JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE
162

Ines Klemme

Polyandry and its Effect on Male and Female Fitness

JYVÄSKYLÄN YLIOPISTO

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi Jyväskylän yliopiston Konneveden tutkimusasemalla
toukokuun 19. päivänä 2006 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2006

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Publishing Unit, University Library of Jyväskylä

Cover picture by Ines Klemme

URN:ISBN:9513925331
ISBN 951-39-2533-1 (PDF)

ISBN 951-39-2449-1 (nid.)
ISSN 1456-9701

Jyväskylä University Printing House, Jyväskylä 2006

ABSTRACT

Klemme, Ines
Polyandry and its effect on male and female fitness
Jyväskylä: University of Jyväskylä, 2006, 28 p.
(Jyväskylä Studies in Biological and Environmental Science,
ISSN 1456-9701; 162)
ISBN 951-39-2533-1
Zusammenfassung: Polyandrie und seine Auswirkungen auf die Fitness von Männchen und Weibchen
Yhteenveto: Polyandria ja sen vaikutukset koiraan ja naaraan kelpoisuuteen
Diss.

Polyandry, i.e., mating with multiple males within one reproductive event, is currently regarded as one of the most significant female reproductive behaviours. Its adaptive functions and its consequences on male reproductive success, however, are still not identified in most species. In this thesis I have studied causes and consequences of polyandry in a small mammal species, the bank vole (*Clethrionomys glareolus*), focusing on two questions. First, are dominance-related traits in males related to reproductive success in polyandrous species and second, which benefits do females gain from mating with multiple males. I conducted five experiments, two under laboratory conditions and three under semi-natural conditions in large outdoor enclosures. I found evidence that two dominance-related traits, male body size and scent marking behaviour, are related to male reproductive success. However, this was only the case under certain environmental and social conditions, suggesting that the strength of sexual selection on these traits is variable. I was further able to show that bank vole females gain direct and genetic fitness benefits from multiple mating, suggesting that polyandry is a beneficial strategy for females. The results of this study may help to understand the evolution of polyandry and its implications on male and female reproductive success, which is of general importance for the study of sexual selection.

Key words: bank vole, *Clethrionomys glareolus*, direct benefits, genetic benefits, male dominance, paternity, polyandry, sexual selection.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on five original papers, which will be referred to in the text by their Roman numerals I-V. I performed a large part of the work in all studies and I am the main writer of all articles.

I Klemme I., Ylönen H. & Eccard J. A. Reproductive success of bank voles (*Clethrionomys glareolus*): the effect of operational sex ratio and male size. Manuscript.

II Klemme I., Eccard J. A. & Ylönen H. Does it pay to be a dominant male in a promiscuous species? Annales Zoologici Fennici (in press).

III Klemme I., Eccard J. A. & Ylönen H. Do female bank voles (*Clethrionomys glareolus*) mate multiply to improve on previous mates? Behavioral Ecology and Sociobiology (in press).

IV Klemme I., Eccard J. A. & Ylönen H. Multiple mating brings direct fitness benefits for female bank voles (*Clethrionomys glaerolus*). Manuscript (submitted).

V Klemme I., Ylönen H. & Eccard J. A. Genetic benefits of polyandry in bank voles (*Clethrionomys glareolus*). Manuscript (submitted).

1 INTRODUCTION

Sexual selection theory predicts divergent mating tactics for males and females (Darwin 1871, Trivers 1972). This is because the asymmetry in gamete size between males and females and associated investment in offspring leads to a differential effort of both sexes for reproduction (Bateman 1948, Trivers 1972, Clutton-Brock & Vincent 1991). Females, who produce large nutrient-rich eggs and often care for the young, allocate typically more resources than males in each offspring. Males are therefore expected to increase their reproductive success by fertilising many females while females are expected to maximize their reproductive success by choosing a high quality mate (Bateman 1948, Trivers 1972). However, molecular evidence combined with behavioural observations has indicated that females of many taxa mate with multiple males during one reproductive event (polyandry) (Birkhead & Møller 1998).

Polyandry expands the scope of classical sexual selection theory. Sexual selection arises from competition over mates, typically through male-male competition and female choice (Darwin 1871). Traditionally success in competition over mates was defined as success in mate acquisition. Thereby dominance, defined as stable asymmetry in agonistic behaviours, is thought to be beneficial for males. First dominant males may be able to exclude their rivals from access to mates and second, since the maintenance of traits reflecting dominance is costly, they are generally thought to signal superior quality to females (reviewed in Qvarnström & Forsgren 1998). However, the fact that females often mate with multiple males implies that sexual selection does not end with copulation. For polyandrous species post-copulatory mechanisms, as sperm competition (Parker 1970) or cryptic female choice (Thornhill 1983, Eberhard 1996), are central parts of sexual selection. Hence, success in competition over mates should be measured by fertilisation success (Parker 1970) and it is therefore unclear whether dominance is advantageous in polyandrous species (Dewsbury 1982).

