Is the female biased sex ratio in wood lemming Myopus schisticolor maintained by cyclic inbreeding?

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The hypothesis is developed where the female biased sex ratio in wood lemming Myopus schisticolor (Lillj.), a cyclic microtine, is maintained through evolutionary time by recurrent inbreeding. If the effects, with respect to sex ratio, of inbreeding are stronger than the effects of outbreeding, then the optimal strategy (being favoured by individual selection) would be to produce as many females as possible; the condition is that a sufficient number of males are present to ensure fertilization of all (or most) daughters. This is ensured by producing enough sons and/or by fathers mating with daughters. Some evidence supporting the occurrence of cyclic inbreeding (both sister-brother and daughter-father matings) during large fractions of microtine cycles in general, is outlined. Female biased sex ratio is predicted to be more common among exaggerated cyclic microtines than appreciated at present. One known case that seems to be similar to the situation in the wood lemming is briefly discussed: The arctic lemming Dicrostonyx torquatus (Pall.) in arctic USSR and North America. Studies aimed at producing data for testing the hypothesized occurrence of inbreeding are sorely needed: Microtines should be studied with respect to breeding structure during low and early increase phases. In addition, breeding experiments for analysing the genetic mechanism are needed.

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Развивается гипотеза о том, что у лесного лемминга, Myopus schisticolor (Lillj.), с циклическим развитием популяции численное преобладание самок поддерживается в ходе эволюции повторным инбридингом. Если влияние инбридинга на численное соотношение полов сильнее, чем влияние аутбридинга, оптимальной стратегией (стимулируемой индивидуальным отбором) была продукция максимального числа самок. Необходимым условием является также наличие количества самцов, достаточного чтобы обеспечить оплодотворение всех (или большей части) дочерних особей. Это обеспечивает ся развитием достаточного количества молодых самцов и/или спариванием дочерних особей с отцовскими. Обсуждаются некоторые материалы на поддержку наличия циклического инбридинга (спаривание сестер и братьев, дочерей и отцов) в течение больших отрезков циклов развития популяции микротин вообще. Тенденция к преобладанию самок в популяции кажется более обычной среди микротин с циклическим развитием чем считается. Кратко описан один известный случай по-видимому сходный с ситуацией у леммингов колычного лемминга Dicrostonyx torquatus (Pall.) в арктических районах СССР и Канады. Необходимы исследования с целью продукции данных для определения гипотетического наличия инбридинга: микротины должны быть исследованы с учетом структуры размножения в течение фаз низкой численности и ее повышения. Кроме того, необходимо проведение опытов по размножению для анализа генетического механизма.
1. Introduction

The wood lemming Myopus schisticolor (Lilljeborg), a cyclic microtine (cf. Krebs and Myers 1974), has been reported to have a female biased sex ratio (20 to 30% males) under both laboratory and field conditions (Kalela and Oksala 1966, Frank 1966, Fredga et al. 1976, 1977). Breeding experiments in the laboratory show that a significant proportion of the females produce only daughters. There is some indication that this sex ratio distortion may be ancient (cf. Fredga et al. 1976) and consequently evolutionarily stable. However, from Fisher (1930) an approximately 1:1 sex ratio is, under most circumstances, expected to be the only evolutionarily stable ratio. I contend that the Fisherian argument does not apply to the wood lemming.

Specifically, the purpose of this paper is to present, in qualitative terms, an evolutionary mechanism for the maintenance of this female biased sex ratio (Sect. 3). Only circumstantial evidence for the validity of the hypothesis is presented. (Sect. 4). However, based on the analysis of Maynard Smith and Stenseth (1978) I consider the hypothesis a plausible one for the wood lemming.

Secondly, I present a general hypothesis stating that cyclic microtines may be expected to have female biased sex ratios at birth. However, I do not maintain that the specific genetic mechanism seen in wood lemmings (Sect. 2; leading to extreme sex ratio distortions) is a general one.

Thirdly, I point out some important, but poorly understood aspects of microtine population biology. As done by Krebs and Myers (1974), the following discussion points to the importance of studying cyclic microtines also when they are rare.

2. Genetic mechanism

Fredga et al. (1976, 1977) have recently reported that some females, producing mainly female offspring, had an XY chromosome constitution. Otherwise both XX and XY females seem to be phenotypically indistinguishable. No difference in litter size was found. Kalela and Oksala (1966) report observations from laboratory experiments that can be interpreted as XY females having a mean litter size equal to 3.94 ± 0.18 (based on 89 litters from 18 different females) whereas the other females (i.e. XX which actually may be of two genetically different types, see below) had a mean litter size equal to 4.00 ± 0.16 (based on 111 litters from 26 different females).

