple mating partners, such as increased resource access. These findings suggest that serial monogamy is also a good reproductive strategy for females (Borgerhoff Mulder, 2009).

### Monogamous populations

Data collected from preindustrial monogamous populations indicate that also in these populations males benefit from having multiple mating partners (Low, 1991; Käär et al., 1998; Courtiol et al., 2012). Both Courtiol et al. (2012) and Käär et al. (1998) investigated the relationship between reproductive

success and mating success in monogamous preindustrial populations in Finland. Courtiol et al. found that the relationship between reproductive success and mating success was stronger in males compared to females, independent of social class (Courtiol et al., 2012). Käär et al. (1998) investigated the consequence of remarriage on reproductive success. The results showed that remarried males had a higher reproductive success than the males who married once. In addition, the reproductive period was, on average, 5 years longer for the remarried males compared to the males that married once. These effects were not present in females (Käär et al., 1998). Low (1991) established that in monogamous Swedish populations in the nineteenth century remarrying was positively associated with number of offspring in males. This effect was not present in females (Low, 1991). These findings suggest that even in a monogamous society the Bateman gradient is stronger in males than in females (Low, 1991; Käär et al., 1998; Courtiol et al., 2012).

### Polygynous populations

Unfortunately, little is known about the relationship between reproductive success and mating success in polygynous populations. However, two studies demonstrate that in males mating success is positively associated with reproductive success (Salzano et al., 1967; Borgerhoff Mulder, 1987). The Kipsigis study of Borgerhoff Mulder in 1987 showed a positive association between wealth and number of offspring in males. Kipsigis wealthy males tend to have more females than males with less wealth. So it is possible that the increase in reproductive success in wealthy males is due to higher mating success (Borgerhoff Mulder, 1987). Complementary, Salzano et al. (1967) found a positive correlation between number of offspring and mating partners among males in the Xavante population (Salzano et al., 1967).

## Conclusion and discussion

The aim of this thesis was to investigate if Bateman's principles (Bateman, 1948) extend to human societies. Furthermore, a distinction was made between populations with different mating systems, with the focus on modern Western populations.

### First principle

The extent to which Bateman's first principle (i.e. males tend to show a higher variance in reproductive success than females) occurs, differs between the different mating systems and populations. In populations with a polygynous mating system there was a greater variance in reproductive success among males than among females. In populations with a monogamous mating system, there was, in general, no difference in variance in reproductive success between the sexes. Evidence was found for Bateman's first principle in most of the investigated serial monogamous societies. When combining data of serial monogamous populations, the sex difference in variance in reproductive success was close to that of polygynous populations. Thus, it is probable that Bateman's first principle extends to human populations with certain mating structures, but a universal pattern across all the different mating systems is unlikely. Nevertheless, when drawing conclusions about Bateman's first principle in human societies, it should be taken into consideration that most databases about reproductive success are biased. Most databases show differences in the number of offspring between male and female. But, this is biologically impossible, assuming there is sexual reproduction. Probably the reason for this is that males tend to forget offspring from previous marriages or extramarital offspring. In this way, the data of variance in reproductive success are underestimated for males, resulting in incorrect conclusions drawn from these data (Rendall, 1999). This is also shown in table 1: in several samples the mean number of offspring was significantly different for the sexes. Additionally, in some populations the sample size was low, making the statistical power weak. Therefore, it remains difficult to determine if Bateman's first principle extends to humans.

### Second principle

The findings of the second chapter indicate that when there is opportunity to remarry and have multiple mating partners during a lifetime, males demonstrate a greater variance in mating success than females in monogamous populations. Even though, little is known about variance in mating success in polygynous populations, it is expected that in such populations sex differences in variance in mating success are highest. Given that in human society polygyny is the most common mating system, it is likely that Bateman's second principle (i.e. the variance in mating success is higher among males than among females) extends to human societies. However, most databases about number of mating partners are biased. For instance, the results of the experiment of Wiederman in 1997 show large differences in self-reported sexual partners between the sexes. Males had, on average, 14.25 sex partners, while females had, on average, 4.81 sex partners. The fact that males reported a higher number of sexual partners than females is impossible, according to the biological principles of sexual reproduction. In addition, the answers did not seem to continue, there seemed to be a preference for numbers such as 5 and 10 (Wiederman, 1997). The difficulty of obtaining correct data was confirmed by Alexander & Fisher (2003). They conducted an experiment using the bogus pipeline method. In the Bogus pipeline method participants are told that they are attached to a lie detector, increasing the possibility to get correct

answers when asking questions about sensible topics, such as sexual behavior. They found differences in reported sexual partners between the control condition and the bogus pipeline condition. Males reported a higher number of sexual partners than females in the control condition, while in the bogus pipeline condition males reported a lower number of sexual partners than females (Alexander & Fisher, 2003). Thus, it is difficult to get correct data about mating success, making it challenging to determine if Bateman's second principle extends to human societies.