Polyandry also challenges the long held view of females as the choosy, monogamous sex and raises the question of why females commonly mate with multiple males. The adaptive basis of polyandry is difficult to understand because multiple mating is contradictory to the conclusion drawn from potential reproductive rates of females (see above). Additionally, mating inevitably involves costs, such as time and energy spent (Daly 1978) as well as risk of predation and disease transmission (Magnhagen 1991). A number of benefit hypotheses, summarized in Table 1, have been proposed to explain why selection should favour the evolution of polyandry. These benefits may increase female fitness either directly, i.e., through immediate benefits, or indirectly, i.e., through genetic benefits for her offspring. There is now a growing body of literature with both empirical and theoretical exploration of the different hypotheses, however the extent to which these hypotheses might apply across taxa is still unclear. Moreover, experimental studies on mammals testing benefit hypotheses of polyandry are almost completely lacking.

Polyandry therefore raises two major questions with implications on sexual selection that I addressed in this thesis. First, which male traits lead to success in competition over mates when females are polyandrous, and second, what are the adaptive functions of polyandry? My model species was the bank vole (*Clethrionomys glareolus*), a promiscuous rodent species. I studied in laboratory and enclosure experiments, combined with genetic paternity analyses, whether dominance-related characters in males are related to male reproductive success (I-III) and what benefits females gain from mating with multiple males (III-V). Answering these questions may help us to understand the evolution of reproductive behaviours of males and females.

TABLE 1 Direct and genetic female benefits proposed to explain polyandry (adapted from Jennions & Petrie 2000, Hosken & Stockley 2003).

direct benefits	Genetic benefits
• increase in parental care[1]	• good genes trading up for "better" genes promotion of sperm competition/cryptic choice sexy sperm
• access to resources/nutrients[1]	
• avoidance of infanticide	
• avoidance of male harassment	• avoidance of genetic incompatibility (including inbreeding avoidance)
• fertilisation assurance	• bet hedging against "bad" or incompatible genes against environmental uncertainty
• ovulation stimulation[2]	

[1] refers only to resource-based mating systems

[2] can be achieved also by repeated mating with the same male

2 METHODS

2.1 Study species

The bank vole is a common sylvatic rodent species that is distributed over most of Europe. Its social organisation has been studied in detail. During the breeding season mature females are territorial and each female's home range overlaps with the home ranges of several males (Bujalska 1973, Bondrup-Nielsen & Karlsson 1985). *Clethrionomys* males, on the other hand, form groups of stable dominance hierarchies (Viitala 1977) and have large home ranges that overlap each other as well as those of several females (Bondrup-Nielsen & Karlsson 1985). On the basis of this spatial distribution, the mating system has been described as promiscuous. Indeed, genetical studies on natural populations showed that males mate with several females (Sikorski & Wójcik 1990) and at least some of the females mate with multiple males as indicated by about 30% of the litters being multiply sired (Ratkiewicz & Borkowska 2000). Males cannot coerce females into copulation, because female cooperation is required for successful copulation (Milligan 1979). Further, males provide no resources for the female or the offspring.

Bank vole males possess no visible weapons or ornaments that may play a role in male-male competition or female choice. Instead, olfactory signals are the common mode for communication in rodents and scent is thought to be a sexually selected trait (Andersson 1994). In bank vole males, the degree of scent marking is positively related to social status (Rozenfeld et al. 1987, Horne & Ylönen 1996). Bank vole females are able to discriminate among dominant and subordinate males in relation to their odours (Hoffmeyer 1982, Kruczek 1997) and prefer males with a more pronounced marking behaviour as mating partners (Horne & Ylönen 1996). Additionally, bank voles exhibit a slight sexual size dimorphism with males being larger than females. Male biased sexual size dimorphism is usually the result of sexual selection by male contest competition (Andersson 1994). Both dominance-related traits, body size and scent marking behaviour, are positively related in bank voles (Horne & Ylönen 1998).

However, there is a lot of variability and relatively small males can - in terms of marking behavior - be dominant over relatively large males (Horne & Ylönen 1998). In two studies of this thesis, both dominance-related traits were measured simultaneously. Body mass was near significantly related to scent marking in one study (III) but not in another (II).

The studies included in this thesis were conducted on a laboratory population that consisted of wild captured individuals trapped in Central Finland (62°37´N, 26°20´E) and their descendants. The laboratory colony was maintained at Konnevesi Research Station and at the Experimental Animal Unit of the University of Jyväskylä.

2.2 Experimental procedure

A simplified overview of the experimental setups and reproductive traits measured in each experiment is given in Table 2.

Male traits related to male dominance were assessed in the laboratory before the actual experiments. We measured body mass using electronic scales for males in studies I-II. For males in studies II-III, we conducted paired trials in the laboratory to estimate the marking pattern of a given pair of males. Earlier studies have shown that dominant males cover large areas of substrate with scent marks in form of fine traces and subordinate males stop marking in the presence of dominant males (Rozenfeld & Rasmont 1991, Horne & Ylönen 1996). These pairs were then used for the actual laboratory or enclosure experiments, during which we measured their reproductive success.

We tested several hypotheses proposed to explain potential benefits of polyandry (Table 2). Female benefits were assessed with either fitness measures such as pregnancy rate and offspring viability or with testing whether females are able to bias paternity towards high quality males or compatible genotypes.

Two studies (III, IV) were conducted in the laboratory facilities of the Konnevesi Research Station. In both studies, we used standard mouse cages (43x26x15 cm) as mating arenas and observed the behaviour of our experimental animals directly. In study III, we manipulated the order in which females encountered males of different dominance status (scent marking). In study IV, we manipulated the number of matings (one or two) and the number of mating partners (one or two) among females using randomly chosen males. After successful copulations, we monitored female reproduction in their home cages.

