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Taina Horne

Evolution of Female Choice  
in the Bank Vole



UNIVERSITY OF JYVÄSKYLÄ

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UNIVERSITY OF JYVÄSKYLÄ

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The Difficulttes of Female Choise

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by Paula Horne

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*This work is dedicated with love to my parents  
Ritva and Reijo.  
And to Winnie and Jekku, whom I selected - naturally.*

## ABSTRACT

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Yhteenveto: Naaraanvalinnan evoluutio metsämyyrällä

Diss.

The aim of this thesis was to test some of the theories proposed to explain the evolution of female choice using the bank vole (*Clethrionomys glareolus*) as the study species. First I conducted a lab experiment to test whether female bank voles show mating preferences on the basis of male urine marking behaviour, which also indicates social status. When male-male competition was excluded, females strongly preferred dominant males but showed no clear preferences if the males were matched for urine marking behaviour. To investigate if male attractiveness is related to fertilizing ability I studied a number of variables reflecting sexual competence in relation to male urine marking value (UMV), but found little evidence for possible direct benefits of mate choice in terms of fertility. Genetic models of sexual selection assume some heritability of the sexually selected male traits. I estimated heritabilities for male UMV and three morphological traits correlated with it using parent-offspring regression. All traits had relatively high heritability values (0.53-0.77) and coefficients of additive genetic variance. To test the idea that sexually selected male traits indicate male genetic quality providing females indirect benefits through offspring fitness I studied components of offspring fitness in relation to male UMV. A laboratory breeding experiment revealed a positive relationship between male UMV and offspring body mass. In order to examine the role of differential maternal investment being responsible for this relationship I conducted a cross-fostering experiment. The results suggested that although females may invest more on offspring of attractive males, male UMV appears to indicate male genetic quality. I studied offspring performance also in natural environment and found that male UMV appears to affect some offspring fitness components. However, the study showed how difficult it is to estimate the net benefits of mate choice to the female due to trade-offs between fitness components and environment-by-genotype interactions. The studies described in this thesis support the idea of genetic mechanisms operating in the evolution of female choice. However, there are several other mechanisms, yet to be tested, and much more work is needed to understand the relative importance of each.

Key words: *Clethrionomys glareolus*; direct benefits; female choice; indicator mechanisms; indirect benefits; male quality; offspring fitness; sexual selection.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to by Roman numerals in the text. I have planned and designed all the experiments, performed all of the work in papers I, II, IV and V, and written all the papers. I performed most of the work in paper III.

- I Horne, T. J. & Ylönen, H. 1996. Female bank voles (*Clethrionomys glareolus*) prefer dominant males; but what if there is no choice? *Behav. Ecol. Sociobiol.* 38: 401-405.
- II Horne, T. J. 1998. Attractive males sire heavier offspring; maternal investment or male genetic quality? Manuscript.
- III Horne, T. J., Luukkonen, M. & Ylönen, H. 1998. Paternal effects on offspring fitness in the bank vole (*Clethrionomys glareolus*). Manuscript (submitted).
- IV Horne, T. J. & Ylönen, H. 1998. Heritabilities of dominance-related traits in male bank voles (*Clethrionomys glareolus*). *Evolution* (in press).
- V Horne, T. J. & Ylönen, H. 1998. Is fertilization ability related to male attractiveness in the bank vole (*Clethrionomys glareolus*)? Manuscript (submitted).

# 1 SEXUAL SELECTION

“... Sexual Selection ... depends not on the struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring.” (p. 136, Darwin 1859).

## 1.1 Theory of sexual selection

Darwin (1859) developed the idea of sexual selection to explain conspicuous male traits that could not be explained by natural selection. Although sexual selection may favour traits that reduce survival and are thus counterselected by other natural selection, these two are not distinct processes and cannot be separated from each other in many cases (Darwin 1871, Endler 1986). Sexual selection is usually divided into intrasexual and intersexual selection (Table 1). Intrasexual selection arises when individuals of one sex compete each other for access to mates, and it affects the evolution of traits that improve success in these combats. Intersexual selection, or mate choice, also involves competition, but in this case individuals of one sex compete to be chosen by the other sex. Thus it leads to selection of traits that increase reproductive success because they are attractive to - and favoured by - the opposite sex. Since in many species females invest more on reproduction, they are often the limiting resource for which males compete. Several different mechanisms, both genetic and non-genetic, may be operating through sexual selection (Table 1), affecting both mating preferences and sexually selected traits. Furthermore, besides sexual selection, there are also other possible selective mechanisms that may favour

male traits and female preferences. Few of these explanations are mutually exclusive and thus the relative importance of each is difficult to assess.

In this thesis I studied sexual selection through female choice, and tested some of the hypothesis proposed to explain the evolution of female choice using the bank vole (*Clethrionomys glareolus*) as the study species. Bank voles are relatively monomorphic, except for the slight size difference between the sexes, and males have no elaborate visual ornaments. The mating system in the bank vole can be considered to be non-resource based. Breeding females are territorial and males offer no material resources to the female or offspring. While an intrasexually exclusive territory is a prerequisite for female breeding, male home ranges are much larger and overlap each other as well as home ranges of several females (Mazurkiewicz 1971, Bujalska 1973, Bondrup-Nielsen & Karlsson 1985). Although there is no direct evidence of multiple paternity, bank vole mating system in nature is most likely promiscuous (Sikorski & Wójeik 1990, see Gipps 1985, Viitala & Hoffmeyer 1985). Both the gestation and lactation periods are 19-21 days and females give birth to litters of 1-10 pups. The young may reach sexual maturity during the same breeding season they were born, or remain immature until the next spring. Most animals breed during one breeding season only (Kaikusalo 1972).

TABLE 1 Possible mechanisms in the evolution of male ornaments and female mating preferences. (Modified from Kirkpatrick & Ryan 1991, Andersson 1994).

- 
- 1) Intrasexual selection (male-male competition)
    - a. Scramble competition
    - b. Endurance rivalry
    - c. Contest competition
    - d. Sperm competition
  - 2) Intersexual selection (female choice)
    - a. Direct phenotypic benefits
      - material resources to female or offspring
      - parental care
      - fertilisation ability or fecundity
      - lower risk of predation or harassment
      - avoidance of disease and parasite transmission
    - b. Indirect genetic benefits
      - Fisherian self-reinforcing mechanism
      - Genetic indicator mechanisms
  - 3) Pleiotropic gene effects
  - 4) Selection for ecological sex differences
  - 5) Mutation pressure
-

## 1.2 Female choice

There is a lot of empirical evidence showing that females discriminate among potential mating partners and affect male reproductive success by favouring some males over others (e.g. Andersson 1994). In many cases female mating preferences have been studied in relation to conspicuous male traits such as coloration, weapons, song or elaborate displays. This may be partly because the theory of sexual selection was first developed to explain the evolution of such traits. However, there are several other factors that can also affect female mating preferences, or dissortative mating may result simply from females being able to detect some males more easily than others (Ryan & Keddy-Hector 1992). Other factors that can influence female mating behaviour and preferences include, for example, age and experience (of both females and males), familiarity and relatedness, male mating status and female hormonal status. Thus female choice for a certain male trait may not be absolute in nature, even if strong preferences are found in controlled experiments.

