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Cytogenetics and sex determination in collared lemmings

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CYTOGENETICS AND SEX DETERMINATION IN COLLARED LEMMINGS

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CYTOGENETICS AND SEX DETERMINATION IN COLLARED LEMMINGS

A

THESIS

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ABSTRACT

Collared lemmings (*Dicrostonyx groenlandicus rubricatus*) from northeastern Alaska were found to have sex chromosomes that differ from those of their Siberian congeners, because of fusion to a particular pair of autosomes. As in Siberian lemmings, sex determination involves an X-linked "male-repressor," which causes carriers to develop as fertile females, despite the presence of a Y chromosome. Genotypic frequencies in offspring are consistent with Mendelian expectations of such a system, hence natal sex ratios normally favor females. X-linkage in Siberia and in Alaska indicates that the male-repressor is probably located on the "original" arms of the X chromosome rather than on the fused autosomal arms, which differ on the two continents.

One consequence of the autosomal fusion to the sex chromosomes is that deleterious recessive alleles on the autosome fused to the X chromosome are more resistant to selection than at truly autosomal loci. Another consequence is that, because males are heterozygous for loci fused to the sex chromosomes, they are more resistant to inbreeding depression than XX females. One inbred line produced a natal sex ratio of 67% males. The male-bias probably resulted from loss of the male-repressor and from

a lethal carried on the formerly autosomal arm of the X chromosome. As inbreeding coefficients approached 0.3, the lethal would have been homozygous in half of the homogametic (female) zygotes. This phenomenon may explain the excess of males and XY females observed in earlier work. Also, if under the natural mating system, inbreeding depression limits fitness, then fusions of autosomal chromatin to the heterochromosomes could be an adaptation to reduce inbreeding depression in heterogametic individuals.

Some other genetic features of collared lemmings do suggest endogamy. Female-biased sex ratios can evolve when mating occurs between neighboring individuals who are more related than if mating occurred randomly. Proposed sources of such "viscous" gene flow in lemmings include cyclical changes in population density and mosaic habitat. Alternatively, cold climate may favor winter aggregation and inhibit the dispersal of winter-born offspring, which would mature and mate with close relatives. Thus, inbreeding would be seasonal rather than density-dependent and it is unnecessary to suppose discontinuous habitat.

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PREFACE

As a teenager, the utter uniqueness of collared lemmings struck me while at the American Museum of Natural History. Familiar with the seasonal molts of mice in temperate climates, I was awed to examine these strange, white, winter study skins. Surely, for their size, no other mammal has longer fur nor shorter legs. At that moment, the Arctic tundra seemed as remote and forbidding as the lunar surface.

I was not disappointed when I finally met collared lemmings on the tundra. By that time, Gerald Shields had ably introduced me to the lore of chromosomes, which, as the substance of heredity, offer crisp character states with which to plumb evolution's mechanisms and history. In Sweden's historic Institute of Genetics at Lund, Karl Fredga persuaded me that lemmings, chromosomes, and sex deserve equal attention.

The continued guidance and support of these two men have been crucial, as has the help of the rest of my committee. John Fox has helped me to fathom the intricacies of population genetics, particularly as it applies to sex ratio theory. Francis H. Fay has been a careful editor providing useful insights from his extensive experience with Alaska's mammals. Of equal importance, has been his

balanced and encouraging perspective during some of the darker moments of the past few years. Edward C. Murphy has provided useful reviews and discussions of various drafts of this work. R. Dale Guthrie inspired an early interest in collared lemmings and has continued to provide useful discussion.

Tom Albert, of the North Slope Borough (NSB), strongly encouraged me to pursue doctoral work; he backed up profuse personal encouragement with a generous fellowship from the NSB, through the Arctic Institute of North America (AINA). AINA also provided two grants-in-aid. Further support has included a grant-in-aid from the University of Alaska Foundation, a Resource Fellowship from the Vice Chancellor for Research and Advanced Study, and a research assistantship from the Dean of the College of Natural Sciences.

Robert Dieterich, the Jim and Tina Helmericks family, and Brendan Kelly, have provided lemmings. Brendan also assisted me with data analysis. Susan DeLisa has helped with animal care and field work. Matthew E. Jones wrote the fortran program for coefficients of inbreeding. Daniel D. Gibson and Brina Kessel have provided useful discussions and editorial assistance.

Chapter I

INTRODUCTION

Collared lemmings (genus *Dicrostonyx* Gloger), known also as varying lemmings, or, in Russian, as hoofed lemmings, superficially resemble other lemmings: short-tailed, short-legged, short-eared northern mice with continuously-growing, high-crowned prismatic molars. But collared lemmings are evolving rapidly, specializing toward new extremes of "lemmingness." All arvicoline rodents are characterized by elaborate prismatic folding of the enamel; but even among the arvicolines, the only species that come close to matching the elaborate level of molar development in collared lemmings are the fossil predecessors of collared lemmings (Guthrie & Matthews, 1971).

Ferguson & Folk (1970) showed that collared lemmings can survive at -40° about three times as long as North American brown lemmings (*Lemmus trimucronatus* [Richardson]) and this is further evidenced by the geographic range of collared lemmings, one limit of which is the northern extent of land (Fig. 7). In Greenland and much of the Canadian Archipelago, they are the only overwintering small homeotherm. Thus, even among lemmings, collared lemmings are the ultimate Arctic specialists.

In that other hallmark of "lemmingness," the potential

to increase rapidly in numbers, collared lemmings have even streamlined their investment in the less limiting of the two sexes. Collared lemmings and their Eurasian cousin, the wood lemming (*Myopus schisticolor* Lilljeborg), are the only known mammals in which genetic sex determination clearly favors females (Fredga, 1983).

Such skewed sex ratios are unusual because sex is the classic example of a balanced polymorphism; by favoring the scarcer sex, natural selection usually promotes equal parental investment in offspring of each sex, irrespective of mating system. Suppose, for example, that the majority of offspring in a population are females. Because, on average, males in this population will mate with more than one female, a parent who produces mostly sons will average more grandchildren than a parent who produces mostly daughters. Therefore, genes favoring the production of sons will spread in the population. The converse is true for a population in which there is an excess of males; genes tending to restore a 1:1 sex ratio will spread. This reason for a balanced sex ratio was understood by Darwin (1871), formalized by Fisher (1930), and widely celebrated by modern theoreticians of biology (e.g., Maynard-Smith, 1978; Charnov, 1982). Hamilton (1967) though, proposed

that parental investment in daughters may be favored when competition for mates occurs among closely related males. Or, if inbreeding is interspersed with episodes of dispersal, groups (or "neighborhoods," Nunney, 1985a) with more females will increase more rapidly and thus will contribute more to the global pool of dispersers. Assuming that sex ratio distortion in collared and wood lemmings is caused by Hamilton's (1967) "viscous gene flow," the ecological factors that would cause such a population structure are unknown. In Chapter IV, I review this problem and suggest that the combined factors of winter aggregation and winter breeding may distinguish these lemmings from ecologically similar rodents with normal sex determination.