Studies I, II and V were conducted in large 0.25 ha outdoor enclosures situated near Konnevesi Research Station. The enclosures are fenced with metal sheets dug in the ground to prevent the escape of the animals. The habitat can be described as homogeneous old field, the vegetation consisting mainly of tall grass and bushes. Twenty-five Ugglan multiple capture live traps per enclosure allowed the monitoring of the enclosure populations. We conducted studies I and II during the breeding season and study V from the end of one breeding season until the beginning of the next, i.e., the animals overwintered in the enclosures. In study I, we manipulated population sex ratios to be either female or male biased. In study II, we manipulated the social relationship of males in our experimental populations (scent marking). Experiment V was a follow-up study of experiment IV and we studied the winter survival and reproductive success at the onset of breeding of individuals arising from different mating treatments. In all three studies, we transferred all animals back to the laboratory at the end of each field period and monitored female reproduction in their home cages.

We estimated paternities of the arising offspring in studies I-III and V using up to six microsatellite markers per study (Gockel et al. 1997, Gerlach & Musolf 2000).

TABLE 2 Simplified overview of the experimental setups in all five studies, including place of the study, which of the two main subjects of this thesis studied, manipulations conducted, male traits measured, female benefit hypotheses tested, and reproductive traits measured in males and females.

	I	**II**	**III**	**IV**	**V**
place	enclosure	enclosure	laboratory	laboratory	enclosure
subject	♂ traits	♂ traits	♂ traits + ♀ benefits	♀ benefits	♀ benefits
manipulation	sex ratio	♂ dominance relationship	♂ dominance relationship	# matings # mates	# mates (follow-up IV)
♂ traits	body mass	body mass + scent marking	scent marking	-	-
♂ measures	RS	RS	RS	-	-
♀ benefits	-	-	good genes	ovulation stimulation	good genes avoid. of genetic incompatibility bet hedging
♀ measures	-	-	pre-copulatory sequential female choice	pregnancy rate	F1 body mass, survival + RS post-copulatory female choice

RS = reproductive success, # = number of

3 RESULTS AND DISCUSSION

3.1 Sexual selection of dominance-related traits under polyandry

Dominance-related traits are potentially favoured under sexual selection because they often predict the outcome of intrasexual competition and/or are preferred by the opposite sex. The strength of sexual selection on phenotypic traits is affected by different factors such as variance in mating success (= opportunity for sexual selection), mating system and aspects of a species' biology (Andersson 1994). Variance in mating success in turn, depends to a large extend on the operational sex ratio, the ratio of fertile males to receptive females (Emlen & Oring 1977). This is because a bias in operational sex ratio will lead to an increased competition among the more abundant sex and monopolization of mates will then cause variance in reproductive success. Our results support the general hypothesis of a relationship between operational sex ratio and the opportunity for selection in males (I). Variance in male reproductive success (number of females fertilised, number of offspring sired) was high in male biased operational sex ratios and small in female biased operational sex ratios (I). Because in mammals maternal investment typically exceeds paternal investment, the operational sex ratio of natural populations should be male biased (Clutton-Brock & Vincent 1991, Clutton-Brock & Parker 1992). We therefore conclude that the opportunity for sexual selection and consequently sexual selection on phenotypic traits should be strong in bank vole males.

In an enclosure study (I) we found evidence that *male body mass was related to reproductive success*. However, this was only the case in female biased and even operational sex ratios, but not in male biased ones, suggesting that there is a decrease in the strength of sexual selection for large body size as operational sex ratio becomes male biased. This seems paradoxically in terms of intrasexual competition, but being a large male and having larger testes (Ylönen et al. 2004) may be advantageous when many females are available and mating demands are high. Larger testes produce, store and ejaculate more sperm (e.g. Ginsberg & Huck 1989) and large males will thus gain a fitness advantage in a social system, where males are not able to monopolize females, by mating with as many females as possible.

In another enclosure study (II), in contrast, *male body mass was not related to reproductive success*, although the sex ratio in this experiment was female biased and the operational sex ratio was on average even. What caused the difference between the two experiments? First, the experiments were conducted in different years and hence the environmental conditions, such as weather or food supply, may have caused differential success of large males. Second, the females used in both experiments differed in reproductive history. In study I all females were sexually experienced and had been breeding at least once before the experiment, whereas all females in study II were sexually inexperienced. Female preferences may alter or choice abilities may improve with reproductive experience. Although we are not able to disentangle the causes for the discrepancy between the two experiments, the results show that the strength of sexual selection for large male body mass does not only depend on operational sex ratio, but also on other factors. However, since operational sex ratio in natural populations of bank voles are rather expected to be male biased (see above), sexual selection on large body size may not be strong.

The relationship between scent marking behaviour and male fitness was investigated in both a laboratory study (III) and an enclosure study (II, note that body mass was not related to scent marking in this study). In the laboratory study females mated sequentially with a given pair of males, with one male showing marking behaviour typical for dominant males (hereafter dominant male) and another male showing marking behaviour typical for subordinate males (subordinate male). We found evidence that *dominant males sired significantly more offspring than subordinate males* (III). The factor(s) determining the increased fertilising success of dominant males remain unclear. We found a small effect of mating order: dominant males sired more offspring when they were second, than when they were first. Moreover dominant males may either have had an advantage in sperm competition and/or females may have cryptically chosen dominant males due to the selection of sperm or selective abortion of embryos. Whatever mechanism underlies our finding shows that male dominance can be advantageous also under polyandry.