In several rodent species females have been found to prefer dominant males as mating partners (e.g. Huck & Banks 1982a,b, Wolff 1985, Shapiro & Dewsbury 1986, Drickamer 1992). In bank voles olfactory cues are important in both intra- and intersexual social relationships. For example, male urine marking behavior is closely related to social status (Desjardins et al. 1973, Rozenfeld et al. 1987) and females prefer odours of dominant males over odours of subordinate ones (Hoffmeyer 1982). In the first paper I investigated female mating behaviour and preferences in relation to male urine marking behaviour. The results indicated that females do discriminate among males according to their urine marking behaviour, and preferably mate with males that mark the most. In nature oestrous females are pursued by several males (Viitala & Hoffmeyer 1985, J Viitala, personal communication), and while males compete each other for access to females, mature females are dominant over males and can prevent males from mating (Gipps 1985, TJ Horne, unpublished data). Thus, both male-male competition and female choice are likely to affect male mating success. Therefore, even though a strong female preference was found in this and subsequent studies (TJ Horne, unpublished data), male-male competition cannot be ignored. Since the male trait favoured by females is closely related to social status, it also affects male mating success through contest competition among males. Other forms of male-male competition may also be operating. For example, the fact that males with high UMV appear to be able to reach more ejaculations before satiety (V), may be an indication of endurance rivalry (Andersson & Iwasa 1996).

## 2 BENEFITS OF MATE CHOICE

“ I strongly suspect that some well-known laws with respect to the plumage of male and female birds, in comparison with the plumage of the young, can be explained on the view of plumage having been chiefly modified by sexual selection, acting when the birds have come to the breeding age or during the breeding season; the modifications thus produced being inherited at corresponding ages or seasons, either by the males alone, or by the males and females...” (p. 137, Darwin 1859).

### 2.1 Direct phenotypic benefits

In order for female mating preferences to be adaptive a choosy female should gain some benefit from mate choice. Potential benefits can be divided in two categories: (1) direct benefits, affecting female reproductive success by enhancing fecundity or survival and (2) indirect benefits affecting the quality of offspring (see below). Direct mechanisms of mate choice are often more obvious, which may be why they have received less attention in both theoretical and empirical studies. The ways in which females may gain direct benefits from mate choice are numerous (see Table 1) and depend strongly on other aspects of the species biology. Some are quite apparent material resources, such as food, good quality breeding territories or parental care. However, benefits related to fertility and reduced risk of predation, disease transmission or harassment may be less obvious, but not less important. Thus even in mating systems where females appear to gain nothing besides genes from their mating partners direct mechanisms may well be operating in the evolution of mating preferences.

Therefore it is necessary to examine these possibilities also in mating systems that seem to be non-resource-based.

In bank voles breeding females defend intrasexually exclusive territories (Bujalska 1973), and males offer no material resources to their mates or offspring. However, there are a number of ways a female could gain from choosing a male on the basis of urine marking behaviour. I tested one of these, the possibility that urine marking behaviour is also related to sexual competence. In a number of laboratory experiments I examined variables associated with pregnancy initiation and fertilizing capacity (V). The results did not indicate that females mating with males with a high urine marking value (UMV) could benefit in terms of increased fertility assurance or fecundity. There was a positive relationship between UMV and the number of ejaculations the male could reach before satiety. In the male's point of view this may be significant, especially if female oestrus is synchronous. However, the female may mate with more than one male, in which case the number of ejaculations will not be a limiting factor for female fertility (see e.g. Davis et al. 1974, Ågren 1990). Multiple matings may be beneficial (for example in terms of reduced risk of infanticide), and at least in the laboratory females readily mate with several mates in succession (TJ Horne, unpublished data).

The fact that this experiment failed to show a positive relationship between male attractiveness and fertilizing ability, does not mean that bank vole females gain no direct benefits from mate choice. Other possibilities include reduced risk of infanticide and harassment from other males during mating. Since urine marking behavior is related to male dominance, mating with a male with high UMV could decrease the probability of interruptions by other males during mating. Furthermore, in some rodents dominant males are more infanticidal than subordinate ones (Huck et al. 1982, vom Saal & Howard 1982), and copulation and/or postmating physical contact inhibit infanticidal behavior in males (Elwood & Ostermeyer 1984, Palanza & Parmigiani 1991, Perrigo et al. 1991). However, these and other possible mechanisms are yet to be studied in terms of providing direct benefits for discriminating bank vole females.

## 2.2 Indirect genetic benefits

Selection through female choice, especially when females gain no direct benefits from mate choice, has risen major theoretical difficulties (Maynard Smith 1991). Two sets of models attempt to explain the evolution of female choice through genetic mechanisms. Fisher (1958) hypothesised that choice may be directed toward features that are simply sexually attractive to females. If these selected male characters are heritable sons of preferred males are attractive to choosy females and gain better reproductive success. When the choosiest females mate with the most attractive males a genetic covariance develops between the mating preference and the preferred male trait (Fisher 1958, O'Donald 1980, Lande 1981, Kirkpatrick 1982). The genetic indicator - or 'good genes' -

hypothesis, on the other hand, proposes that the male characters preferred by females indicate fitness enhancing genes that are passed on to the offspring (Andersson 1982,1986, Hamilton & Zuk 1982, Heisler 1984, Kodric-Brown & Brown 1984). The male traits favoured by female mate choice reflect males' ability to cope with environmental stresses and thus depend on environmental conditions. These traits are not necessarily heritable as such but exhibit heritability when linked with a particular fitness component (Hamilton & Zuk 1982).

Maynard Smith (1978, 1985) argued that heritable variation of the preferred male traits would decrease as these traits became fixed leaving no genetic advantages for the choosy females compared to those mating at random. The controversy over the question of heritability of sexually selected traits remains although mechanisms for maintaining genetic variation in characters closely related to fitness have been proposed (e.g. Dingle & Hegman 1982, Cade 1984). During the past two decades a number of studies have demonstrated that, contrary to the predictions, heritabilities of several sexually selected traits can be relatively high (review in Pomiankowski & Møller 1995, see however Alatalo et al. 1997).

Both major theories assume some heritability in the male traits. I estimated heritability values ( $h^2$ ) for UMV and three morphological traits using parent-offspring regression analysis (IV). The  $h^2$  values were relatively high (0.531-0.767) for all traits measured and the coefficients of additive genetic variance indicated high levels of additive genetic variance in the variables related to male attractiveness.

The idea that the sexually selected male trait serves as an indication of male quality was tested both in laboratory and field experiments (II, III). A laboratory breeding experiment (II) showed that males with high U MVs sire heavier offspring, and suggested that even though females mated to attractive males appear to invest more on the offspring during lactation period, the positive relationship between male U MV and offspring size is partly genetically determined. In the field experiment (III) I examined components of offspring fitness (growth, survival, reproduction) in relation to the U MV of their father. The experiment consisted of two replicates carried out in large outdoor enclosures. Probably due to environmental conditions the overall performance of offspring differed significantly between the replicates. Under more favourable conditions father U MV was negatively correlated with offspring survival, but there was indirect evidence for a positive relationship between father U MV and the reproductive success of male offspring. In the second replicate where the overall performance was significantly poorer, father U MV was positively correlated with growth and reproductive condition of male offspring. The results show that female choice is reflected in offspring fitness, and that the male trait preferred by females best predicts offspring performance. However, the net benefit of female choice is difficult to estimate due to the trade-offs between life history traits and genotype-by-environment interactions.

These studies give some support for the idea of sexually selected male traits indicating male genetic quality, but in order to be able to estimate the

relative importance of each mechanism involved, more research is needed. For example, the male trait that serves as an indicator of genetic quality (providing discriminating females indirect benefits) may also be selected by natural selection, increase male reproductive success via male-male competition, and provide some direct benefits for the mate. Thus several mechanisms can work simultaneously, and therefore the results must be interpreted as only part of the picture. On the other hand, statistically non-significant results of an experiment do not necessarily mean that the mechanism studied has no significance in the evolutionary sense.



### 3 CONCLUSION

Several mechanisms have been proposed to be operating in the evolution of sexual selection, modifying both male traits and female preferences. The aim of this thesis was to study some of those mechanisms. The results provided evidence for female choice and indicated that genetic mechanisms may be operating in sexual selection in the bank vole. However, many questions remained to be answered, and most of the hypotheses proposed (see Table 1) were not addressed at all. Thus much more research is needed for understanding the relative importance of the different mechanisms.