Natural populations of adult arvicoline rodents often have more females than males, due to greater male dispersal and mortality; thus, early observations (e.g., Manning, 1954) suggestive of unusual primary sex ratios in lemmings apparently excited little interest. Kalela & Oksala (1966) made definitive field observations and captive breeding experiments, showing an unequivocal surplus of daughters at birth in wood lemmings. At the same time, they showed normal sex ratios in the closely related Norway lemming (*Lemmus lemmus* [Linneaus]).

Following up Kalela & Oksala's (1966) findings, Fredga, Gropp, Winking & Frank (1976) revealed the presence of female wood lemmings with XY chromosomes and proposed an aberrant mode of sex determination (Fredga, Gropp, Winking & Frank, 1977). In normal mammalian sex determination, females have two X chromosomes and therefore all ova carry the X. Males are heterogametic, producing equal quantities of X and Y sperm. The Y chromosome is thought to be male-determining, thus XY zygotes would normally become males. But, in wood lemmings, a mutant X chromosome, conventionally designated "X*," apparently suppresses the male-determining aspect of the Y chromosome; X*Y zygotes develop into females having normal fertility. X*Y female wood lemmings avoid the problem of inviable YY zygotes by producing only X* ova; their Y chromosome usually segregates to the polar body (Gropp, Fredga, Winking & Frank, 1978). Hence their offspring are all daughters: either X*Y females or X*X° females ("X°" denotes a normal X chromosome). X*X° females produce a Mendelian ratio of three daughters to one son (25% X*X° daughters, 25% X*Y daughters, 25% normal X°X° daughters, and 25% X°Y sons). This scheme is diagrammed in Fig. 1.

Gileva and her coworkers (Gileva & Chebotar, 1979;

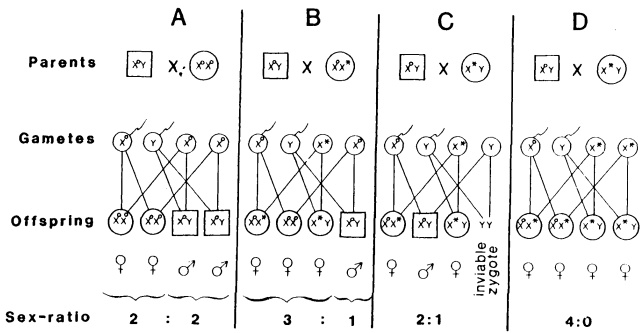

Figure 1. Sex determination schemes (Gileva & Chebotar, 1979) of collared lemmings (Gileva & Chebotar, 1979) and wood lemmings (Fredga *et al.*, 1977). *A* shows the normal mammalian sex-determining mechanism proposed for X^0X^0 females of collared and wood lemmings. *B* shows the mechanism of a 0.25 sex ratio from X^0X^* females of collared and wood lemmings. *C* shows the mechanism of a 0.33 sex ratio from X^*Y collared lemmings. *D* shows the mechanism, invoking meiotic drive, for a 0 sex ratio (all daughters) from X^*Y female wood lemmings.

Gileva, Benenson, Konopistseva, Puchkov & Makaranets, 1982), working with karyotypes more complex than those of wood lemmings, proposed an analogous (and perhaps homologous) system of sex determination for collared lemmings in Siberia. While wood lemmings prevent the formation of YY zygotes by meiotic drive for the X* chromosome, Gileva's data (Gileva *et al.*, 1982) show that X*Y female collared lemmings do produce Y ova, but compensate for the loss of inviable YY zygotes by increased ovulation. Thus, instead of X*Y females producing all daughters, as in wood lemmings, X*Y female collared lemmings should produce two thirds daughters (Fig. 1C). In collared lemmings, X-linkage of the male-suppressor is inferred from Gileva & Chebotar's (1979) breeding experiments.

Another difference between collared lemmings and wood lemmings is that, in wood lemmings, there is a visible difference, detectable with G-banding, between the X* and X° chromosomes (Herbst, Fredga, Frank, Winking & Gropp, 1978). Since they cannot be differentiated visually in collared lemmings, the symbol X, without superscript, is used either as an inclusive term for both the X* and the X° of collared lemmings, or when the genotype of the X chromosome is unknown.

Bengtsson (1977) showed that the theoretical equilibrium sex ratio for wood lemmings is 0.25 males. (Sex "ratio" is conventionally defined as the proportion of males.) For collared lemmings, the expected figure is 0.42 (Bull & Bulmer, 1981).

Bull & Bulmer (1981) reviewed data from both collared and wood lemmings and concluded that sex ratios agreed with expected values in some captive colonies, but in others there were significant surpluses of X*Y females and sex ratios were significantly lower than expected. This has recently been affirmed for collared lemmings by Gileva (1987) in a reevaluation of her earlier data (Gileva & Chebotar, 1979).

Over the holarctic range of collared lemmings, and perhaps complementary to their rapid rate of morphological change, there is a striking diversity of karyotypes (See Fig. 7). The magnitude of chromosomal variation is similar to that in some fossorial rodents and contrasts with low chromosomal diversity in the "true" (Norway and brown) lemmings of the genus *Lemmus* (Gileva, 1983). As in many rodents, the most pervasive chromosomal changes among collared lemmings are of the centric fusion/fission, or "Robertsonian" (Rb) type. In this kind of mutation, two

telocentric chromosomes may fuse at their centromeres to form a single biarmed or mediocentric chromosome. Conversely, a biarmed chromosome may split at the centromere to form two telocentric chromosomes. Thus, these fusion and fission events change the diploid number, but the number of chromosome arms is the same. The number of chromosome arms is therefore the fundamental number, or "NF," after Matthey's (1945) *nombre fundamentale.*

Involvement of the sex chromosomes of collared lemmings in Robertsonian fusions complicates chromosomal nomenclature. I have used the standard mammalian XX/XY terms, following Gileva (1987). Earlier, Gileva and her co-workers (Gileva, 1980; Gileva & Chebotar, 1979; Gileva *et al.*, 1982) described collared lemmings as having XX/XO sex determination because no Y chromosome is consistently apparent. *Dicrostonyx torquatus chionopaes* (as described by Gileva and her coworkers), and the animals discussed herein, have their X chromosomes fused to different telocentric autosomes. The apparently unfused autosomal homologues are present as independent telocentric chromosomes in individuals with heterochromosomes. These unfused "autosomes" might be fused to a vestigial Y chromosome (Fredga, 1983 and this study), thus making it a "neo-Y," in the sense of White (1973). Thus, use of the

standard mammalian XX/XY nomenclature for lemmings with X/autosome fusions implies a Y/autosome fusion. Given these uncertainties and the diversity of poorly understood sex chromosomes in several other arvicoline rodents (Fredga, 1983), use of the XX/XY nomenclature is provisional. Regardless of its other merits, this simplification facilitates comparative discussion of collared lemmings and wood lemmings. In the latter species, a normal Y chromosome is clearly present.