Furthermore, Wachtel et al. (1976) have demonstrated that XY females are H-Y antigen negative while XY males are H-Y antigen positive (cf. Silvers and Wachtel 1977). Presuming that the H-Y antigen is the gene product of the Y chromosome, responsible for initiating testicular differentiation and male development (cf. Brøgger and Aagenæs 1964, Crew 1965, Ohno 1976), the observations of Wachtel and his co-workers indicate that the Y-gene(s) either is (are) absent, or not operating in XY females.

Fredga and his co-workers hypothesized that (1) there is an X-linked factor (or gene, called X* whenever necessary in the following) which represses the male determining effect of the Y-chromosome; (2) this X-linked factor is transferred by the XY-females to all of their eggs, presumably by the operation of a meiotic drive (Sandler and Novitski 1957) causing mainly X-carrying eggs to be produced. Thus mainly (or only, if the meiotic drive is 100% effective) female offspring result. Clearly, a population where X* has gone to fixation is dead; there will be no male in such a population. Thus, a polymorphism is expected.

It should be pointed out that Fredga and his co-workers do not show any evidence, other than circumstantial, for the existence of a mutant X gene. Thus, the mutant gene suppressing the male determining genes on the Y chromosome might equally well be on an autosomal chromosome. However, Bengtsson (1977) gives strong reasons to believe that the mutant gene is unlikely to be an autosomal one. Thus, Bengtsson (1977: 339) demonstrates that an autosomal sex reversal gene, A* will always be selected against and will disappear from the population under the condition that the sex reversed animals have lower fertility than other animals. What will happen if such a reduced fertility is not connected with sex reversal remains to be analyzed. The general hypothesis presented below, for the evolutionary maintenance of the female biased sex ratios applies whether the sex reversing gene is autosomal or not.

In a population with X*, X, and Y, three types of matings are possible:

- **XX ♀ × XY ♂ giving 1 ♀ : 1 ♂**
- **X*X ♀ × XY ♂ giving 3 ♀♀ : 1 ♂♂**
- **X*Y ♀ × XY ♂ giving only ♀♀**

Bengtsson (1977) has shown that in a random mating population the frequencies of the four different genotypes X*X, XX, X*Y, and XY all are expected to be close to 0.25. Thus, there will be approximately 25% males in the population. Simulations indicate that this result does not depend on whether or not inbreeding occurs (Maynard Smith and Stenseth 1978); the only condition is that all females are potentially mated. The latter condition is likely to be valid, an inference based on the observed greater home range of males compared with females in many microtine species (e.g. Myllymäki 1975). Furthermore, Skarén (1964) observed 100% pregnancy among wild caught wood lemmings. Thus, Fredga and his co-workers' hypothesis may be concluded to result in an ecologically stable system in a global sense. This is an important property of a genetic system to operate in cyclic fluctuating species like the wood lemming: The frequencies of the different genotypes in a population may be radically changed due to migration.
(the tendency to disperse seems to be unevenly distributed over different genotypes (cf. Krebs et al. 1973)), or due to drift and founder effects (which might be of great importance just after the crash).

However, it should be emphasized that the hypothesis of Fredga and his co-workers treats the genetic mechanism underlying the observations on wood lemmings only. They did not consider the evolutionary stability of the postulated system. If the Fisherian argument applies, modifiers suppressing the X linked gene would be expected to be selected.

The model presented by Bengtsson (1977) demonstrates only the ecological stability of the genetic system suggested by Fredga and his co-workers. To me it seems that Bengtsson's model is insufficient to explain evolutionary stability. The ecological stability of the system is a necessary but insufficient condition for stability in evolutionary time. In order to study the evolutionary stability of a system it is necessary to consider what happens in the case of new genetic material being introduced into a population consisting of X*, X, and Y. Bengtsson (1977) does this for a panmictic population and Maynard Smith and Stenseth (1978) for a population with different degrees of inbreeding. For the system to be stable or "unbeatable" in evolutionary time, it must resist the introduction of mutants tending to normalize the sex ratio: Bengtsson (1977: 341) and Maynard Smith and Stenseth (1978) demonstrate that genes suppressing the X* gene are likely to be established in a panmictic population.