In the enclosure study (II), in which one dominant and one subordinate male competed for four females, *reproductive success of dominant and subordinate males did not differ significantly*. This although females seemed to mate again commonly with both males, as indicated by 33% of the litters sired multiply. Again there are several possible explanations for the discrepancy between both experiments. First, the number of females males competed for, differed between experiments, and different operational sex ratios may lead to varying selection pressures (see above). Second, again females used in both experiments had different reproductive histories: females in the enclosure experiment were sexually inexperienced, whereas females in the laboratory experiment had been breeding prior to experimentation. Alternatively, female preferences may alter with environmental conditions or might be density dependent (Qvarnström & Forsgren 1998). Especially in the wild, where many uncontrollable factors influence individual behaviour, female choice decisions might be different to those observed under stable laboratory conditions.

There have been only few studies on promiscuous mammals investigating the relationship of dominance and siring success, and a positive relationship was found in all these studies (deer mice: Dewsbury 1981, yellow-toothed cavy: Keil et al. 1999, Soay sheep: Preston et al. 2003). However, in the study on deer mice, reproductive success of dominant males was also context dependent, i.e., a positive relationship was found in outdoor enclosures, but not in small cages in the laboratory (Dewsbury 1981). Our results show that dominance-related traits can be positively correlated to male reproductive success in polyandrous species, but the strength and direction of sexual selection on these traits seems to depend on many factors. All three studies (I-III) showed that female bank voles generally mate with multiple males regardless of obvious differences in size and dominance of available mates.

3.2 Benefits of polyandry

The evolution of polyandry is focus of much current work in sexual selection and several hypotheses have been proposed to explain the phenomenon (Table 1). We conducted three studies to determine benefits of multiple mating in bank voles (III-V). First we tested the trade-up hypothesis under which females are expected to re-mate when a new male encountered is a superior genetic source to a previous mate (Halliday 1983). If so, females could maximize the genetic benefits to their offspring. In a sequential mate choice experiment (III) we found that the majority of females (92%) *actively engaged in mating with multiple males, irrespective of male quality* (dominant vs. subordinate) of the first or second male offered. Therefore, multiple mating in bank voles cannot be explained by the trade-up hypothesis based on dominance rank. Since mating *per se* is costly (Daly 1978, Magnhagen 1991) and mating with low quality males may decrease a female's fitness, specific benefits of polyandry may outweigh these potential costs.

Among the hypotheses proposed to explain the benefits of polyandry, direct benefits are thought to be the origin of polyandry. Although in many polyandrous species males seem to provide only non-nutritious ejaculates to the female, it must be noted that direct benefits often can be inconspicuous. Indeed we found in a laboratory study (IV) that bank vole females gain direct benefits from multiple mating. When mating multiple times, either repeatedly with the same male or with different males, females *increased the probability of pregnancy initiation* (IV). This is in accordance with the stimulation of ovulation hypothesis proposed for mammals with induced ovulation (Hunter et al. 1993). As has been also shown in other rodent species, a certain amount of stimulation from the male is needed to initiate pregnancy and may be only achieved by multiple matings (Dewsbury 1979, Huck et al. 1986, Ågren 1990, Wolff & Dunlap 2002). However, an appropriate stimulus for pregnancy initiation can be achieved by multiple mating with the same male (IV). Mating with multiple males seems inevitably costlier than repeated mating with the same male, yet female bank voles are found to mate commonly with multiple males. In a female choice study, where four males were simultaneously offered to a single bank vole female, females mated up to seven times including all four males (Klemme I., Kataja-aho S., Eccard J. A. & Ylönen H. unpublished).

In a combined laboratory study (IV) and field study (V) we tested potential genetic benefits of multiple mating, that can only be achieved by multiple mating with different males, including i) the good genes hypotheses: promotion of sperm competition or female choice of sperm to increase the probability that eggs are fertilised by sperm of high quality males (Birkhead et al. 1993), ii) the sexy sperm hypothesis: sons of multiply mated females produce competitively superior sperm or ejaculates (Keller & Reeve 1995), iii) the avoidance of genetic incompatibility hypothesis: polyandrous females exploit post-copulatory mechanisms to minimize the risk of fertilisation by genetically incompatible males (Zeh & Zeh 1996) and iv) the bet-hedging hypothesis: multiple paternity increases the likelihood that at least some of the offspring are sired by males with good or compatible genes, or at least some of the offspring will survive in an unpredictable environment (Watson 1991). There are some theoretical difficulties associated with genetic benefits and therefore genetic benefits may not explain the evolution of polyandry in the first place (Yasui 1998). For example female abilities for biasing paternity – a premise for the cryptic choice of good genes hypothesis or genetic incompatibility hypothesis – are not expected to have evolved without polyandry. Further, theoretical models have shown that the bet hedging hypothesis cannot explain the origin of polyandry unless populations are very small and there are no costs of mating (Yasui 1998). Once evolved, however, polyandry can generate genetic benefits which may lead to the maintenance of polyandry.