One of the most interesting aspects of female choice is the variation in the within and between individual variation in mating preferences among females and the consequences of such variation. The different types of intrasexual selection and their role in determining male life time reproductive success are also an interesting, yet little studied, aspect of sexual selection. As for the benefits of mate choice, many remain to be tested empirically. Although the mechanisms and theories of sexual selection are often categorized by different criteria, as in Table 1, they are not mutually exclusive and are not necessarily distinctive processes. Therefore, evidence for or against one hypothesis is hardly enough for understanding how the system works. In experimental studies confounding variables are often excluded in order to test a particular hypothesis. However, the effect of these variables, and others that were not tested, should not be forgotten when interpreting the results. The experiment described in the third paper of this thesis well demonstrated the significance of environmental factors. Had only one of the replicates been carried out, the interpretation of the results would have been rather different.

In this thesis I used a mammal as the study species. In previous studies of sexual selection mammals have been rather poorly represented (see e.g. chapter 6 in Andersson 1994). But should the theories be tested also in mammals for the results to be applicable to them? And should several theories be studied in one organism or one theory in several organisms? No doubt a large variety of organisms provides more possibilities for studying different aspects of sexual selection, but the results can hardly be generalised throughout the taxa. One major challenge, that may lead to better understanding of the relative importance of different mechanisms within and between species is to relate sexual selection to other aspects of species biology, such as endocrinology, life-history, environment, ecology and population fluctuations.

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# YHTEENVETO

## Naaraanvalinnan evoluutio metsämyyrällä

Seksuaalivalinta on osa luonnonvalintaa, jossa valinta suosii ominaisuuksia, jotka parantavat yksilön menestystä kilpailussa parittelukumppaneista. Vaikka luonnonvalinta ja seksuaalivalinta voivat suosia samoja ominaisuuksia, voi niiden vaikutus tietyn ominaisuuden evoluutioon olla myös päinvastainen. Seksuaalivalinnan teoria kehitettiin aluksi selittämään koiraiden ornamentteja, jotka alentavat niiden hengissäsäilymistodennäköisyyttä ja joiden evoluutiota ei näinollen voida luonnonvalinnalla selittää. Seksuaalivalinta jaetaan yleensä intra- (naaraanvalinta) ja interseksuaaliseen (koiras-koiras kilpailu) valintaan. Evoluutio seksuaalivalinnan kautta voi tapahtua useiden eri mekanismien välityksellä muokaten sekä naaraan parinvalintaa että koiraan toissijaisia seksuaaliominaisuuksia. Jotta naaraanvalinta olisi adaptiivista, tulisi naaraalle olla hyötyä valinnasta. Hyödyt voivat olla suorina, vaikuttaen naaraan lisääntymismenestykseen tai sen hengissäsäilyvyyteen, tai epäsuorina geneettisiä hyötyjä, jotka tulevat esiin jälkeläisten parempana kelpoisuutena.

Väitöskirjatyössäni tutkin naaraanvalintaa metsämyyrällä (*Clethrionomys glareolus*) ja testasin joitain seksuaalivalinnan mekanismeista esitettyjä hypoteesejä. Ensimmäisessä osatutkimuksessa tarkastelin naaraanvalintaa suhteessa koiraan jättämien virtsamerkkien määrään ja laatuun, jotka heijastavat myös koiraan sosiaalista asemaa. Tulokset osoittivat metsämyyränaaraiden valitsevan parittelukumppaneikseen koiraita, jotka virtsamerkkien perusteella ovat dominanteja muihin koiraisiin nähden. Koska tämä ja myöhemmät tutkimukset osoittivat koiraan virtsamerkkien heijastavan parhaiten niiden parittelumenestystä naaraanvalinnan kautta, käytin tätä ominaisuutta (urine marking value, UMV) koiraan laadun mittana selvittäessäni seksuaalivalinnan mekanismeja väitöskirjatyöni muissa osatutkimuksissa.

Toisessa ja kolmannessa osatutkimuksessa tarkastelin koiraan laadun vaikutusta jälkeläisten menestymiseen sekä laboratoriossa että luonnonmukaisissa olosuhteissa. Naaraan fenotyypisten ja genotyypisten vaikutusten kontrolloimiseksi jaoin poikueet molemmissa kokeissa imetysaikana eri naaraiden kesken. Laboratoriotutkimuksen tulokset osoittivat sekä koiraan geneettisen laadun että naaraan panostuksen osaltaan vaikuttavan poikasten painoon ja kasvunopeuteen. Tulokset viittaavat siihen, että naaraat voivat hyötyä parinvalinnasta jälkeläisten paremman geneettisen laadun kautta. Kenttäkoe toteutettiin kahtena toistona, joissa olosuhteet myyrille poikkesivat toisistaan. Isän laadun vaikutus jälkeläisten kelpoisuuteen tuli esille epäsuotuisammassa olosuhteissa niin, että isän UMV korreloi positiivisesti koirasjälkeläisten menestyksen kanssa, kun taas suotuisammassa olosuhteissa eroja ei havaittu. Se, että isän UMV:n ja jälkeläisten hengissäsäilyvyyden välillä

oli negatiivinen korrelaatio molemmissa toistoissa viittaa siihen, että korkeasta dominansiasemasta voi olla kustannuksia. Tämä tutkimus osoitti, että naaraanvalinnan geneettisiä hyötyjä, jotka tulevat esille jälkeläisten kelpoisuutena on vaikea mitata johtuen ympäristön ja genotyypin vuorovaikutuksista ja elinkierto-ominaisuuksien välisistä allokaatio-kustannuksista.

Seksuaalivalinnan geneettisiin hyötyihin perustuvat hypoteesit olettavat koiraan ominaisuuksien olevan jossain määrin periytyviä. Neljännessä osatutkimuksessa mittasin UMV:n ja kolmen morfologisen ominaisuuden periytyvyyttä isältä koirasjälkeläisille. Kaikilla mitatuilla ominaisuuksilla oli suhteellisen korkeat heritabiliteettiarvot. Tulokset viittaavat siihen, että kyky saavuttaa korkea sosiaalinen asema on jossain määrin periytyvä ominaisuus. Lisäksi se, että naaraiden parinvalinnassaan suosima ominaisuus periytyy koirasjälkeläisille voi parantaa näiden paritutumismenestystä. Tämä tukee ajatusta geneettisten mekanismien osallisuudesta seksuaalivalinnassa.

Parinvalinnasta naaraalle koituvia mahdollisia suoria hyötyjä on useita. Paritutumissysteemeissä, joissa koiras tarjoaa naaraalle tai jälkeläisille materiaalisia hyötyjä (esim. ravintoa tai hyvän reviirin) voivat erot koiraiden välillä vaikuttaa suoraan naaraan lisääntymismenestykseen ja/tai hengissä-säilymistodennäköisyyteen. Väitöskirjani viidennessä osatutkimuksessa tutkin koiraan hedelmöittämissä vaikuttavia tekijöitä suhteessa naaraiden suosimaan ominaisuuteen (UMV). Vaikka tulokset osoittivat koiraiden välillä olevan suuriakin eroja parittelukäyttäytymisessä, en löytänyt todisteita siitä, että naaraiden suosimilla koirilla olisi parempi hedelmöittämissäkyky. Tämä viittaa siihen, että metsämyyränaaraat eivät saavuta suoria hyötyjä lisääntyneen fertiilitetin muodossa valitessaan parittelukumppaninsa hajujälkien perusteella. On kuitenkin mahdollista, että valinnasta koituu muita suoria hyötyjä naaraalle, mutta näiden osoittaminen vaatii lisätutkimuksia.