3. A hypothesis for the evolutionary stability of the female biased sex ratio

Tactically, the Fisherian argument for a 1:1 sex ratio assumes that mating is random (panmictic). No other restrictions with respect to the mating system (e.g. monogamy or not) seem necessary (cf. Maynard Smith and Ridpath 1972). The Fisherian argument goes as follows in the case of equal expenditure on both sexes until weaning (cf. MacArthur 1965) (J. Maynard Smith pers. comm.): Let s < 1 be the expected sex ratio in the population. That is, s = 1 is the expected sex ratio at birth (or weaning) for any individual in the population. If s > 1, it will pay (in an evolutionary sense) to produce females, because females have more offspring; i.e. if s > 1, an individual producing daughters will have more grandchildren. Thus, if s > 1 selection will reduce s. By similar arguments, if s < 1, selection will increase it. Only s = s* = 1 is an evolutionarily stable strategy, or an ESS (cf. Maynard Smith 1972, Lawlor and Maynard Smith 1976). Maynard Smith and Stenseth (unpubl.) show that this argument can be made genetically correct for, at least, autosomal genes: Thus, if the production of males and females is genetically determined by autosomal genes, in a random mating population, the ESS will be found to be s* = 1. All genes in the homogametic parent, autosomal genes in the heterogametic parent, and genes determining the sex of the individual, will tend to produce a 1:1 sex ratio at birth. The only genes distorting sex ratio, which would at first be selected, are those on the X and Y chromosome of the heterogametic sex (Maynard Smith 1978, Maynard Smith and Stenseth unpubl.). However, mutants suppressing these latter genes may always be expected as selected in a random mating population.

Hamilton (1967) pointed out that the Fisherian argument fails under inbreeding: In such situations it is individually beneficial to produce as many daughters as possible. Thus, Hamilton’s argument and the one presented in this paper only need to assume the operation of individual selection. In addition, a sparse patchily distributed population may be presumed to have group selective advantages of female biased sex ratio. Hamilton’s argument does not depend on arrhenotoky, i.e. a sex determining mechanism in which fertilized diploid eggs develop as females and unfertilized haploid eggs as males (cf. Maynard Smith and Stenseth 1978, unpubl.): Hamilton’s arguments are likely to apply whenever genes (autosomal or not) in the gametophyte can influence the sex ratio. The condition for optimizing the strategy of producing as many daughters as possible is that enough males are present to ensure fertilization of all (or most) daughters. This is ensured by producing an adequate number of sons, possibly in combination with fathers mating with daughters, or sons with their mothers.

Based on Hamilton's original suggestion I hypothesize that the peculiar sex ratio seen in wood lemmings is maintained through evolutionary time by recurrent inbreeding (i.e. mating between close relatives) during most of the cyclic periods. Inbreeding results from extremely low densities and patchy distribution during the low phases.

Several features of the situation discussed by Fisher and Hamilton differ from the wood lemming case, particularly with respect to the genetic system assumed (Sect. 2): The Fisher–Hamilton arguments were originally put forth for (autosomal) genes determining the sex ratio of the offspring, and not for genes determining sex in the individual carrying it. Hamilton's model assumes that an autosomal gene (m, say) may, if it operates in males, cause (through the operation of a meiotic drive) fewer sperms carrying a Y chromosome than an X chromosome to be produced, but all XY individuals are males. Alternatively, if the gene, m, operates in the females, she may be able to differentiate between "XY-embryos" and "XX-embryos" and cause more of the latter type to be implanted. This would be a form of differential parental care, but without any significant cost (due to the early operation).

However, Maynard Smith and Stenseth (1978) demonstrate that Hamilton's argument is also applicable to a genetic mechanism as hypothesized by Fredga and his co-workers; that is, where a gene exists that both determines the sex ratio at birth and the sex itself.
Ecologically, my hypothesis is also somewhat different from Hamilton’s: I have hypothesized mating to occur between close relatives like brothers and sisters, or daughters and fathers. Hamilton, on the other hand, supposed that the population consisted of groups of n families whose members mated randomly. A female then has a probability of 1/n of mating with her brother. Hamilton obtained \( s^* = (n-1)/2n \). Maynard Smith and Stenseth (unpubl.) demonstrate that this result is generally applicable for brother-sister mating in diploids, i.e. for the situation hypothesized in this paper.

An important point of great theoretical implication concerning the discussion of sex and optimal sex ratios in wild populations is apparent: The problems of breeding structure and grades of relationship between mating individuals. This has most often been neglected by proponents of both group selection and individual selection when discussing optimal sex ratios (cf. Williams 1971, ch. 4, but see Hamilton 1975)). Although the existence of a non-random breeding structure has vaguely been appreciated by field biologists, they have, unfortunately, given the problem too little consideration.