In a field study (V) we found evidence for genetic benefits of polyandry in bank voles. After controlled matings in the laboratory (IV), the offspring of polyandrous females and monandrous females were released to outdoor enclosures to overwinter. At the onset of breeding we found that progeny of polyandrous females *were significantly more successful at reproduction* than progeny of monandrous females. Moreover progeny (F1) of polyandrous females showed a *reduced variance among litters in body mass* before the field experiment. In our analysis we tried to disentangle different genetic benefit hypotheses to explain our findings, however, the mechanisms underlying our findings are not entirely clear (V). There has been only one experimental study on mammals testing potential genetic benefits of polyandry. In their study on yellow-toothed cavies, Keil and Sachser (1998) found that nestlings of polyandrous females had an increased viability compared to nestlings of monandrous females, suggesting that also females of this rodent species gain genetic benefits from polyandry.

Few hypotheses proposed to explain female multiple mating remain so far untested for bank voles (Table 1). We can exclude the increase in parental care hypothesis and the resources hypothesis because the mating system of our study species is nonresource-based. We can further exclude the avoidance of male harassment hypothesis, because bank vole females actively solicit multiple mating (Klemme I., Kataja-aho S., Eccard J. A. & Ylönen H. unpublished). The assurance of fertilisation hypothesis (males may be sperm depleted or sterile) cannot be ruled out for our study species. Although we found that females were not limited by sperm and able to reproduce successfully in highly female biased sex ratios (I), little is known about male sterility in bank voles. Lastly, the avoidance of infanticide may, in addition to the benefits found, also play a major role in the evolution or maintenance of polyandry in bank voles. Infanticide committed by males is common among mammals (reviewed in Ebensperger 1998b) and has been also shown to occur in bank voles (Ylönen et al. 1997). In species with male infanticide, polyandry may serve to confuse paternity and thereby prevent males from killing potential young (Ebensperger 1998a). Indeed a recent enclosure study showed that the presence of unmated bank vole males in a female's vicinity significantly reduced offspring recruitment (Reckord A., Klemme I., Eccard J. A. & Ylönen H. unpublished). This also suggests that mating with multiple (all available) males may be an advantageous strategy for females.

4 CONCLUSIONS

In this thesis I have studied implications of polyandry on male and female reproductive success in a small rodent species, the bank vole. I have mainly focused on the strength of sexual selection on male characters related to male dominance, and on the evolution of female multiple mating. I have approached this with experimental studies in both the laboratory and in a semi-natural environment in large outdoor enclosures. *First*, the results of my study add new support for a strongly promiscuous mating system in bank voles. I found that most of the females engaged in mating with multiple males. Moreover, males are capable of fertilizing many females within a short time, suggesting that males possess large sperm storages. There is now considerable evidence that polyandry, and hence a high risk for sperm competition, selects for large testes, which are related to the production of numerous sperm. *Second*, I found evidence that traits related to male dominance in bank voles can be related to male reproductive success, but the strength and direction of sexual selection on these traits seem to depend on many factors. I conclude that variation in population structure, known to exist in small rodent species, may explain variation in fitness related traits found in natural populations. However, since the advantage of dominance-related traits was observed under conditions not expected to be natural (in female biased sex ratios, in the laboratory), it is questionable whether these traits play a significant role in sexual selection. In the future it will be crucial to investigate sperm competition and cryptic choice in order to understand the paternity patterns observed in this study. *Third* I was able to show that polyandry is evidently beneficial for bank vole females. The hypotheses proposed to explain polyandry are not mutually exclusive and the results on bank voles show that females can gain diverse benefits from polyandry. Multiple mating in bank voles may have evolved in the first place due to the direct benefit of ovulation stimulation, but genetic advantages in addition to the stimuli needed, may contribute to the maintenance of polyandry.

Acknowledgements

Setting out in the right way is just as important as the opening lines in a book.

This is the way to start a new life,
with a hurricane lamp shining at the top of the mast,
and the coastline disappearing behind one
as the whole world lies sleeping.

Moominpappa

It was a grey day in February four years ago when a ferry left Germany on its way to Finland. The evening had been stormy, and I was standing on deck looking silently to the coastline disappearing behind me as the whole world lied sleeping. And in spite of all the preparations and visions I had had during the previous weeks and months, it was only then that I realised this journey is a journey into a new life. A new life, started to write the book you are holding in your hands. The fear that struck me on the ferry disappeared quickly. I set out just in the right way, and the new life with the book and everything else it contained, turned out to be most wonderful.

I thank my supervisors Hannu and Jana, for believing in me and giving me the opportunity to come here and work with little hairy animals. Thank you also for motivating me again and again and for teaching me to work independently. Hannu, special thanks for your guidance and advices, your endless optimism, for “Multamäkis”, for sending me to congresses, and for maintaining this friendly and familiar vole group. Jana, although we almost never were in the same place (physically), thanks for being always ready to help. Thanks also for your everlasting idea pool, for your interest, for the long e-mail debates, for being critical and for leading me to think.

I am grateful to the numerous people that have also helped and supported me in various ways during this project. Special thanks to Aira, Niina and Raisa, for their practical help, for their friendship, and for the most wonderful summer I have ever had. Without you three, Finland would not mean the same to me. Also, “suuri kiitos” to the three masters students involved in this project: Annika, Saana and Onerva. Thanks for your interest in mating voles and for helping to learn more about them. Special thanks to Saana for shared non-scientific hobbies and to Onerva for all the laughter. I also owe much thank to the other - previous and present - members of our vole group for their practical and mental help and for many hours of fun in Konnevesi: Dorota, Lenka (special thanks for Slovakian cuisine), Janne and Marko. And it would yet take another four years to finish this work without all the students and trainees that never got tired of cleaning cages, checking traps, carrying dominance arenas back and forth, doing PCR’s and much more. Thank you Anni (also for joined mushroom hysteria), Borbla, Dagmar, Elina P. (also for nice chats), Elina R.,

Eveliina, Henni, Jossu (also for EachOneTeachOne full of giggle moments), Kaisa, Saara, Susanne and Tuija.