Tässä väitöskirjassa kuvaillut tutkimukset tukevat osin geneettisiin mekanismeihin perustuvia hypoteesejä naaraanvalinnan evoluutiosta. Seksuaalivalinnassa toimivat mekanismit ja niistä esitetyt hypoteesit eivät kuitenkaan ole toisiaan poissulkevia, ja yhtä hypoteesiä tukevat tulokset eivät välttämättä edusta kaikkia tutkitun ominaisuuden evoluutioon vaikuttavia tekijöitä. Jotta eri mekanismien suhteellinen merkitys voitaisiin arvioida, tulee useita mekanismeja testata samalla lajilla ja huomioida myös muut lajille ominaiset tekijät, jotka voivat olla seksuaalivalinnan kannalta merkittäviä.

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ORIGINAL PAPERS

I

**Female bank voles (*Clethrionomys glareolus*) prefer dominant males;  
but what if there is no choice?**

by

Taina J. Horne and Hannu Ylönen

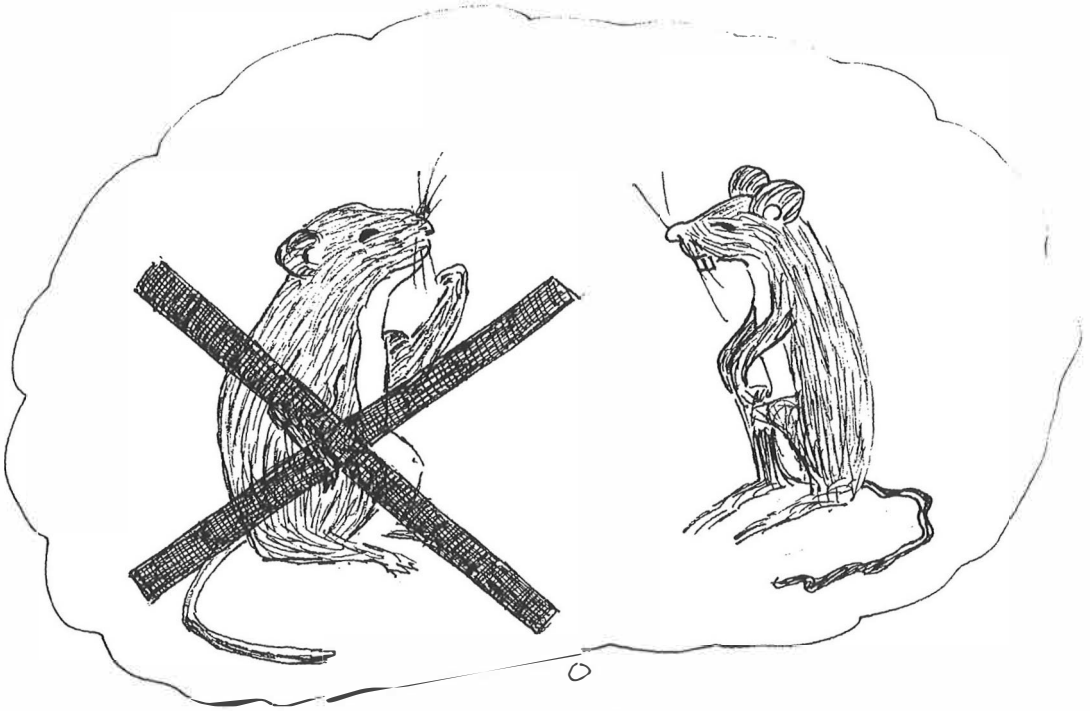
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Behav. Ecol. Sociobiol. 38: 401-405, 1996

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**WHAT IF THERE IS NO CHOICE ?**

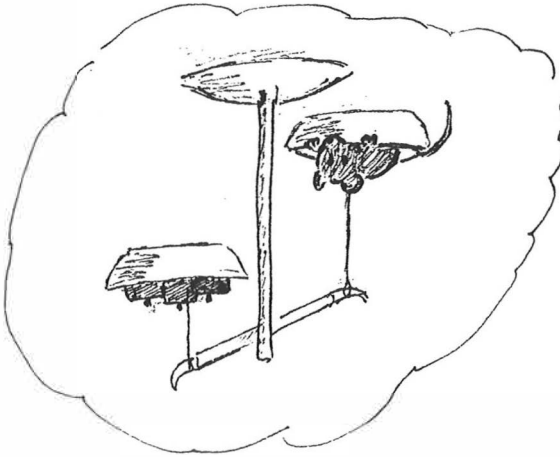
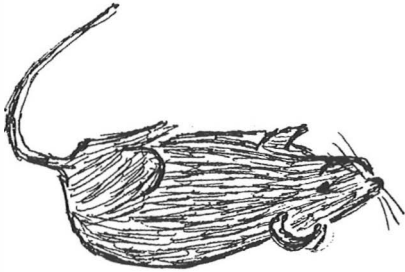
II

**Attractive males sire heavier offspring; maternal  
investment or male genetic quality?**

by

Taina J. Horne

Manuscript, 1998



# ATTRACTIVE MALES SIRE HEAVIER OFFSPRING; MATERNAL INVESTMENT OR MALE GENETIC QUALITY?

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## ABSTRACT

One of the most controversial topics in the theory of sexual selection has been the idea of genetic mechanisms being responsible for the evolution of female mating preferences and sexually selected male traits. The genetic indicator models propose that sexually selected traits express male genetic quality and thus choosy females may gain indirect benefits in terms of offspring fitness. However, besides male genetic quality, offspring performance is determined also by genetic and material maternal effects which may be related to male quality. Previous studies have provided evidence for male genetic quality to predict components of offspring fitness, but the role of differential maternal investment has not been determined. I conducted controlled breeding and cross-fostering experiments in which both the effects of male genetic quality and maternal invest on offspring mass and growth could be examined using the bank vole (*Clethrionomys glareolus*) as the study species. Data from 233 litters (of 114 males) bred in a laboratory showed that offspring body mass from birth to 30 days of age was positively correlated with the sexually selected male trait, urine marking behaviour. The results of the cross-fostering experiment revealed some indications that females mated to 'better' males invest more on the offspring. However, male genetic quality appears to have a significant effect on offspring size and growth. In pups that were raised by foster females, offspring body mass was positively related to urine marking value of the father, whereas the relationship with that of the foster female's mate was negative. The results suggest that choosy females may gain indirect benefits from mate choice and may promote differences in male reproductive success by investing more on the offspring of attractive males.

## INTRODUCTION

Indicator models of sexual selection propose that sexually selected male traits express male quality and thus discriminative females may gain through increased fitness of offspring (Andersson 1982,1986; Hamilton & Zuk 1982;

Heisler 1984; Kodric-Brown & Brown 1984). Although several empirical studies have given support for indicator models, only few have provided evidence for genetic benefits of mate choice (see however Norris 1993; Petrie 1994). If the preferred male trait also indicates the quality or quantity of material resources available to the female or the offspring, mate choice may be based on direct rather than genetic benefits. Such phenotypic benefits may be enough to explain female preferences even when no genetic benefits are involved (Reynolds & Gross 1990; Andersson 1994). However, a correlation between the expression of the preferred male trait and offspring performance is not necessarily evidence for a genetic indicator process even in non-resource based mating systems. For example, if preferred males mate with higher quality females (Møller 1991) and/or maternal investment differs in relation to the male trait, maternal and male genotypic effects on offspring performance may be difficult to distinguish.