4. Inbreeding in cyclic microtine populations

I have been unable to locate data to test the hypothesized occurrence of inbreeding directly. Studies aimed at producing such data are sorely needed: Microtines should be studied with respect to their breeding structure during low and early increase phases.

In the following I will briefly outline some evidence supporting the occurrence of cyclic inbreeding during the greater part of microtine cycles (i.e. low and increase phases) in general:

(1) After a crash of cyclic microtines, a metapopulation (cf. Levins 1970) is presumed to exist in survival pockets (Lidicker 1973) consisting of only a few individuals which may be closely related.

(2) In increasing populations selective pressures exist for allocating as many resources as possible to increasing the current reproductive output (see Pianka and Parker 1975). Thus there is a tendency for a pregnant female, with a newly weaned litter to migrate to another place prior to giving birth (Stenseth 1978). Empirical evidence suggests that many rodent species display this behaviour (Lidicker 1975). The offspring (possibly only daughters) are likely to continue to reside in the proximity of their birthplace. This is particularly true for the daughters. Lloyd and Christian (1967: 268) working with the house mouse Mus musculus L. observed that “litters tended to remain together in nest sites long after weaning and after subsequent litters had been born”. This tendency was common at low densities. Since pregnancy (of the mother) occurred at all, a reproductively active male is likely to be available when the weanlings mature at an age of approximately one month (Ilmén and Lahti 1968), thus ensuring their fertilization.

(3) New demes may also be formed by the weanlings. An open question is whether or not these new demes tend to be established by close relatives (e.g. brothers and sisters). No relevant data from free-living microtines seem to exist. Preliminary (unpubl.) analysis of a current experiment with freely-growing confined root vole populations Microtus oeconomus (Pall.) indicates that siblings tend to stay where they were born, or else move together to another place in the population cage. Similar observations on the Norwegian lemming Lemmus lemmus (L.) have been made by A. Semb-Johansson (pers. comm.).

If sisters only establish a new deme, then reproduction may not occur. Thus there would be a tendency to produce, in effect, non-reproductive offspring. I contend that this effect is slight. Particularly may this be assumed to result from the greater mobility of males compared to that of females (cf. Myllymäki 1975): By their greater mobility, males are likely to find any females that are within reasonable distances.

(4) The average low density in the habitat dictates that the probability is low for an individual emigrating from one deme into another established deme. The probability would be further reduced since residents repel strangers (Lidicker 1975).

(5) From any of the three mating types in the system hypothesized by Fredga and his co-workers for the wood lemming, males will sooner or later be born. Thus, any group may be quite likely to contain at least one male. Based on information collected and interpreted by Stenseth et al. (1977: Sect. 7), these males may be assumed to be driven away at their age of maturation, unless the old male should die. This, presumably general tendency further assures the fertilization of all females.

(6) In cases of low density, these young dispersing males may be likely to find their mothers who dispersed earlier when pregnant. This further contributes to the degree of inbreeding.

Consequently, during the low phase, inbreeding in the metapopulation may be extensive. In particular, it follows from the above circumstantial evidence that daughters are unlikely to be inseminated by non-related males in most cases. During the peak phase, the likelihood for outbreeding increases. Thus the crux is how will the effects of inbreeding and outbreeding balance? The structure of the metapopulation facilitating inbreeding is, however, likely to exist for 2/3 or more of the whole cyclic period: Microtines are only observed as common every third or fourth year.

It might be argued, that since microtines exhibit density cycles and are extremely abundant every third or
fourth year, these species ought to exhibit little inbreeding compared with other “stable” populations, being fairly rare all the time. This I do not believe is a valid criticism of the hypothesis. Thus, A. Myllymäki (pers. comm.) has data for the field vole *Microtus agrestis* (L.) which indicate a relatively close demic structure (and presumably some inbreeding) even at peak densities. Rasmussen (1964) found extensive inbreeding in fairly dense populations of deer mouse *Peromyscus maniculatus* Wagner. Thus there is, I believe, no reason to expect the degree of inbreeding to be less in cyclic microtines.

5. Conclusion and discussion

My arguments can be summarised as follows:

(1) Fisher’s (1930) argument for the selection of a 1:1 sex ratio has panmixis as a prerequisite.

(2) Hamilton (1967) has shown that inbreeding leads to selection of female biased sex ratios. This biased sex ratio is evolutionarily stable. This is true if the genes determining the sex ratio are autosomal (Hamilton 1967, Maynard Smith and Stenseth unpubl.) or sex linked (Maynard Smith and Stenseth 1978).