Most of this work has been conducted at Konnevesi Research Station, which is (as Jana has said earlier) probably the best place on earth to do science. This is because this station is placed at a beautiful shoreline, it is cosy and it has all one can dream of, including the best sauna in the world. But mostly this is because of the people that work there. Thanks to Jussi and Hannu - the earlier and the present leader of the station, to Helinä, Irja, Raija, Tarja and to the "pojat" Janne, Jyrki and Risto for making life so easy and for the warm and friendly atmosphere at the station.

When not in Konnevesi, I enjoyed being at our Department, another wonderful place to work. Thanks to its leaders during the last four years: Jonna and Rauno, and to all the nice and friendly researchers, teachers, staff and fellow PhD students. Special thanks to those of you who have read and improved parts of my thesis: Marjo, Tanja, Mikael, Rauno and the Journal Club, and to those who have improved my English: Emily, Suzie and John. Thanks also to the "outside" people that have invested time and energy on reading drafts of my manuscripts: Elina K., Karen, Paula and Sebastian. And thanks to Hannu for writing the Finnish summary of my thesis.

I am very thankful to the institutions and foundations that thought this project is worth of being supported financially: the Academy of Finland, the University of Jyväskylä, the Graduate School in Evolutionary Biology, the Marie-Curie Foundation and the DAAD Foundation.

Outside of Science are also a number of people that I would like to express my thanks to. "Lieben Dank" to my parents and my sisters for their love, for their interest in both my work and my new home, for millions of hours on the phone and for providing me with essential nutrients like "Rostbratwurst", "Thüringer Klöße" and chocolate. Thanks and hugs also to my best friend Karen. She desired this PhD position at least as much as I did. There was only space for one of us, and still she is my best friend. I am thankful for this and happy that you made your way to Finland.

But my warmest thanks go to Sven for his love, his endless support and encouragement, for liking this country as much as I do, and for being with me on deck of the ferry that particular evening.

It's funny about paths and rivers.
You see them go by,
and suddenly you feel upset and want to be somewhere else –
wherever the path or river is going, perhaps…

Sniff

(PS and I thank Tove Jansson for her beautiful literature)

ZUSAMMENFASSUNG (RÉSUMÉ IN GERMAN)

Polyandrie und ihre Auswirkungen auf die Fitness von Männchen und Weibchen

Theoretische Überlegungen zur sexuellen Selektion besagen, dass Männchen und Weibchen unterschiedliche Fortpflanzungsstrategien verfolgen sollten. Männchen haben relativ viele Gameten für die Fortpflanzung zur Verfügung und sollten sich mit möglichst vielen Weibchen verpaaren, um ihren Fortpflanzungsserfolg zu maximieren. Im Gegensatz dazu verfügen Weibchen über relativ wenige Gameten in die sie normalerweise mehr Ressourcen investieren als Männchen. Weibchen sollten sich daher nur so oft verpaaren wie zur Fertilisation nötig ist und können ihren Fortpflanzungsserfolg durch eine gute Partnerwahl maximieren. Genetische und verhaltensbiologische Studien der letzten Jahre haben allerdings gezeigt, dass sich Weibchen vieler Taxa innerhalb einer Fortpflanzungsperiode mit mehreren Männchen verpaaren (Polyandrie). Diese Verhaltensstrategie wirft verschiedene Fragen auf, denen ich in meiner Doktorarbeit nachgegangen bin.

Einerseits wurde bisher angenommen, dass soziale Dominanz bei Männchen ein sexuell selektiertes Merkmal ist. Dominante Männchen gehen häufig als Sieger im Konkurrenzkampf um Weibchen hervor und Weibchen bevorzugen oft dominante Männchen als Paarungspartner. Wenn sich Weibchen aber mit mehreren Männchen verpaaren, kann der Fortpflanzungserfolg nur durch andere Mechanismen, wie Spermienkonkurrenz und kryptischer Weibchenwahl, bestimmt werden. Es ist deshalb unklar, ob Dominanz auch bei polyandrischen Arten positiv mit dem Fortpflanzungserfolg korreliert.

Andererseits stellt sich die Frage, warum sich Weibchen mit mehreren Männchen verpaaren, da eine einzige Kopulation in der Regel ausreicht, um alle Ova zu befruchten. Außerdem entstehen bei Mehrfachverpaarungen zusätzliche Kosten für das Weibchen wie zum Beispiel ein erhöhter Zeit- und Energieaufwand sowie ein erhöhtes Predations- oder Infektionsrisiko. Es wurde eine Vielzahl verschiedener Hypothesen aufgestellt, um den Vorteil von Mehrfachverpaarungen zu erklären. Weibchen könnten ihre Fitness entweder durch direkte Vorteile oder aber indirekt durch genetische Vorteile für ihre Nachkommen erhöhen.