I became interested in the collared lemmings of northern Alaska because Rausch & Rausch (1972) found unusual sex chromosomes, suggestive of XY females, and female-biased sex ratios in collared lemmings from Umnak Island, Alaska. The mechanisms proposed by Gileva & Chebotar (1979) appeared to apply to collared lemmings in Alaska, but the sex chromosomes in Alaska appeared distinct from those of Gileva & Chebotar's Siberian lemmings (Rausch & Rausch, 1972 and my own preliminary observations).

Most discordantly, I had observed that a captive colony of collared lemmings maintained for veterinary research at the Institute of Arctic Biology (IAB) was producing a significant surplus of males. This phenomenon was obviously important but, at least initially,

inexplicable. Could unidentified modifiers of the proposed female-biased system of sex determination exist in response to frequency-dependent selection for a balanced sex ratio?

In taking on this project, I hoped to determine if the morphologically distinct sex chromosomes of collared lemmings in Alaska resulted in sex determination similar to that proposed for the races in Siberia. Because it seemed probable, based upon Rausch & Rausch's (1972) early work, that XY females would be found in northern Alaska, a clean test of Gileva & Chebotar's (1979) hypothesis would be to find such females and demonstrate X-linkage of the male-repressor by karyotyping and breeding experiments. The genotypic ratios predicted by the male-repressor hypothesis are consistent with either an X-linked or an autosomal dominant gene. If the male repressor was an autosomal dominant, then only half of the XX daughters of XY females should be capable of producing XY daughters. But if the male-repressor is X-linked, then all XX daughters of XY females should be $X^{*}X^{o}$, and all should be able to produce XY daughters.

The chromosomal variation reported for North American collared lemmings by Rausch & Rausch (1972) and Rausch (1977) was described on the basis of unbanded chromosomes, with little more than diploid numbers published. Depending

on the availability of specimens, I hoped to contribute further description of these geographic complexities.

The most challenging aspect of this project was the male-biased colony at the IAB. I realize now that I was naive to assume such a problem could be tractable and yet not a trivial anomaly, but luck may have compensated for naivete. I offer a credible explanation of the phenomenon: autosomes attached to the X and Y chromosomes cause males, on average, to be more heterozygous than XX females. Hence, females are more sensitive to inbreeding depression because they are more likely be homozygous for deleterious recessive and lethal alleles. This explanation denies that the male-bias is an evolved response to balancing selection for an even sex ratio. Hence, it is not the "theoretically significant solution" I once envisioned. For a time it seemed a dreaded "trivial anomaly," but Gileva's (1987) recent reanalysis of Gileva & Chebotar's (1979) breeding records clarifies inconsistencies noted by Bull & Bulmer (1981) in the original analysis; heterozygotes (males, $X^{*}Y$ females, and $X^{*}X^{o}$ females) are overrepresented. Gileva (1987) attributes this to "meiotic drive," but the effect that I have described is a more specific alternative. Given autosomal fusions to the sex chromosomes, sex ratio

distortion may be a frequent consequence of inbreeding depression because of the relative difficulty of eliminating lethals from the autosomal part of the X chromosome.

The inbreeding depression, which I believe directly raised the proportion of males in the IAB colony, should not be confused with the long-term, selective pressure from small effective population size. That is, it is distinct from Hamilton's (1967) "viscous gene flow," which favors the evolution of female-biased sex determination.

The following three chapters represent manuscripts prepared for publication. They have been somewhat modified for this thesis. Chapter IV was published (Jarrell, 1987) in the *Biological Journal of the Linnean Society*. Chapter III is under review and Chapter II has not yet been submitted.

Chapter II

THE CYTOGENETICS OF COLLARED LEMMINGS (*Dicrostonyx groenlandicus rubricatus*) FROM NORTHEASTERN ALASKA

In lemmings from Umnak Island, Alaska, Rausch & Rausch (1972) observed irregular sex chromosomes and female-biased primary sex ratios. But in Siberian lemmings (Gileva & Chebotar, 1979), the sex chromosomes were clearly different from those of Alaskan lemmings described by the Rauschs. The objectives of this portion of the study were to determine whether collared lemmings from Alaska share the same sex-determining system as their Siberian congeners and to describe further the chromosomal diversity of collared lemmings. Breeding experiments were used to test the prediction that an X-linked male-suppressing gene overrides the normal mammalian sex determining system as proposed for Siberian collared lemmings by Gileva & Chebotar (1979).

MATERIALS & METHODS

A breeding colony of captive lemmings was established using eleven of the fourteen wild-caught collared lemmings listed in Table 1, plus three lemmings from a colony that had already been established at the IAB, University of Alaska. This earlier IAB colony originated from lemmings captured at Prudhoe Bay, Alaska. Its unusual history is

Table 1. Karyotypes of wild-caught collared lemmings.

LOCATION	SPEC.NO	2N=	SEX	SEX CHROM.	Rb DISTINCTIONS
Kaktovik	GHJ795	30	M	XY	
Kaktovik	GHJ794	30	F	XX	
Kaktovik	#2	31	F	$X^{a}X^{a}$	heteroz 17.11
Kaktovik	#4	31	M	XY	heteroz 17.11
Kaktovik	#7	30	M	XY	
Kaktovik	#8	31	M	XY	heteroz 17.11
Prudhoe	GHJ875	30	F	XX	
Prudhoe	#3	30	F	XX	
Colville	#57	31	M	XY	heteroz 17.11
Colville	#59	30	F	XY	
Colville	#60	31	F	XX	heteroz 17.11
Colville	#61	31	M	XY	heteroz 17.11
Colville	#62	32	F	XY	homoz 17, 11
Toolik	"T1"	37	M	XY	heteroz 17.11, 12.10, 18.9

described in Chapter III. Voucher specimens of the three wild-caught lemmings that were not bred (identified in Table 1 by my field numbers) are deposited in the University of Alaska Museum (UAM catalog numbers 13696, 13697, and 15757). "Prudhoe #3" (Table 1) was born to GHJ875 just after capture. Thus, for sampling purposes, "Prudhoe #3" represents only half of an independent sample, since her maternal genome is already represented by GHJ875.

Captive animals were raised by routine procedures (Dieterich, 1975; Hasler & Banks, 1975). Most chromosome preparations were made from bone marrow, often using the yeast stimulation method of Lee & Elder (1980). When key animals died unexpectedly, lung fibroblasts were grown in tissue culture. Later, marrow was used in short-term culture (Fredga, 1987) for animals that had been dead for as long as 48 hours. Trypsin G-bands were made by the method of Wang & Fedoroff (1972), C-bands by the method of Sumner (1972), and silver staining by the method of Bloom & Goodpasture (1976). Once the parental karyotypes were known, most preparations were homogeneously stained with Wright's stain.