### Third principle

It is highly possible that Bateman's third principle (i.e. the relationship between reproductive success and mating success is stronger in males than in females) extends to humans, even if there are differences in mating system across the different human populations. Even in modern Western societies the Bateman gradient was stronger in males than in females. In our current Western society remarrying is probably a good strategy for males to increase reproductive success. As Bateman's third principle is most important for sexual selection, these findings highlight the opportunity for sexual selection mechanisms to work in humans. In modern Western societies there will be sexual selection pressure on traits that increase the probability of getting remarried in males. However, it should be taken into account that in some samples individuals with many mating partners were rare. In both the study of Forsberg & Tullberg and Borgerhoff Mulder there were only a few people with three or more mating partners. This could have led to less powerful statistical evidence (Forsberg & Tullberg, 1995; Borgerhoff Mulder, 2009; Jokela et al., 2010).

### General limitations

When investigating if Bateman's principles are present in human societies, it should be taken into account that Bateman's methodological procedures were limited by the used methods of that time. Gowaty et al. (2012) argued that Bateman's experiment had some serious methodological problems. Therefore, a replication study was done. In this study the phenotypic differences among the offspring were inconsistent with the expected frequencies, according to Mendelian inheritance. It seems that Bateman did not check if his frequencies of the offspring carrying two dominant marker alleles were in line with the expected frequencies. Probably the assumption that there were no effects of marker combinations on offspring survival was incorrect. Therefore, it is likely that his results of mating success and reproductive success were biased: the number of flies with no sexual partner was overestimated and the number of flies with one or more sexual partners was underestimated (Gowaty et al., 2012). Dewsbury (2005) agreed with the thought of methodological limitations in the Bateman experiment, because the matings that did not lead to offspring production were not included in Bateman's data. Thus, only the sexual partners which led to offspring production were calculated as mating partners (Dewsbury, 2005). Complementary, Snyder et al. (2007) claimed that it is possible that the sex differences in mating success and reproductive success found in Bateman's experiments were influenced by differences in mating behavior and attractiveness between the flies with different marker mutations or even by chance. They used a simulation model to determine if Bateman's results could be explained by chance effects. The simulation model showed that it is possible that sex differences in mating success derived from chance effects, such as individual differences in the amount of meetings with a potential mating partner (Snyder et al., 2007). The findings of Gowaty et al., Dewsbury and

Snyder et al. indicate that the experimental evidence upon which Bateman based his principles are not as strong as generally assumed. This should be taken into consideration when interpreting evidence found for Bateman's principles in human societies. Nonetheless, some studies show that animals exhibit patterns in reproductive behavior and mating behavior consistent with Bateman's predictions (Trivers, 1972; Jones et al., 2002). For instance, in the rough-skinned newt males showed a higher variance in number of offspring and number of mating partners and a stronger relationship between number of offspring and number of mating partners than females (Jones et al., 2002).

### Implications for further research

As a consequence of the previous described limitations, further research on Bateman's principles in human societies should be done to determine the differences in mating and reproductive behavior between the sexes and to see if these differences are to the same extent present in different human populations. Data about other aspects of populations, such as population density or sex ratio, could be added, because for example it is known that the sex ratio influences the strength of competition (Brown et al., 2009). Moreover, there is need for databases with unbiased data about number of offspring and number of mating partners. Otherwise it remains impossible to draw valid conclusions. The findings of this thesis and those obtained from further research will contribute to a better understanding of sexual selection mechanisms working in human societies.

## References

- Alexander MG, Fisher TD. 2003. Truth and consequences: Using the bogus pipeline to examine sex differences in self-reported sexuality. *The journal of sex research*. 40(1):27-35.
- Andersson M, Iwasa Y. 1996. Sexual selection. *Trends in Ecology and Evolution*. 11(2):53-58.
- Andrade MCB, Kasumovic MK. 2005. Terminal investment strategies and male mate choice: extreme tests of Bateman. *Integrative and Comparative Biology*. 45:838-847.
- Arnold SJ. 1994. Bateman's principles and the measurement of sexual selection in plants and animals. *The American naturalist*. 144:126-149.
- Arnold SJ, Duvall D. 1994. Animal mating systems: a synthesis based on selection theory. *The American naturalist*. 143(2):317-348.
- Barthold JA, Myrskylä M, Jones OR. 2012. Childlessness drives the sex difference in the association between income and reproductive success of modern Europeans. *Evolution and human behavior*. doi:10.1016/j.evolhumbehav.2012.03.003.
- Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity*. 2:349-368.
- Betzig L. 2012. Means, variances, and ranges in reproductive success: comparative evidence. *Evolution and human behavior*. 33:309-317.
- Borgerhoff Mulder M. 1987. On cultural and reproductive success: Kipsigis evidence. *American anthropologist*. 89(3):617-634.
- Borgerhoff Mulder M. 2009. Serial monogamy as polygyny or polyandry?. *Human nature*. 20:130-150.
- Brown GR, Laland KN, Borgerhoff Mulder M. 2009. Bateman's principles and human sex roles. *Trends in Ecology and Evolution*. 24(6-14):297-304.
- Buckle L, Gallup GG Jr, Rodd ZA. 1996. Marriage as a reproductive contract: patterns of marriage, divorce and remarriage. *Ethology and Sociobiology*. 17:363-377.
- Courtial A, Pettay JE, Jokela M, Rotkirch A, Lummaa V. 2012. Natural and sexual selection in a monogamous historical human population. *Proceeding of the National Academy of Sciences*. 109(21):8044:8049.
- Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Dewsbury DA. 2005. The Darwin-Bateman paradigm in historical context. *Integrative and Comparative Biology*. 45:831-837.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*. 197:215-223.