This study was designed to investigate the roles of a sexually selected male trait and differential maternal investment on offspring size and growth in the bank vole (*Clethrionomys glareolus*). Bank voles have a non-resource-based mating system; females defend breeding territories (Bujalska 1973) and males offer no material resources for females or offspring. Oestrous females are pursued by several males (Viitala & Hoffmeyer 1985; J Viitala personal communication), and while males compete each other for mating opportunities, mature females are dominant over males and can prevent males from mating (Gipps 1985). In laboratory studies oestrous females have been shown to exercise choice among possible mating partners (Horne & Ylönen, 1996; TJ Horne, unpublished data). Thus, both male-male competition and female choice determine which males are able to mate. In this study I first investigated whether the male trait associated with attractiveness is related to offspring birth mass and growth. In order to examine maternal investment in relation to mate quality, I conducted a cross-fostering experiment and compared mass gain during lactation between siblings raised by different females.

## **MATERIALS AND METHODS**

The animals used in this study were laboratory-born bank voles from a population maintained at the Experimental Animal Unit, University of Jyväskylä. They were housed in standard mouse cages (43 x 26 x 15 cm) with wood shavings as bedding and dry hay for nest building. Food and water were continuously available. The colony was maintained under 18L:6D photoperiod and air in the animal rooms was changed 15 times per hour.

### **Male urine marking behaviour**

Urine marking behaviour is related to male social status (Johnson 1975; Brinck & Hoffmeyer 1984; Rozenfeld et al. 1987), and reflects male attractiveness to females (Hoffmeyer 1982; Horne & Ylönen 1996) and thus represents a male trait that affects male mating success via both male-male competition and

female choice. The apparatus and the method used to estimate male urine marking behavior were similar to those used in our earlier work (Horne & Ylönen 1996,1998). Males were tested as pairs in arenas divided in two by a wire-mesh wall. Each male was given a score (1-6) according to the amount and the pattern of urine marks he left. All males were tested against at least five different, randomly chosen males and the urine marking value (UMV) of each individual was determined as the mean of these tests. The males used as fathers in the study were also weighed in order to test for effects of male body mass on offspring mass.

### **Breeding experiment**

All animals used in the study were sexually experienced and had given birth or sired at least one litter. Females were randomly allocated to males and the male-female pairs were housed together until the female was found to be pregnant. Pregnant females were separated from their mates and checked daily for parturitions. Females were mated in post-partum oestrus (see below), and returned to their nest boxes immediately after mating. All pups were weighed, sexed and individually marked at birth. The pups were weighed also at 10 (total dependency) and 20 (weaning) days of age. A total of 233 litters from 127 females and 114 males were produced. Each male sired 1-3 litters; the mean of all litters of a male was used in analysing the data.

### **Cross-fostering experiment**

To investigate the role of differential maternal investment during lactation on offspring growth I conducted a cross-fostering experiment in 90 litters. Females housed apart from mature males (see above) were mated in post-partum oestrus to randomly selected experimental males of known UMV. The pups were individually marked and weighed within 24 hours after birth. The litters were then cross-fostered so that about half of the pups of two litters born the same day were exchanged between the mothers while maintaining the original litter size of each mother. Thus each female raised a litter consisting of both her own and cross-fostered pups.

Due to the cross-fostering design the UMV of the foster female's mate was higher than that of the father of the pups in approximately half of the cases and lower in the other half. All pups were weighed at birth, 10 days of age and 20 days of age. Foster females readily accept strange pups and, in a series of experiments conducted in our laboratory we have found no evidence that females are able to distinguish between their own and strange pups (Koskela 1998; TJ Horne, unpublished data).

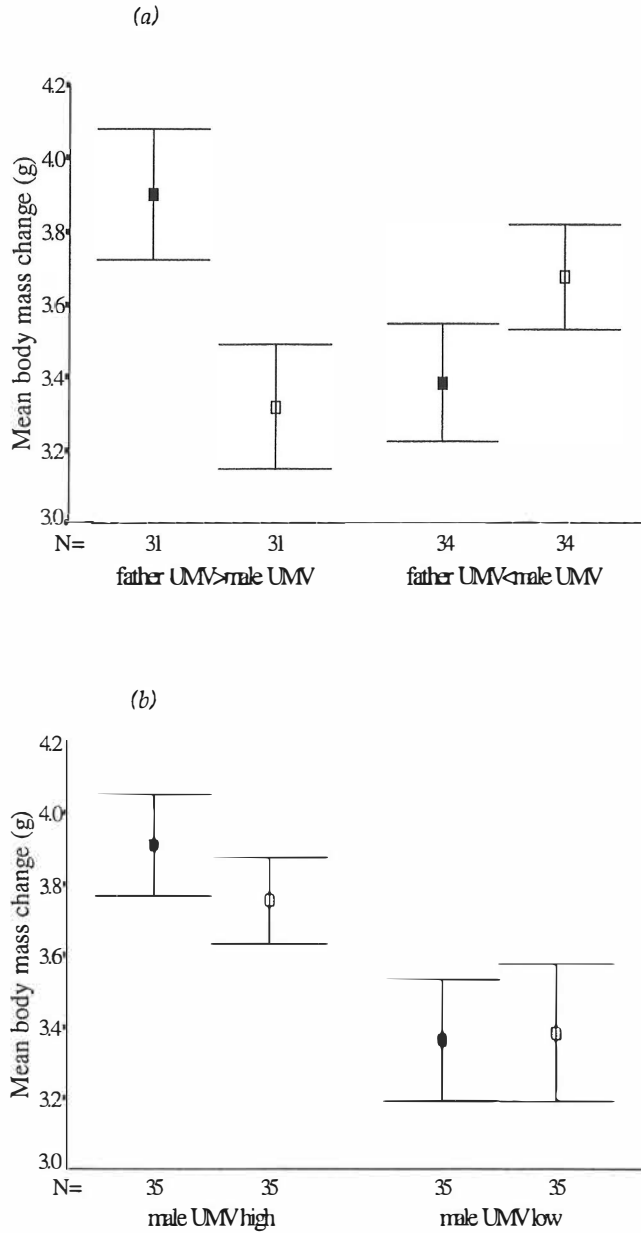


FIGURE 1 Comparisons of offspring body mass change at 10 days of age in the cross-fostering experiment (a) Comparison between sibling groups raised by different females (■ = mother, □ = foster; UMV change negative:  $t = 2.61$ ;  $df = 36$ ;  $p = 0.014$ ; UMV change positive:  $t = -1.36$ ;  $df = 33$ ;  $p = 0.182$ ). (b) Comparison between offspring born to different parents but raised by the same female (■ = father UMV high, □ = father UMV low; for significance see text). 'Male' implies the mate of the foster female.

## RESULTS

### Male UMV and offspring growth

Male UMV was not related to litter size ( $r_s = 0.053$ ;  $n = 114$ ;  $p = 0.575$ ), nor litter sex ratio (percentage of sons:  $r_s = 0.075$ ;  $n = 89$ ;  $p = 0.486$ ). There was a significant negative correlation between litter size and the mean birth mass of pups ( $r_s = -0.1791$ ;  $n = 248$ ;  $p = 0.005$ ). Therefore litter size was entered in a multiple regression analysis together with male UMV to test for the effects on offspring mass. Since male body mass was correlated with UMV ( $r_s = 0.319$ ;  $n = 113$ ;  $p = 0.001$ ) and it is a heritable trait in the bank vole (Horne & Ylönen 1998), it was also included in the analysis. After controlling for the litter size and male body mass, male UMV appeared to have a positive effect on offspring body mass from birth to weaning (Table 1).

TABLE 1 Results from multiple regression analyses with mean offspring body mass at different ages as dependent variables and litter size and the body mass and UMV of the father as the independent variables.