In order to facilitate comparison with karyotypes of collared lemmings in the literature, measurements were made of the chromosome arms of ten G-banded karyotypes in which

the identity of each arm was unambiguous. The two pairs of small metacentrics (chromosomes M1 and M2, Fig. 2) were not measured because they are a distinctive and consistent feature of all published collared lemming karyotypes. The four smallest chromosomes and the short arms on chromosomes 2 and 19 (Fig. 2) were not measured, both because they appear to be labile features and because they are too small to be identified consistently from either measurements or banding patterns. Measurements from 3000X micrographs were taken to the nearest 0.5 millimeter and transformed to relative lengths of each haploid set (exclusive of chromosomes M1, M2, the four microchromosomes, and the small arms of 1 and 19, Fig. 2).

A Barr body, also called sex chromatin, is the condensed and inactivated X chromosome visible in the interphase nuclei of some mammalian cells (Barr & Bertram, 1949). XY females do not have Barr bodies (Rausch & Rausch, 1972). In order to test X-linkage of the male-repressor, it was necessary to distinguish between XX females and XY females without killing the individual for a karyotype. Hair-sheath cells of vibrissae or of hairs from the tail were examined for the presence or absence of a Barr body by the method of Schmid (1967). Barr bodies in

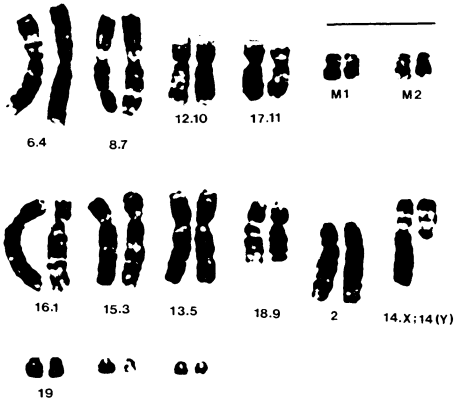

Figure 2. A G-banded karyotype of a typical 2n=30 male collared lemming from Prudhoe Bay, Alaska. The numbering system (described in the text) indicates the twenty largest chromosome arms. The biarmed chromosome 6.4, for example, consists of arm number 6 fused to arm number 4. Chromosomes M1 and M2 appear to be a consistent feature of all collared lemming karyotypes. Bar = 10μm.

lemming hair were difficult to detect relative to those in human squamosal epithelia, for example. The Schmid procedure was most successful when done at room temperature, without heating the preparation. Kohler illumination was essential. I felt confident when Barr bodies were discerned, but diagnosing XY females by failure to discern a Barr body was inconclusive. Determinations were verified by karyotyping after the desired breeding was completed. Of 19 females examined, only one (an XX female) was misevaluated as XY.

RESULTS

The basic NE Alaska karyotype

Most individuals had 2n=30 karyotypes similar to that described by Modi (1987a) in collared lemmings from Barrow (See Fig. 2). There are ten pairs of biarmed autosomes, a distinctive large pair of telocentrics (pair 2), a much smaller pair of telocentrics (pair 19), and four microchromosomes. Variations from this basic karyotype are described below.

Measurements of the twenty largest chromosome arms (Table 2 and Fig. 3) indicated that these arms cannot all be distinguished on the basis of size, there being no significant size difference among several arms. Thus, in

Table 2. Relative sizes of the major chromosome arms in collared lemmings.

#	MEAN SIZE	S.D.	#	MEAN SIZE	S.D.
1	8.332	5.048×10^{-1}	11	5.117	4.118×10^{-1}
2	8.012	5.702×10^{-1}	12	3.778	2.617×10^{-1}
3	7.763	5.342×10^{-1}	13	3.648	2.792×10^{-1}
4	7.115	4.292×10^{-1}	14	3.481	2.179×10^{-1}
5	6.609	6.399×10^{-1}	15	3.411	2.196×10^{-1}
6	6.443	4.840×10^{-1}	16	3.224	2.335×10^{-1}
7	6.002	6.050×10^{-1}	17	2.965	3.631×10^{-1}
8	5.876	3.682×10^{-1}	18	2.717	2.885×10^{-1}
9	5.255	2.484×10^{-1}	19	2.680	2.022×10^{-1}
10	5.225	3.145×10^{-1}	20	2.347	2.012×10^{-1}

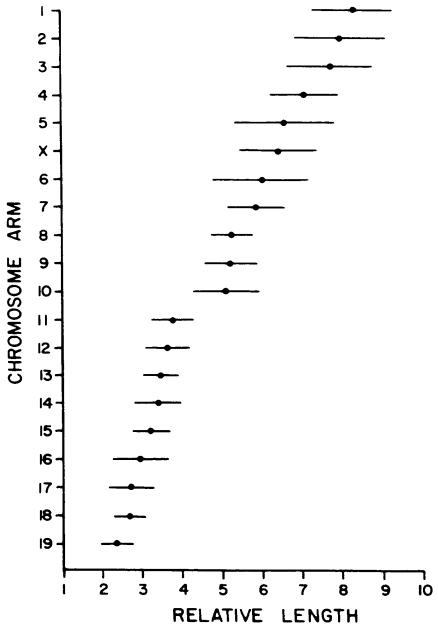

Figure 3. Graph of relative sizes of chromosome arms with 95% confidence intervals.

Table 3 (page 1 of 2). Proposed nomenclature for major chromosome arms in collared lemmings. Based upon measurements in Table 2 and probable homologies with two other nomenclatures.

ARM #	RAM N	Gileva & Chebotar 1979	*Peromyscus* (Committee, 1977)
1	1	A5	8 & 14?
2	2	A3	3
3	3	A7	?
4	4	A6	4 (dist) & ?
5	5	A10	1 (distal portion)
6	7	A8	5
7	8	A9	4 (proximal portion) & 19
8	9	A11	12
9	10	A4	11
10	11	A12	7
11	12	A13	9

Table 3 (page 2 of 2).

ARM #	RAN K	Gileva & Chebotar 1979	*Peromyscus* (Committee, 1977)
12	13	A16	2 (distal portion)
13	14	A14?	13
14	15	A15	16
15	16	A17?	6 (distal portion)
16	17	A18 or A19	18
17	18	A18 A20?	?
18	19	A18 or A19	15
19	20	A21 or A23	?
M1	–	A1	21 (pericentric inversion)
M2	_	A2	22
X	6	X	X

the absence of banded karyotypes, centric fusion/fission polymorphism cannot be evaluated adequately. Nonetheless, these measurements are offered as the basis for a chromosomal-arm nomenclature (Table 3), which will be necessary if Robertsonian variation in collared lemmings is eventually to be described in the same detail as it is in house mice (*Mus musculus*, *M. domesticus* etc.), and in common shrews (*Sorex araneus*).