Die Beantwortung dieser Fragen ist von genereller Bedeutung für ein besseres Verständnis über die Evolution von Fortpflanzungsstrategien bei Säugetieren. In meiner Doktorarbeit habe ich die Auswirkungen von Polyandrie auf die Fitness von Männchen und Weibchen untersucht. Meine Modellart war die Rötelmaus (*Clethrionomys glareolus*), ein häufig vorkommendes Nagetier in der Holarktis. Rötelmäuse haben ein promiskuitives Paarungssystem, das heißt, sowohl Männchen als auch Weibchen verpaaren sich mit mehreren Partnern. Ich habe fünf experimentelle Studien im Labor sowie in großen Außengehegen unter seminatürlichen Bedingungen durchgeführt.

In den Studien, in denen der Zusammenhang von sozialer Dominanz und Fortpflanzungserfolg der Männchen zu untersuchen war, habe ich zwei Merkmale sozialer Dominanz, die Körpergröße und das Markierungsverhalten von den zu testenden Männchengruppen erfasst. Der Fortpflanzungserfolg wurde nach jedem Experiment mit Hilfe von genetischen Vaterschaftstests ermittelt. Es zeigte sich, dass soziale Dominanz auch in polyandrischen Arten positiv mit dem Fortpflanzungserfolg korreliert sein kann. Dies war jedoch nicht in allen Studien der Fall und schien von anderen Faktoren beeinflusst zu werden, wie zum Beispiel von dem operationalen Geschlechterverhältnis einer Population. Soziale Dominanz bei Rötelmausmännchen scheint daher weniger sexuell selektiert zu sein als bisher angenommen. Es ist möglich, dass andere Merkmale, als die von mir untersuchten, stärker selektiert sind. Denkbar ist ebenfalls, dass der Vorteil von Polyandrie für Weibchen den möglichen Nachteil von Verpaarungen mit untergeordneten Männchen ausgleicht.

In weiteren Studien habe ich die Anzahl der Fortpflanzungspartner von Weibchen experimentell manipuliert und die Fitness von mehrfach und einfach verpaarten Weibchen verglichen. Es zeigte sich, dass Weibchen eindeutig von Mehrfachverpaarungen profitieren. Polyandrische Rötelmausweibchen wurden mit einer höheren Wahrscheinlichkeit trächtig als monandrische Weibchen. Hierbei war es egal, ob in die Mehrfachverpaarung nur ein oder mehrere Männchen involviert waren. Dieser direkte Vorteil lässt sich durch eine erhöhte Stimulation bei Mehrfachverpaarungen erklären, die anscheinend essentiell für die Ovulation ist. Weiterhin scheinen Rötelmausweibchen auch genetische Vorteile für ihre Nachkommen aus Mehrfachverpaarungen zu ziehen. In einem Experiment konnte ich zeigen, dass Nachkommen von polyandrischen Weibchen einen signifikant höheren Fortpflanzungserfolg hatten als Nachkommen von monandrischen Weibchen. Darüber hinaus zeigten Nachkommen von polyandrischen Weibchen eine geringere Varianz in ihrer Körpergröße im Vergleich zu Nachkommen von monandrischen Weibchen. Die verschiedenen Hypothesen zum Vorteil von Polyandrie schließen sich nicht gegenseitig aus und die Ergebnisse dieser Studien belegen, dass Rötelmausweibchen gleichzeitig mehrere Vorteile aus Mehrfachverpaarungen ziehen können. Diese Vorteile könnten die Evolution oder zumindest das Vorkommen von Polyandrie bei Rötelmäusen erklären.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Polyandria ja sen vaikutukset koiraan ja naaraan kelpoisuuteen

Seksuaalivalinnan teorian mukaan koiraiden ja naaraiden tulisi omaksua erilaiset lisääntymisstrategiat parhaan lisääntymistuloksen saavuttamiseksi. Koirailla siittiöiden tuotanto on suurta, joten sukusolujen käytettävissä oleva määrä ei rajoita lisääntymiskumppanien lukumäärää. Siksi koiraan tulisi paritella mahdollisimman monen naaraan kanssa maksimoidakseen lisääntymismenestyksensä. Naarailla sitä vastoin on vähän munasoluja, joihin naaras joutuu investoimaan paljon resursseja. Tästä johtuen naaraan tulisi valikoida erittäin tarkasti laadukas pariutumiskumppani, ja parittelujen määrän tulisi riippua ainoastaan hedelmöitymisen varmistamisesta. Kuitenkin geneettiset ja käyttäytymisekologiset tutkimukset ovat viimeaikoina osoittaneet, että monien lajien naaraat parittelevat useiden koiraiden kanssa yhden lisääntymiskerran aikana. Väitöskirjatyössäni olen tutkinut tämän lisääntymisstrategian, polyandrian, vaikutuksia sekä naaraiden että koiraiden lisääntymismenestykseen.

Näihin päiviin saakka on oletettu, että koiraiden sosiaalinen dominanssi on seksuaalivalinnan kautta muodostunut ominaisuus. Dominantit koiraat selviävät useimmin voittajina kilpailutilanteissa ja taisteluissa, ja naaraat suosivat dominantteja koiraita lisääntymiskumppaneina. Dominanssin merkitys kuitenkin hämärtyy kun naaras parittelee useamman koiraan kanssa. Tällöin yksilön lisääntymismenestys määräytyy eri mekanismien, kuten spermakilpailun tai naaraan kryptisen valinnan kautta. Tämä johtaa yhteen väitöskirjatyöni kysymykseen siitä, korreloiko dominanssi enää koiraan lisääntymismenestyksen kanssa tilanteessa, jossa naaras parittelee usean koiraan kanssa yhden lisääntymiskerran aikana.