Independent variable	Mean offspring body mass (g)								
	at birth			at 10 days			at 20 days		
	$\beta$	$t$	$p$	$\beta$	$t$	$p$	$\beta$	$t$	$p$
Litter size	-0.06	-3.46	<0.001	-0.30	-4.47	<0.001	-0.62	-3.93	<0.001
Male body mass	0.01	0.58	0.560	0.02	0.43	0.666	0.05	0.55	0.584
Male UMV	0.04	2.47	0.015	0.15	2.21	0.029	0.39	2.51	0.014
	$F_{3,107} = 5.82$ ; $p = 0.001$			$F_{3,91} = 8.16$ ; $p < 0.001$			$F_{3,88} = 7.53$ ; $p < 0.001$		

### Cross-fostering experiment

The positive relationship between male UMV and the mean birth mass of offspring was apparent also among the cross-fostered litters (controlling for litter size:  $\beta = 0.041$ ;  $t = 2.06$ ;  $p = 0.045$ ). To examine the role of maternal investment on offspring growth during lactation, I compared the mean body mass change of the pups that were cross-fostered to that of pups that were raised by the mother. The litters were analysed as two groups; those in which the UMV of the foster female's mate was higher than the UMV of the father (UMV change positive), and those in which it was lower (UMV change negative). The mean birth body mass did not differ between the pups that were cross-fostered and those raised by the mother in either group (UMV change positive:  $t = -0.09$ ;  $df = 40$ ;  $p = 0.925$ ; UMV change negative:  $t = -0.21$ ;  $df = 39$ ;  $p = 0.836$ ). Among the litters where UMV change was negative the cross-fostered



pups gained significantly less mass during the first ten days than their siblings raised by the mother (Fig. 1a). In the other group of litters, where UMV change was positive, the cross-fostered pups tended to grow faster than their litter mates, but the difference was not significant (Fig. 1a). Thus the trend in both groups was faster growth of pups raised by the female that had mated with a male with a higher UMV. However, when the whole lactation period (20 days) was examined, the mean body mass change did not appear to differ between the pups that were cross-fostered and those that were raised by the mother in either group (UMV change positive:  $t = 1.29$ ;  $df = 16$ ;  $p = 0.215$ ; UMV change negative:  $t = 0.35$ ;  $df = 14$ ;  $p = 0.729$ ).

A comparison between pups that were born to different parents but were raised by the same female provides an indication of the competitive ability of the young sired by different males. In the group where the UMV change was positive, (foster females mated on average with 'good males') the pups sired by males of higher UMV tended to grow faster (10 days:  $t = 1.92$ ;  $df = 34$ ;  $p = 0.063$ ; Fig. 1b; 20 days:  $t = 3.47$ ;  $df = 18$ ;  $p = 0.003$ ). In the other group (foster females mated with 'poorer males') there were no difference between the litter mates (10 days:  $t = -0.13$ ;  $df = 34$ ;  $p = 0.900$ ; Fig. 1b; 20 days:  $t = 0.14$ ;  $df = 20$ ;  $p = 0.892$ ).

Even when maternal effect during lactation was randomised (i.e. excluding all pups raised by their mother from the analysis) a positive relationship between the mean body mass of offspring and the UMV of their father was apparent both at 10 days (multiple regression, controlling for foster female's litter size:  $\beta = 0.271$ ;  $t = 2.33$ ;  $p = 0.022$ ;  $F_{2,87} = 7.26$ ;  $p = 0.001$ ) and at 20 days of age (Fig. 2a). The UMV of the foster female's mate was not related to mean pup body mass at 10 days of age ( $\beta = -0.002$ ;  $t = -0.02$ ;  $p = 0.981$ ;  $F_{2,81} = 2.17$ ;  $p = 0.12$ ), and in fact negatively correlated at weaning (Fig. 2b).

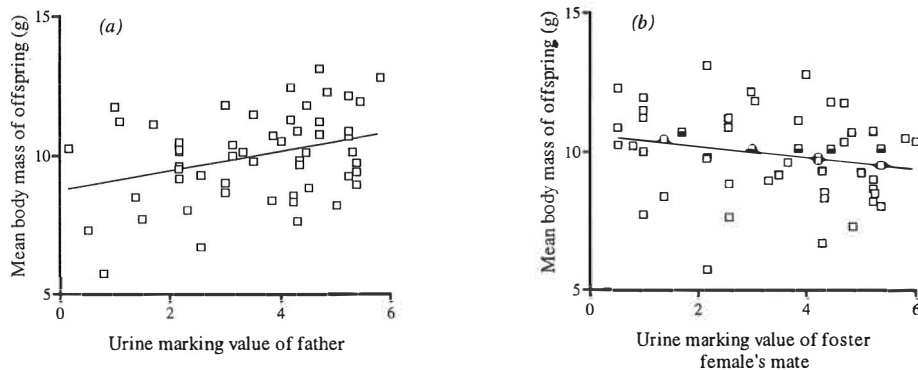


FIGURE 2 The relationships between mean offspring body mass at weaning (20 days of age) and the urine marking value of (a) their father (multiple regression, controlling for foster female's litter size:  $\beta = 0.27$ ;  $t = 2.06$ ;  $p = 0.044$ ;  $F_{2,51} = 6.01$ ;  $p = 0.005$ ) and (b) the mate of the foster female ( $\beta = -0.37$ ;  $t = -2.64$ ;  $p = 0.011$ ;  $F_{2,49} = 4.90$ ;  $p = 0.012$ ). Only pups that were cross-fostered are included in the analysis.

## DISCUSSION

A relationship between a sexually selected male trait and offspring size is not necessarily evidence for a genetic indicator mechanism even when the male offers no material resources or parental care. If the most attractive males mate with high quality females, differences in offspring size can be due to genetic or phenotypic characteristics of the mother. There is evidence for this sort of assortative mating to occur (Møller 1991). Furthermore, maternal investment may depend on male phenotypic quality. In this study males with high urine marking value, a trait reflecting attractiveness, sired offspring that were heavier at birth and remained heavier until independent. Assortative mating was controlled for in the experimental design by allocating females randomly to males. There were some indications of differential maternal investment during the first half of the lactating period, but the mean mass gain from birth to weaning did not support the idea that females mated to 'better' males would allocate more resources to their offspring. Body mass of cross-fostered pups at weaning was positively correlated to the UMV of their biological father and negatively to the UMV of the foster female's mate. These results suggest that male genetic quality does have a significant effect on offspring size and growth, and indicate that differential maternal investment may further promote this tendency.

It must be noted that prenatal maternal investment on offspring size could not be controlled for in this study. However, it is likely that investment during lactation well represents the total investment, and at weaning accounts for a major part of maternal investment (see El Oksh et al. 1967). Besides offspring size, another possible way to increase reproductive success is to increase litter size. However, male quality does not appear to be related to litter size, which suggests that females mated to 'better' males do not, or can not, increase their reproductive effort by producing more young.

But what is the significance of offspring size in terms of fitness? Size at birth is often considered as an important fitness component (Roff 1992). However, there are only few studies on mammals in which the influence of size at birth on future performance has been examined. Lower birth mass of young in large litters has been found to decrease early survival in some rodent species (Myers & Master 1983; Kaufman & Kaufman 1987). In bank voles body mass at birth appears to affect female maturation (Koskela 1998) and reproductive success (M Luukkonen, TJ Horne & H Ylönen, unpublished data). Koskela (1998) also found weaning mass to predict over-winter survival in females. Thus the results of this study suggest that there may be genetic mechanisms through which mating preferences provide benefits to females by increasing offspring fitness.