The combination of size and G-bands permitted visual matching of many chromosome arms to the mostly telocentric chromosomes of the Siberian race, *Dicrostonyx torquatus chionopaes* (Fig. 2 in Gileva & Chebotar, 1979). Also, many arms can be matched to homologues in the well-studied karyotypes of *Peromyscus* (Modi, 1987a). These homologies are indicated in Table 3, and the arm nomenclature therein is used throughout the rest of this paper. Biarmed chromosomes are indicated by the two arm numbers separated by a period (.), as in the *Mus* literature.

Robertsonian dimorphisms

Robertsonian dimorphism in chromosome 17.11 was found in about half of the wild-caught individuals from Colville Village, Kaktovik, and Toolik Lake. The frequency of the metacentric is 0.67. Five of 13 were homozygous for the

metacentric chromosome and only one individual was homozygous for the telocentrics (Table 1). These genotypic frequencies, including the haploid genome represented by "Prudhoe #3," agree with Hardy-Weinberg expectation (X^2 = 0.375, 2 d.f.). Captive breeding data for the 17.11 dimorphism indicate that the metacentric form is transmitted randomly in meiosis. Heterozygous males transmitted the metacentric chromosome to 20 offspring and the telocentrics to 21. Heterozygous females transmitted the metacentric chromosome to 27 offspring, but the telocentric chromomsomes to only 18; not a significant distortion of random segregation (X^2 = 1.8). But the female with the most karyotyped offspring produced 7 heterozygotes and 15 homozygotes (X^2 = 2.91, $p < 0.1$), at least suggesting distortion similar to that described in Robertsonian heterozygotes of mice (Gropp & Winking, 1981) and shrews (Searle, 1986a). Two additional Robertsonian dimorphisms (12.10 and 18.9) occurred in the individual from Toolik Lake (Fig. 4).

Microchromosomes and supernumerary chromosomes

The four smallest chromosomes of the standard karyotype are somewhat enigmatic. Because of differences in centromere position, definitive identification of

homologues is uncertain in some individuals. C-banding revealed that one arm of each of these chromosomes is usually heterochromatic (Fig. 5). This is in contrast to the finding of Modi (1987b), who described virtually identical karyotypes of collared lemmings from Barrow as entirely C-band negative. Both silver nitrate staining (Bloom & Goodpasture, 1976) and observation of associations in nucleoli, with each other and with chromosomes 2 and 19, show that these smallest chromosomes often have nucleolus-organizing regions. One wild-caught individual (GHJ875) had a conspicuous secondary constriction on one of these chromosomes, similar to that described in chromosome M6 of collared lemmings from Wrangel Island (Kozlovskii & Khvorostyanskaya, 1978).

Two individuals in this study were definitely missing one of these smallest elements (2n=29). One of these was a male from the inbred male-biased line (Chapter III); his parents were not karyotyped but one of his brothers was 2n=30 as were 43 other karyotyped individuals in this line. A 2n=29 female was sired by a wild-caught 2n=30 male; the mother and 11 siblings were also 2n=30. Nevertheless, these smallest chromosomes do pair normally in male meiosis (Fig. 6; also Fig 5b in Jarrell & Fredga, in press) and they were retained through several generations of

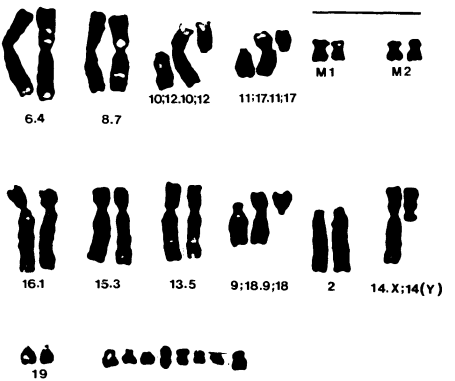

Figure 4. G-banded karyotype of male collared lemming from Toolik Lake, Alaska. The diploid number of 2n=37 results from three Robertsonian dimorphisms and four probable supernumerary chromosomes which are not distinct from the four normal microchromosomes. Bar = 10μm.

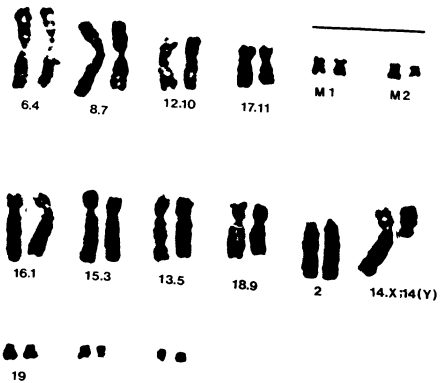

Figure 5. C-banded karyotype of a 2n=30 male collared lemming from Prudhoe Bay, Alaska. Centomeric C-bands are present in chromosomes 17.11 and 13.5. The short arm of chromosome 14 (Y) is positively stained, and may represent the ancestral Y chromosome. Bar = 10µm.

inbreeding in the male-biased line.

The 2n=28 karyotype of collared lemmings on Wrangel Island (Kozlovskii, 1974; Kozlovskii & Khvorostyanskaya, 1978; Chernyavskii & Kozlovskii, 1980) differs in diploid number from the 2n=30 karyotypes of Alaska in that one of these smallest pairs is absent.

Missing microchromosomes have been reported in wood lemmings; Gileva, Bolsjakov, Sadykov & Omariev (1983) found three individuals missing one of their smallest chromosomes with no apparent phenotypic effect. The microchromosomes in wood lemmings are similar in size and in C-banding pattern to those of collared lemmings.

The inconsistent presence of these chromosomes suggests a relatively weak distinction between the microchromosomes and supernumerary chromosomes in collared lemmings. Some microchromosomes are apparently extraneous to a normal phenotype, but their segregation is far less haphazard than that of "true" supernumeraries.

Though true supernumerary chromosomes are ubiquitous in the collared lemmings of mainland Siberia (See Table 5), they have not been documented previously in North America. A male from Toolik Lake, in the northern foothills of the Brooks Range, had a total of eight microchromosomes (Fig. 4); four of these are assumed to be the normal

microchromosomes of the 2n=30 karyotypes, but they could not be paired definitively. In 17 offspring from crosses with 2n=30 females, this male sired 2 offspring without supernumerary chromosomes, 5 offspring with one B chromosome, 5 with two, and 5 with three.

Sex chromosomes

The heterochromosomes in Figures 2, 4, and 5 are arranged to show that arm 14 is common to both chromosomes; thus the "Y" is inverted (short arm down) in these figures. C-banding (Fig. 5) shows that the long arm (Yq = arm 14) of the Y is entirely euchromatic while the short arm is the largest positively-stained region in the karyotype and might be the "original Y." Fredga (1983) suggested that the original Y chromosome of some races of collared lemmings might be retained as a vestigial attachment to certain autosomes.

Modi (1987a) described the entire karyotype of collared lemmings from Barrow as devoid of C-bands, but in my preparation, C-bands are visible at the centromeres of autosomes 17.11 and 13.5 (Fig. 5), as well as the short arm of the Y. Such differences between preparations, particularly those from different laboratories, are not unusual and can result from many factors. Overtreatment

can cause negative staining, which perhaps is more likely than a false positive result.