Toinen kysymys on se miksi naaras ylipäätään parittelee usean koiraan kanssa, jos oletetusti jo yhden parittelun siittiömäärä voi hedelmöittää kaikki naaraan munasolut. Lisääntymistapahtuma siihen liittyvine käyttäytymismalleineen ja parittelut itsessään aiheuttavat naaraalle mm. aika- ja energiakustannuksia ja altistavat naaraan saalistukselle sekä mahdollisesti lisäävät erilaisten tautien riskiä. Seksuaalivalinnan teorian jatkumona onkin esitetty monia hypoteeseja, jotka selittäisivät monen koiraan kanssa parittelun edullisuuden naaraan kannalta. Naaraat voivat saada joko suoria kelpoisuusetuja tai epäsuoria, geneettisiä etuja, jotka ilmenisivät jälkeläisten parempana laatuna.

Ylläesitettyjen kysymysten tutkimuksella on yleistä merkitystä nisäkkäiden lisääntymiskäyttäytymisen evoluution ymmärtämisessä. Tässä tutkimuksessa olen tarkastellut naaraiden polyandrian vaikutusta molempien sukupuolten, koiraiden ja naaraiden lisääntymismenestykseen. Mallilajina olen käyttänyt metsämyyrää (*Clethrionomys glareolus*), joka on holarktisen metsähabitaatin yleisimpiä nisäkkäitä. Uusimpien tutkimusten mukaan metsämyyrä lisääntyy sekasopuisesti, eli niin koiraat kuin naaratkin parittelevat useiden eri yksilöiden kanssa yhden lisääntymistapahtuman aikana. Väitöskirjatyöni sisältää viisi kokeellista tutkimusta, jotka tehtiin laboratoriossa ja suurissa luonnonmukaisissa ulkotarhoissa.

Tutkimuksissa, joissa tarkasteltiin sosiaalisen dominanssin vaikutusta koiraan lisääntymismenestykseen, käytin kahta sosiaalisen dominanssin muuttujaa tarkastelun kohteena, koiraan painoa ja hajumerkintäkäyttäytymistä. Yksilön lisääntymismenestys määritettiin geneettisten isyystestien avulla. Tutkimukset osoittivat, että myös polyandrisesti käyttäytyvillä naarailla koiraan dominanssi saattaa vaikuttaa sen lisääntymismenestykseen, mutta vaikutus ei ollut yksiselitteinen vaan riippuvainen monista sosiaalisen ympäristön tekijöistä, kuten populaation operationaalisesta sukupuolisuhteesta, eli siitä kuinka monta potentiaalista lisääntymiskumppania kulloisenkin lisääntymiskerran aikana oli tarjolla. Tutkimusten tulokset viittaavat siihen, että metsämyyrän sosiaalinen dominanssi ei olisikaan niin selkeästi seksuaalivalinnan kautta kehittynyt ominaisuus kun on tähän asti uskottu. On myös mahdollista, että naaras hyötyy monien koiraiden kanssa parittelusta, mutta koiras-koiras kilpailu johtaisi siihen, että pääasiassa dominantit koiraat pääsevät parittelemaan tietyn kiimasyklin aikana.

Seuraavissa tutkimuksissa tarkastelin naaraan lisääntymismenestystä tilanteissa, joissa naaras paritteli kontrolloidusti joko yhden tai useamman koiraan kanssa. Tulosten mukaan naaras yksiselitteisesti hyötyi useammasta parittelusta, mikä ilmeni korkeampana hedelmöitymisprosenttina. Paritteliko naaras useamman kerran yhden vai useamman koiraan kanssa ei ollut merkitystä. Naaraan saama suora etu useasta parittelusta selittyy mitä luultavimmin munasolun irtoamisen stimulaatiolla, joka on voimakkaampaa usean parittelukerran myötä ja joka parantaa munasolun hedelmöitymismahdollisuutta. Kuitenkin tulokset myös osoittivat sen, että metsämyyränaaras sai geneettistä etua siitä, että se paritteli useamman koiraan kanssa. Tämä ilmeni kokeessa, jossa seurattiin niiden poikueiden lisääntymismenestystä pitkäkestoisessa tarhakokeessa, jotka olivat syntyneet parittelusta yhden tai useamman koiraan kanssa. Jälkimmäisten poikueiden lisääntymismenestys oli selkeästi korkeampi. Lisäksi useamman koiraan kanssa parittelun tuloksena syntyneiden poikueiden koon vaihtelu oli vähäisempää, mikä saattaa vaikuttaa yksilöiden säilyvyyteen luonnonoloissa.

Tutkimukseni osoittavat, ettei mikään yksittäinen tähän mennessä esitetty hypoteesi pystyne selittämään polyandrian evoluutiota ja etuja. Metsämyyränaaraat saavat niin suoria kuin epäsuoriakin etuja useista paritteluista samoin kuin paritteluista useiden koiraiden kanssa, mutta nämä edut eivät ilmenny samaan tapaan erilaisissa sosiaalisissa oloissa. Havaitut selkeät edut naaraalle voivat kuitenkin yhdessä selittää polyandrian evoluution ja esiintymisen metsämyyrällä.

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