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III

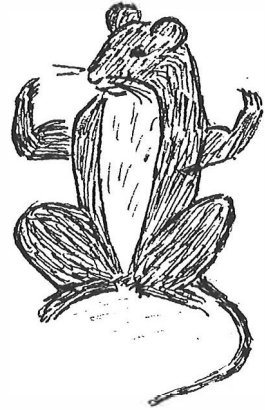
**Paternal effects on offspring fitness in the  
bank vole (*Clethrionomys glareolus*)**

by

Taina J. Horne, Marjaana Luukkonen and Hannu Ylönen

Manuscript (submitted), 1998

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IV

**Heritabilities of dominance-related traits in male  
bank voles (*Clethrionomys glareolus*)**

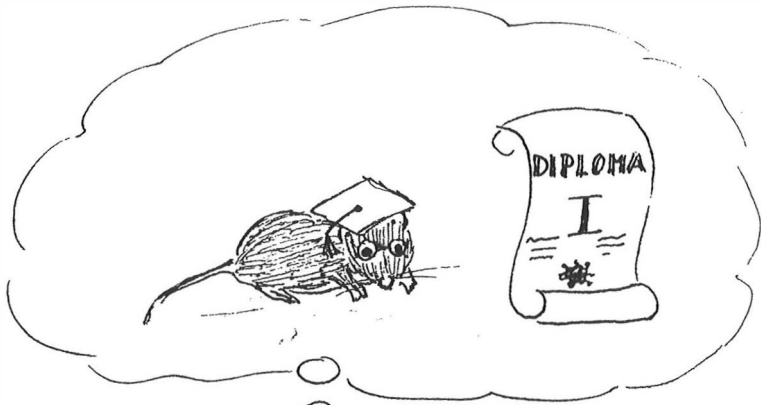
by

Taina J. Horne and Hannu Ylönen

<https://doi.org/10.1111/j.1558-5646.1998.tb03714.x>

Evolution (in press), 1998

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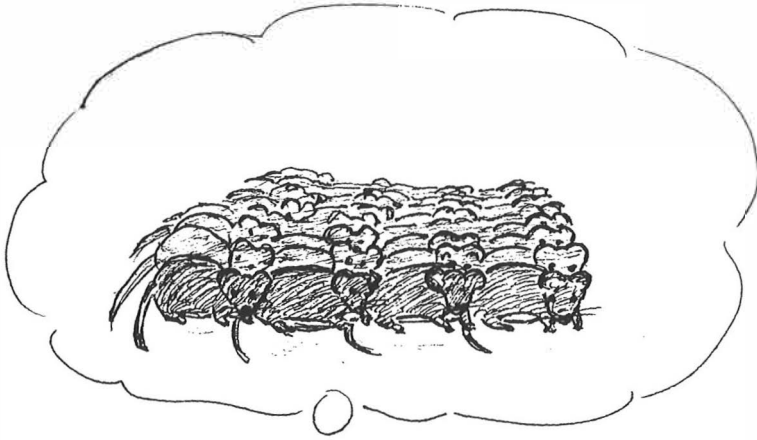
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**Is fertilization ability related to male attractiveness in  
the bank vole (*Clethrionomys glareolus*)?**

by

Taina J. Horne and Hannu Ylönen

Manuscript (submitted), 1998



# IS FERTILIZATION ABILITY RELATED TO MALE ATTRACTIVENESS IN THE BANK VOLE (*CLETHRIONOMYS GLAREOLUS*)?

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## ABSTRACT

Much of the research on the evolution of female mating preferences has concentrated on the role of indirect mechanisms in recent years. However, there are several ways by which a female may benefit also directly from her choice, such as better resources, increased fertility, and/or decreased risk of predation or disease transmission. As the various models proposed to explain the evolution of female preferences make few mutually incompatible predictions, several mechanisms can operate simultaneously. Our previous work has indicated that in bank voles (*Clethrionomys glareolus*) male urine marking predicts both male reproductive success via female choice and offspring performance. The objective of this study was to investigate if this male trait is related to male fertilizing capacity, indicating direct benefits of mate choice. The copulatory behavior of small rodents has been studied extensively and several aspects have been found to affect fertility. In our study there were large differences in the copulatory behavior between males but we found little indication of them being related to male attractiveness. Males with high urine marking value were able to reach more ejaculates before satiety, but did not perform better in respect to other variables related to mating. Our results suggest that discriminating females gain no direct benefits in terms of increased probability of fertility, litter size or litter sex ratio by mating with a male with high urine marking value.

## INTRODUCTION

Most research on sexual selection in recent years has concentrated on theories involving indirect selection of female choice. Especially mating systems where females get little more than genes from their mates have generated controversy over the mechanisms operating in the evolution of female preferences (Kirkpatrick & Ryan 1991). However, despite the great interest, indirect selection is not the most important form of sexual selection, but several

different mechanisms can affect the evolution of mating preferences (Kirkpatrick & Ryan 1991; Maynard Smith 1991).

There are several possible direct benefits that female choice can promote, even in species where males offer no resources (reviewed by Reynolds & Gross 1990; Kirkpatrick & Ryan 1991; Andersson 1994). Males may, for example, differ in their fertilizing ability or fecundity, and discriminating females can thus avoid infertile matings. Mating and copulatory behavior has been studied extensively in small rodents. In most species copulatory patterns are complex, consisting of multiple intromissions and multiple ejaculations (Dewsbury 1975). Several different functions have been suggested for these copulatory patterns, such as a role in pregnancy initiation, fertility assurance and sperm competition (Dewsbury 1981). A sufficient number of pre-ejaculatory intromissions seems to be essential for successful initiation of pregnancy (Toner & Adler 1985; Huck et al. 1986 and references therein). The multiple intromission pattern triggers female neuroendocrine reflexes needed for ovulation and implantation, and facilitates sperm transport in the uterus (e.g. Adler 1969; Chester & Zucker 1970; Gray et al. 1977). Multiple ejaculations also appear to increase the probability of pregnancy and/or affect litter size in some species (Davis et al. 1974; Gray et al. 1977; Dewsbury 1979; Ågren 1990). Despite the numerous studies on copulatory behaviors in small rodents, they have not been studied in relation to sexually selected male traits.

Our previous work has indicated that in bank voles (*Clethrionomys glareolus*) females discriminate among possible mating partners (Horne & Ylönen 1996) and that females may gain genetic benefits from their choice (Horne & Ylönen 1998; TJ Horne, M Luukkonen, H Ylönen, submitted; TJ Horne, submitted). However, even if there exists evidence for one mechanism, it does not exclude the possibility of other mechanisms. The male trait that best predicts both male mating success by female choice and offspring quality is urine marking behavior. The objective of this study was to investigate if this male trait also reflects male sexual competence, providing selective females direct benefits in terms of increased fertility. The copulatory behavior of bank voles is characterized by multiple intromissions and multiple ejaculations (pattern number 13, see Dewsbury 1972), and at least in laboratory both sexes readily mate with several partners in succession. We studied a number of variables that are related to fertilizing ability in relation to male urine marking behavior.

## METHODS

### Experimental animals

All animals used in the experiment were laboratory-born bank voles from a population maintained in the Experimental Animal Unit, University of Jyväskylä. The laboratory population was bred from voles originally trapped in Konnevesi, central Finland. The animals were housed in standard mouse cages

(43 x 26 x 15 cm) with wood shavings as bedding and dry hay for nest building. Food and water were continuously available. The colony was maintained under 18L:6D photoperiod and air in the animal room was changed 15 times per hour. All experimental males were of proven fertility and had been housed individually for at least one week before testing in order to ensure they were sexually rested when tested. The females used in the experiments were sexually experienced and none were primiparous. All behavioral tests were conducted in neutral cages, similar to those used for housing, with a thin layer of wood shavings on the floor.

### **Measures of copulatory behavior and fertility**

Males were tested for differences in their copulatory behavior that might indicate better sexual competence. Thirty-seven males were mated to estrous females and their mating behavior was recorded by a single observer. Each male was tested with 1-3 different females, and a total of 71 tests were performed. In cases where the same male was used for more than once, a period of at least two weeks separated the successive tests. The experimental females were housed individually or in pairs and were brought into behavioral estrus by an injection of 0.1 mg estradiol benzoate 48 hours before testing. Of the standard measures of copulatory behavior used in several studies with different rodent species (see e.g. Austin & Dewsbury 1986) we used those relevant to this study. These included intromission frequency (the number of intromissions before ejaculation), ejaculation latency (latency from the first intromission to ejaculation) and ejaculation frequency (number of ejaculations prior to attainment of the satiety criterion). Sexual satiety was defined as 30 minutes without an intromission or 60 minutes without ejaculation (Austin & Dewsbury 1986). Intromission frequency and ejaculation latency were recorded for 31 different males in 62 tests. Ejaculation frequency was recorded in all 71 tests.