The long arm of the X has a characteristic G-banding pattern (Figs. 2 and 3) similar to that found in the telocentric X chromosomes of many other rodents (e.g., Pathak & Stock, 1974).

Sex chromosomes similar in size and centromere position to those described here appear in unbanded karyotypes of collared lemmings from Wrangel Island (Chernyavskii & Kozlovskii, 1980) and from several Nearctic populations (Rausch & Rausch, 1972). Further evidence that an autosome has become fused to the mammalian "original X" (Ohno, Becak & Becak, 1964 *et seq.*) in Alaskan collared lemmings can be derived from Rausch & Rausch's (1972) work on the sex chromosomes of collared lemmings from Umnak Island: tritiated thymidine labelling indicated that only the long arm of the X was late replicating. Also, using Rausch & Rausch's measurements, if one subtracts their relative length of the Y chromosome in males (4.3%), or the Y chromosome in XY females (their "deleted X," 3.8%), from their length of the X chromosome (8.75%), the remainder is similar in length (4.45 and 4.95%) to Ohno's "original X" (5%).

In male meiosis, the autosomal arms of the X and Y synapse and may form a spoon-shaped bivalent in diakinesis (Fig. 6), similar to but smaller than that described by Gileva (1980, Fig. 3a). The end-to-end pairing described by Rausch & Rausch (1972) also is seen (e.g., Fig. 5b in Jarrell & Fredga, in press) but probably represents terminalization of a single chiasma.

The X chromosome described here is distinct from that of *Dicrostonyx t. chionopaes* and *D. t. torquatus* (Fig. 2, Gileva, 1980), in that these Siberian forms have the original telocentric X fused to arm 1 rather than to arm 14.

XY females

XY females or females who bore XY daughters were obtained from Kaktovik and the Colville River delta (Table 1).

In order to test for X-linkage of the male-repressor, XX daughters of XY females were were selected (by the presence of a Barr body) to be bred until they bore either 8 successive XX daughters, or at least one XY daughter. Under X-linkage, all XX daughters of XY females should be $X^{*}X^{o}$ and a third of their daughters should be XY. Hence, the probability of an $X^{*}X^{o}$ female producing 8 successive XX

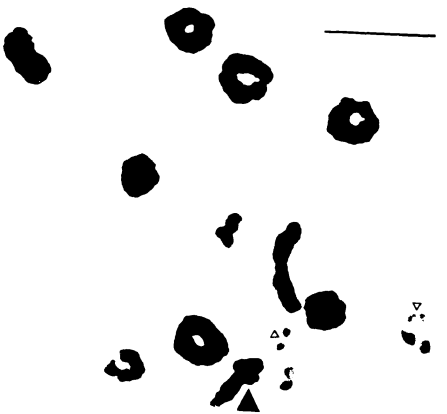

Figure 6. Diakinesis in a 2n=30 male collared lemming. The large solid triangle indicates the sex bivalent. The two small triangles indicate bivalents formed by the four microchromosomes. Bar = 10µm.

daughters is, $(2/3)^8 \cong 0.039$. Under autosomal linkage of the male-repressor, half of the XX daughters of XY females should lack the male-repressor and be unable to bear XY daughters.

None of the five selected XX daughters of XY females produced 8 successive XX daughters; one or more XY daughters by each indicates a probability of autosomal linkage of $(1/2)^5 = 0.03125$.

XX females who bore one or more XY daughters, and XX females who were the daughters of XY females are thus defined as $X^{*}X^{o}$. The sex ratios and the ratios of XY daughters to XX daughters obtained from the three female genotypes are shown in Table 4. For $X^{o}X^{o}$ females, a ratio of 39M:39F in the first generation of outbreeding from inbred females assumed to be $X^{o}X^{o}$ is described in Chapter III. To those data, I have added the data from two additional females diagnosed as $X^{o}X^{o}$ by their production of eight or more XX daughters and no XY daughters ($p \cong 0.039$). Not included in Table 4 is the 11M:11F ratio produced by a female from whom seven daughters were identified as XX ($p = (2/3)^7 \cong 0.0585$); the other four were not karyotyped.

Table 4. Progeny sex ratios (males:females) and ratios of XY to XX daughters from three female genotypes.

Sex ratios:

	---MATERNAL GENOTYPES---		
	$X^{m}Y$	$X^{m}X^{o}$	$X^{o}X^{o}$
expected	1:2	1:3	1:1
observed	46:101	30:74	63:63
χ^2	0.276	0.820	0.000

Ratios of XY to XX daughters:

	---MATERNAL GENOTYPES---		
	$X^{m}Y$	$X^{m}X^{o}$	$X^{o}X^{o}$
expected	1:1	1:2	---
observed	26:29	23:34	---
χ^2	0.164	1.263	---

DISCUSSION

Taxonomic implications of chromosomal variability

Within the genus *Dicrostonyx*, the Ungava lemming, *D. hudsonius*, is the only morphologically diagnosed species. The molar structure is simpler than in the *D. torquatus* morphospecies. However, this character deserves further scrutiny; both Peterson (unpubl. thesis cited in Rausch, 1963) and Youngman (1975), using large samples, suggested that the key dental characters are not discrete. The rest of the living members of the genus have most frequently been regarded as representing one (Ognev, 1948; Rausch, 1963) or possibly as many as three (Hall, 1981) weakly differentiated species.

The work of Rausch & Rausch (1972) rendered the number of species in the *D. torquatus* morphospecies even more tentative. The diploid numbers and results of breeding experiments in that work, along with subsequent data (Rausch, 1977; Chernyavskii & Kozlovskii, 1980; Scott & Fisher, 1983), indicate a complex of intersterile chromosomal races, suggestive of a holarctic superspecies, *D. torquatus*. Since chromosomal differences frequently are associated with taxonomic differences at the species level, Johnson (p. 482 in Honaki, Kinman & Koeppl, 1982) provisionally elevated most nominal subspecies to full

species.

The data presented here, while not substantial from a geographic perspective, do offer some insights into the probable nature and taxonomic significance of chromosomal variation in *Dicrostonyx*. Previous work in North America revealed little definitive Robertsonian variation and no supernumerary chromosomes; these two factors may account for much of the reported chromosomal variability.

Given the three Robertsonian dimorphisms at Toolik Lake (Fig. 4), plus the three whole arm translocations (forming biarmed chromosomes 16.4, 11.6, 17.1) characterizing the Seward Peninsula (Jarrell & Fredga, in press), then just within northern Alaska, ten of the twenty major chromosome arms (Table 3) are involved in Robertsonian mutations. This strongly suggests a "Robertsonian fan" (Matthey, 1973) as complex as those in the murine rodents, *Mus* and *Leggada*, and in the common shrew, *Sorex araneus*.