(3) Fredga et al. (1976) have hypothesized on the basis of observations that the genetic basis for the female biased sex ratio in wood lemmings is sex linked.

(4) I have, by means of examples, substantiated the hypothesis that inbreeding may be fairly common in cyclic microtines in general and in wood lemmings in particular.

(5) I propose therefore that a contributing factor to the evolutionary stability of the observed female biased sex ratio in wood lemmings is extensive inbreeding, presumably during the low phases of the density cycle.

A few words about *stability* are necessary at this point to avoid confusion. (I am indebted to B. O. Bengtsson for pointing out some of the difficulties to me.) I have used the term “evolutionary stability” in the following meaning: Given a complete description of all strategies (genotypes/phenotypes) constituting the “fitness set” (cf. Levins 1968), the strategy maximizing individual fitness will represent an evolutionarily stable, or unbeatable, strategy; that is an ESS in the terminology of Maynard Smith (1972). Defined thus, an ESS is that strategy which, if adopted by all individuals in the population, is proof against further evolution (for a given long-term consistent environmental pattern) because any mutant would be less fit than the remaining members of the population (e.g. León 1976). However, to describe all possible strategies is an impossible task. Realizing this, one has to restrict oneself to a subset of the possible strategies. In this paper I have had in mind one class of such strategies, i.e. those suppressing the effect of the X*-mutant. Then, what I have suggested is that strong inbreeding will prevent such suppressor genes being established in the population. I have disregarded strategies due to “hitch-hiking” with other advantageous genes. I contend that this is not of major importance because, as I have pointed out in Sect. 3, individual selection will, in the case of inbreeding favour a female biased sex ratio. Thus it might be argued that selective pressure favours a decoupling of the two genes. Much further work is certainly needed at this point.

Inbreeding often results in excessive homozygosity and may therefore result in reduced individual fitness. Inbreeding is therefore likely to be fairly rare in nature, a presumption supported by empirical information (cf. Wilson 1975: 79, Jacquard 1974). Nevertheless, during periods of low density and for certain spatial distributions, inbreeding may be a “statistical necessity”: The only individuals around may be close relatives and a given individual may have the choice between not re-producing at all, or mating with a close relative like one of its parents or a sibling. This I believe is just the situation in many cyclic microtine species and in the wood lemming in particular. In such a system, deleterious genes are likely to have been strongly selected against.

But if inbreeding overrides outbreeding with respect to sex ratio, then why are female biased sex ratios not observed in more cyclic microtine populations? First, as stated above, I contend that the lower the density during a cyclic low, the greater the likelihood will be of extensive inbreeding, causing a sex ratio distortion. Thus, it should be noted that the wood lemming exhibits density cycles which are even more exaggerated than those of the legendary Norwegian lemming (Kalela and Oksala 1966). However, as is apparent from the discussion in Sect. 4, whether or not this happens depends on the particular behaviour and population dynamics of the species being considered.

Secondly, sex ratio distortions among small rodents are not extensively sought after. Nevertheless, a few cases resembling the female dominance in the wood lemming apparently exist among other microtines: Fredga et al. (1976) cites Gileva and Lobanova’s (1974) observations on the arctic lemming *Dicrostonyx torquatus* (Pallas) in the arctic tundra of USSR. Similar observations are reported for the arctic lemming in Alaska (Rausch and Rausch 1972). Another possibly similar situation may be found in the root vole in Alaska (R. L. Rausch, cited from Whitney 1973: 221). This female biased sex ratio may, however, not be evolutionary stable (cf. Maynard Smith and Stenseth 1978). I predict that female biased sex ratios (possibly with different genetic basis) are likely to be observed in other microtine populations exhibiting exaggerated styles. Field and laboratory studies testing this prediction are badly needed.

Two general problems ought to be investigated in connection with the hypothesis discussed in this paper.
Genetic analysis of the offspring from different types of matings in order to investigate the genetic mechanism (Sect. 2), and

(2) The mating structure of the population in order to investigate the occurrence of inbreeding; i.e. studies of the social organization, breeding biology and movement patterns, particularly during the low phases of microtine cycles.

The latter issue might be investigated by the occurrence of different genotypes (cf. Rasmussen 1964) within a geographical area: If, for instance, a shortage of heterozygous individuals is observed, and this shortage cannot be accounted for by differential survival, inbreeding is likely to occur. Particularly, if the genetic variability within groups is significantly smaller than the genetic variability between groups, inbreeding is likely to occur in a metapopulation. The application of blood protein as markers seems to be the obvious device.

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