Since mating in hormone induced estrus does not result in impregnation, we used females that were in post-partum estrus for testing fertility. Females were used in tests within 24 hours after parturition. Sixty male-female pairs were allowed to mate until the occurrence of the first ejaculation. Both animals were then immediately returned to their home cages and the female was allowed to raise her new-born litter until the pups were 18 days of age (the gestation period is 19-22 days). Females were checked daily for parturitions and the number, sex and body mass of the pups were recorded the day they were born. These tests were conducted to see if the fertilizing capacity of the first ejaculate differed between males. However, since multiple ejaculations commonly occur, we also tested the fertility of successive ejaculates. Males were mated to 2-5 females in succession. The last female in each test was in post-partum estrus while estrus in the others was induced by hormone injections (see above).

### **Sperm counts**

Sperm counts were conducted for 25 males. Each male was mated to a female in hormone induced estrus and the pair was allowed to copulate until the completion of the first ejaculatory series. Sperm counts followed the method described by Matthews and Adler (1978) with slight modifications. Females were killed by cervical dislocation immediately after the test. The reproductive tract of the female was removed and placed in a saline bath of known volume. The uterus was opened and sperm was removed from the uterine horns by squeezing. To homogenize the solution it was shaken vigorously for 2 minutes. Two samples were taken from the center of the solution using a hypodermic needle. Sperm numbers of these samples were counted in a haemocytometer and the average of the two samples was used as the sperm count of the ejaculate. To get an estimate of sperm numbers in the ejaculate, the mean value of the two samples was multiplied by the ratio of the total saline volume to the volume of the haemocytometer sample.

### **Male urine marking value**

The apparatus and the method used to estimate urine marking behavior were similar to those used in our earlier work (Horne & Ylönen 1998). Males were tested as pairs in arenas divided in two by a wire-mesh wall. Each male was given a score (1-6) according to the amount and pattern of urine marks left. All males were tested against at least five different, randomly chosen, males and the urine marking value (UMV) of each individual was determined as the mean of these tests. Under the housing conditions used in this study the marking behavior of individual males remain relatively constant over long periods of time (Horne & Ylönen 1998).

## **RESULTS**

### **Copulatory behavior**

The mean ( $\pm$  SE) intromission frequency in the first ejaculatory series of the 62 tests was 43.35 ( $\pm$  4.02), ranging from 12 to 172. Male UMV was not significantly correlated with the mean intromission frequency ( $r = -0.215$ ;  $n = 31$ ;  $p = 0.245$ ), nor with ejaculation latency ( $r = 0.05$ ;  $n = 31$ ;  $p = 0.795$ ). Males reached 1-5 ejaculations prior to satiety. Urine marking value was positively related with the number of completed ejaculatory series before the satiety criterion was reached ( $r = 0.377$ ;  $n = 37$ ;  $p = 0.02$ ; Fig. 1).

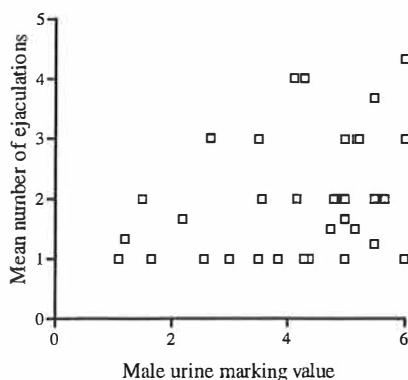


FIGURE 1 The correlation between male urine marking value and the number of ejaculations before satiety. Each male was used in 1-3 tests, the mean number of ejaculations is presented for males tested more than once. Spearman rank correlation  $r = 0.377$ ,  $n = 37$ ,  $p = 0.02$ .

## Fertility

Of the 60 females 37 (62%) became pregnant when mating with a male for his first ejaculatory series. One female died during the experiment and in 22 cases ejaculation did not result in pregnancy. Male urine marking behavior was negatively related to the probability of pregnancy, but the relationship was not significant (logistic regression  $\chi^2 = 1.77$ ;  $df = 1$ ;  $p = 0.183$ ). There was a lot of variability between males in sperm numbers of the first ejaculate (mean  $\pm$  SE ( $\times 10^6$ ):  $12.5 \pm 2.1$ ; range 0.0-33.7). Sperm counts did not reveal a significant relationship between the UMV and the number of spermatozoa in the ejaculate ( $r = 0.229$ ;  $n = 25$ ;  $p = 0.272$ ). Fertilizing capacity did not seem to decrease with successive ejaculations. Three out of 7 ejaculations in the second ejaculatory series, 2/2 in the third, 3/4 in the fourth and 1/3 in the fifth ejaculatory series resulted in female pregnancy. Litter size was not correlated with male UMV ( $r = 0.069$ ;  $n = 37$ ;  $p = 0.700$ ), which indicates that preferred males do not sire larger litters.

## DISCUSSION

We found little evidence to show that the trait preferred by females would express male fertilizing capacity. Male urine marking value was not significantly related to pre-ejaculatory behaviors, sperm numbers or fertility of the first ejaculate. It must be noted, however, that we examined copulatory behaviors in a one male-one female situation. In rats mating in a multiple male-multiple female situation dominant males had twice as many intromissions

before ejaculation than did subordinate ones (McClintock et al. 1982). Since urine marking behavior is related to social status in male bank voles (Bronson & Marsden 1973; Johnson 1975; Brinck & Hoffmeyer 1984; Viitala & Hoffmeyer 1985), male copulatory behavior may depend on the other males present.

The only thing indicating better sexual competence of males with high UMV was the number of completed ejaculatory series before satiety. Ability to complete more than one ejaculatory series may be significant as multiple ejaculations can increase fertility probability, which after one ejaculation was only 62%. For example, fertility after just one ejaculation was 35-70% in Mongolian gerbils (Ågren 1990), 22.2-70% in meadow voles (Gray et al. 1977), 25% in montane voles (Davis et al. 1974), and 42% in deer mice (Dewsbury 1979) whereas two or more ejaculations resulted in 100% fertility in all species, but the deer mouse (92%).

The number of ejaculatory series may also affect litter size; in Mongolian gerbils litter size increased with an increasing number of ejaculations received by the female (Ågren 1990). However, litter size does not appear to depend on the preferred male trait even indirectly. In this study we found no correlation between litter size and male UMV, and data from a more extensive breeding experiment (Horne TJ, submitted), where the pairs were allowed to mate freely, gave similar results.

The fact that the preferred male trait does not seem to indicate better reproductive capacity, does not mean that discriminating females could not gain other direct benefits. Breeding bank vole females defend intrasexually exclusive territories, and in fact such a territory is a prerequisite for breeding (Bujalska 1973). Thus choosy females do not gain in terms of territory quality nor do males offer other material benefits. However, since urine marking behavior is related to male dominance (see above), mating with a male with high UMV could decrease the probability of interruptions by other males during mating. Female choice for males with high UMV might also decrease the risk of infanticide. At least in some rodents dominant males are more infanticidal than subordinate ones (Huck et al. 1982, vom Saal & Howard 1982), and copulation and/or postmating physical contact inhibit infanticidal behavior in males (Elwood & Ostermeyer 1984; Palanza & Parmigiani 1991; Perrigo et al. 1991). However, these and other possible mechanisms are yet to be studied in terms of providing direct benefits for discriminating bank vole females.

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