In a classic Robertsonian fan, the diploid number may vary, depending on the relative numbers of biarmed versus telocentric chromosomes. The number of chromosome arms (FN) should remain constant. As shown in Table 5, FNs are not constant in the existing literature on collared

Table 5 (Page 1 of 2). Summary of reported karyotypes for collared lemmings. Diploid number (2n), number of supernumerary chromosomes (B), the "corrected" diploid number (2n - B), and the reference are shown.

Locality	2n	B	2n - B	FN	Ref.
Beringia:					
Umnak Island	34	0	34	54	1
Saint Lawrence Island	34	0	34	54	1
Seward Peninsula	30	0	30	54	1
Barrow	30,33	0	30,33	54	1,3
Beaufort Lagoon	32-33	0	32-33	55	1
Prudhoe Bay, Barter Island	29-32	0	29-32	-	4
Toolik Lake, Brooks Range	37	4	33	52	4
Anaktuvuk Pass, Brooks Range	34-35	0	34-35	54	1
Wrangel Island, NE Siberia	28	0	28	54	5
Eastern Arctic:					
Churchill, Manitoba	42-44	0	42-44	50,52	1,9
Banks Island	47	0	47	56	2
Devon Island	46	0	46	52	2
Hudson Bay Coast, Ungava	48	0	48	54	11

Table 5 (Page 2 of 2).

Locality	2n	B	2n - B	FN	Ref.
Palearctic:					
Pechora inlet coast	53-60	7-15	45-46	51-52	6
Middle Yamal	48-54	3-8	45-46	51-52	6
Polar Urals	46-49	1-3	45-46	51-52	7
Buor-Khaya inlet coast	48-53	2-7	46	51-52	6
Big Rautan Island	47-48	0-1	47-48	51-52	8
Chaun inlet coast	57-60	10-13?	47-48?	51-52?	10
Lawrence Lagoon	84-85	37-38?	47-48?	51-52?	5

Key to references:

1 Rausch & Rausch, 1972

2 Rausch, 1977

3 Modi, 1987a; 1987b

4 This study.

5 Chernyavsky & Kozlovskii, 1980

6 Gileva, 1983

7 Gileva, 1973

8 Gileva, 1980

9 Malcolm, Brooks & Bogart, 1986

10 Kozlovskii, 1974

11 Krohne, 1982

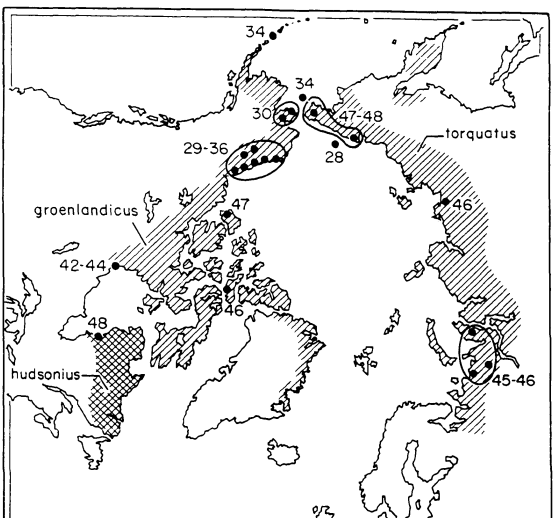

Figure 7. Geographic distribution of diploid numbers in collared lemmings. Diploid numbers are given exclusive of supernumerary (B) chromosomes. For references, see Table 5.

lemmings, but much of the reported variation may result from inconsistent scoring among authors. Undetected supernumeraries are possible, but microchromosomes and small arms on "subtelocentric" chromosomes seem to be the points of confusion.

For example, Rausch & Rausch (1972) described the smallest pair of chromosomes in lemmings from Umnak Island as biarmed, though this can hardly be perceived from their published photographs and presumably is based on direct measurements with an optical micrometer. Consequently they reported an FN of 54. I have found the centromere position in the smallest chromosomes to be variable, and Kozlovskii (1974) has described the smallest chromosomes in lemmings from Wrangel Island as dimorphic for the presences of a nucleolus organizing region. If such small chromosomes are inconsistently biarmed, and the individual arms are small and indistinct, then they might best be ignored from the standpoint of evaluating Robertsonian change. Thus, I consider the karyotypes from Umnak Island (Rausch & Rausch, 1972) to be consistent in FN, however scored, with my preparations from northern Alaska.

Also, Rausch & Rausch (1972) reported a fundamental number of 50 at Churchill, while Malcolm, Brooks & Bogart (1986) reported 52. Malcolm *et al.* scored one of the

largest chromosomes as a subtelocentric, but their preparations show variability in the short arms of this chromosome. I noticed similar variability in chromosome 2 of the animals in this study. Again, a nucleolus organizing region is present. Hence, I suggest that these short arms are an inconsistent character and that Rausch & Rausch's FN of 50 is the more consistent scoring.

Determinations of fundamental numbers are apparently imprecise when small chromosome arms are present. Thus, the Robertsonian pattern among *Dicrostonyx* populations is more consistent than is apparent from reported FNs. Nevertheless, the amount of chromatin in *Dicrostonyx* karyotypes is variable, and I have suggested that the distinction between supernumerary chromosomes and autosomal microchromosomes is not absolute. For example, the 2n=28 karyotype found on Wrangel Island may differ from a 2n=30 karyotype of the Alaska mainland simply by the absence of one pair of microchromosomes. The two 2n=29 individuals described here suggest the intermediate step.

In summary, chromosomal variation in collared lemmings is primarily caused by centric fusions, fissions, and/or centric transpositions. The situation is complicated by the variable presence of microchromosomes and supernumerary

chromosomes and by the variable presence and variable scoring of small chromosome arms. As mentioned above, this pattern of chromosomal variation, a Robertsonian fan, is well-documented in several other species of small vertebrates.

Robertsonian variation has been proposed as a possible basis for stasipatric (White, 1978) and parapatric speciation (Capanna, 1982; Baker & Bickham, 1986). Nevertheless, some studies indicate that high levels of chromosomal polymorphism are not necessarily an insurmountable barrier to gene flow.

For example, Sites, Porter & Thompson (1987), studying the Mexican lizard, *Sceloporus grammicus*, found little evidence of underdominance in Robertsonian heterozygotes and, despite cytotypes varying in diploid number from 32 to 46; allelic variability is suggestive of "relatively large, random-mating breeding units." Frykman & Bengtsson (1984) suggested that some genetic exchange occurred between two chromosomal races of *Sorex araneus* distinguished from each other by several monobrachial fusions.

Searle (1986b) has described how Robertsonian fans may produce a clinal gradient in the degree of intersterility among populations and individuals. Such variability does not suggest discrete populations isolated by discrete

barriers to interfertility. Thus, intersterility among individuals captured at some distance from each other, such as that reported by Rausch & Rausch (1972), is not conclusive evidence of blocked gene flow. If the sampled populations are only slightly intersterile with unsampled adjacent populations, then genes might be shared across a clinal gradient of intersterility. Thus, elevation of the nominal subspecies in the *torquatus* group, as proposed by Johnson (in Honaki *et al.*, 1982) seems premature; they might better be regarded as cytotypes of one or two widespread species.