Forsberg AJL, Tullberg BS. 1995. The relationship between cumulative number of cohabiting partners and number of children for men and women in modern Sweden. *Ethology and Sociobiology*. 16:221-232.

Geary DC. 2000. Evolution and proximate expression of human paternal investment. *Psychological Bulletin*. 126(1):55-77.

Godin JJ, McDonough HE. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral ecology*. 14(2):194-200.

Gowaty PA, Kim YK, Anderson WW. 2012. No evidence of sexual selection in a repetition of Bateman's classic study of *Drosophila Melanogaster*. *Proceedings of the National Academy of Sciences*. doi: 10.1073/pnas.1207851109.

Hewlett BS. 1988. Sexual selection and paternal investment among Aka pygmies. *Human reproductive behaviour: a Darwinian perspective*. 263-276.

Hrdy S. 1997. Raising Darwin's consciousness. *Human nature*. 8(1):1-49.

Jokela M, Rotkirch A, Rickard IJ, Pettay J, Lummaa V. 2010. Serial monogamy increases reproductive success in men but not in women. *Behavioral ecology*. 21(5):906-912.

Jones AG, Roman Arguello J, Arnold SJ. 2002. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough-skinned newt. *Proceedings of the Royal Society of London B: Biological sciences*. 269:2533-2539.

Käär P, Jokela J, Merilä J, Helle T, Kojola I. 1998. Sexual conflict and remarriage in preindustrial human populations: causes and fitness consequences. *Evolution and human behavior*. 19:139-151.

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

Marlowe F. 2000. The patriarch hypothesis: an alternative explanation of menopause. *Human nature*. 11(1):27-42.

Minnesota Population Center, with the help of National Institute of Statistics and Censuses Argentina, National Bureau of Statistics Austria and the Bureau of the Census United States. 2011. Integrated Public Use Microdata Series, International: Version 6.1 [Machine-readable database]. Minneapolis: University of Minnesota.

Murdock, GP. (1967). *Ethnographic atlas*. University of Pittsburgh Press.

Pettay JE, Kruuk LEB, Jokela J, Lummaa V. 2005. Heritability and genetic constraints of life-history trait evolution in preindustrial humans. *Proceedings of the National Academy of Sciences*. 102(8):2838-2843.

Quinlan RJ, Flinn MV. 2005. Kinship, sex, and fitness in a Caribbean community. *Human nature*. 16(1):32-57.

Rendall MS, Clarke L, Peters HE, Ranjit N, Verropoulou G. 1999. Incomplete reporting of men's fertility in the United States and Britain: a research note. *Demography*. 36(1):135-144.

Salzano FM, Neel JV, Maybury-Lewis D. 1967. Further studies on the Xavante Indians. I. Demographic data on two additional villages: genetic structure of the tribe. *American journal of human genetics*. 19(4):463-489.

Schmitt DP. 2005. Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and brain sciences*. 28:247-311.

Snyder BF, Gowaty PA. 2007. A reappraisal of Bateman's classic study of intrasexual selection. *Evolution*. 61(11):2457-2468.

Tang-Martinez Z, Ryder TB. 2005. The problem with paradigms: Bateman's worldview as a case study. *Integrative and Comparative Biology*. 45:821-830.

Trivers RL. (1972). Parental investment and sexual selection. In *Sexual selection and the descent of man*. Chicago: Aldine publishing company.

Weeden J, Abrams MJ, Green MC, Sabini J. 2006. Do high-status people really have fewer children?. *Human nature*. 17(4):377-392.

Wiederman MW. 1997. The truth must be in here somewhere: examining the gender discrepancy in self-reported lifetime number of sex partners. *The journal of sex research*. 34(4):375-386.

Weir LK, Grant WJA, Hutchings JA. 2011. The influence of operational sex ratio on the intensity of competition for mates. *The American naturalist*. 177(2):167-176.