The chromosomal data from Alaska, including Umnak and Saint Lawrence Islands, and from Wrangel Island in the Siberian Chukchi Sea indicate a related complex of cytotypes distinct from *D. torquatus, sensu stricto*, of mainland Siberia (Fig. 7). This complex appears to be characterized by a preponderence of biarmed chromosomes, resulting in relatively low diploid numbers of 28 to 37, and probably by the 14.X centric fusion. The total intersterility of the 2n=28 race on Wrangel Island with the adjacent race on mainland Siberia (Chernyavskii & Kozlovskii, 1980), in contrast to the usual sterility of F_1 hybrids among North American races (Rausch & Rausch, 1972),

further suggests a major discontinuity between Beringian and Siberian races. Beringian races appear to have been displaced from eastern Siberia by the western Siberian race after the most recent establishment of the Bering Strait.

In *D. torquatus, sensu stricto*, and in the eastern Arctic forms, judging from the reported diploid and fundamental numbers (Table 5), most chromosomes are telocentric. Gileva (1983) has commented upon the similarity of Siberian karyotypes to the unbanded karyotype of *D. hudsonius* (Krohne, 1982).

The sharp distinctions between Beringian populations and populations of mainland Siberia, as well as the total intersterility between them (Chernyavskii & Kozlovskii, 1980), suggest two species in the *torquatus* complex. On the other hand, the apparent similarity between Siberian and the far-less-studied eastern Arctic forms is intriguing. Could these widely separated races be interfertile?

A reasonable compromise between the extreme lumping of Ognev (1948) and the extreme splitting of Johnson (in Honaki *et al.*, 1982) is offered by Hall (1981) who steadfastly maintains *D. groenlandicus* for North America and *D. torquatus* for Siberia. Because crosses between lemmings from the Seward Peninsula and lemmings from Saint

Lawrence Island produced fertile progeny (Rausch & Rausch, 1972), Hall's *D. exsul* should be submerged in *D. groenlandicus*. Also, the similarity between the chromosomes of lemmings from Wrangel Island and those of northern Alaska suggests that *D. vinogradovi*, elevated to specific rank by Chernyavskii & Kozlovskii (1980), might also belong with Beringian forms in *D. groenlandicus*.

Sex ratio phenomena

The sex ratios, and ratios of XX to XY daughters, in this study (Table 4) qualitatively support Mendelian predictions under the X-linked male-suppressor scheme proposed for *D. torquatus* in Siberia (Gileva & Chebotar, 1979). This in turn, supports the idea that one sex-determining system is characteristic of all collared lemmings. These data are too scant to evaluate the inconsistencies with the male-suppressor hypothesis shown by Bull & Bulmer (1981) and by Gileva (1987), but Chapter III proposes an explanation for these phenomena.

The probable X-linkage of the male-repressor in both the 1.X races of Siberia (Gileva & Chebotar, 1979; but see Bull & Bulmer, 1981), and in the 14.X race, described here, indicates that the locus is probably on the true X arm of these derived chromosomes, rather than on arm 1 in Siberia

and on arm 14 in Alaska.

Chapter III

A MALE-BIASED NATAL SEX-RATIO IN INBRED COLLARED LEMMINGS, *Dicrostonyx groenlandicus*

Collared lemmings have a gene that causes a female phenotype in some individuals with XY chromosomes; hence, their sex ratio normally favors females (Bull & Bulmer, 1981). This is a report of a captive colony that was producing a surplus of males. The classical arguments for frequency-dependent selection on sex ratio predict a 1:1 sex ratio (Fisher, 1930; Charnov, 1982). Therefore, modifiers of the known female-biased sex-determining system might be favored by frequency-dependent natural selection. However, a simpler explanation can be inferred from the karyotype of the lemmings in this male-biased captive colony. A pair of autosomes fused to both sex chromosomes gave males two copies of many (formerly autosomal) X-linked loci; under inbreeding, males apparently remained more heterozygous at these loci, and hence were less subject than XX females to inbreeding depression.

History of the colony

The captive colony of collared lemmings that eventually produced male-biased progenies was established from two males and three females captured in summer 1973 at

Prudhoe Bay, Alaska (70°22'N, 148°22'W). The lemmings were maintained in captivity for veterinary research by the methods of Dieterich (1975). Originally, the sex ratio of offspring favored females. In 1982, caretakers noticed that about twice as many males as females were being born. I reconstructed the colony's pedigree from incomplete caretaker's records. It frequently happened that the sex recorded for a lemming when it was weaned and toe-clipped differed from the sex recorded later when it was a breeder. Where this occurred, I assumed the later sex of the individual to be correct. Sexes were not recorded for 15% of the 2348 recorded births; many of these were lemmings that died before weaning. Mortality before weaning does not appear to affect the sex ratio in collared lemmings (Hasler & Banks, 1975; Gileva, Benenson, Pokrovskii & Lobanova, 1980). Though some errors exist in the breeding records of this colony, there is no reason to believe that these create a systematic bias.

Generations overlapped, so in analyzing the pedigree, I assigned generations matrilineally with males going to the same generation as their sisters. Coefficients of inbreeding (F) were calculable for all but a few of the animals that bred. This core pedigree contained 398 individuals. The F values shown in Table 6 are the

averages for the parents born in that generation (and fertile in the next generation). The slight decrease in average F value between the ninth and tenth generations is an artifact of assigning generations.

One of the three wild-caught females produced only two offspring (1M:1F) and only her son bred. Also, descendants of one of the two original males did not breed after three generations. Thus, subsequent generations are the product of only three and a half individual genomes. The other two wild-caught females produced a surplus of daughters (6M:16F and 2M:8F), which suggests that both carried the male-suppressor chromosome. The females of generations two through five (Table 6) produced 39% males, not significantly different ($X^2 = 1.23$) from the equilibrium sex ratio of 42% predicted by the male-suppressor hypothesis (Bull & Bulmer, 1981). In the sixth through eighth generations, male-biased sibships appeared while some sibships continued to be female-biased.

A shortage of breedable females resulted in a "genetic bottleneck" in the ninth generation (Table 6). In generations nine through eleven, the sex ratio was almost exactly two-to-one in favor of males. After the eleventh generation, some pairs produced an even sex ratio and

Table 6. Summary of pedigree data.

Generation number	# Females bred	# Offspring of known sex	Average F value	% Male offspring
1	3	34	0.000	26%
2	11	121	0.000	43%
3	13	102	0.120	36%
4	10	69	0.134	43%
5	15	130	0.207	36%
6	13	100	0.233	52%
7	13	106	0.243	52%
8	22	113	0.273	54%
9	5	45	0.328	69%
10	8	88	0.324	65%
11	13	121	0.377	64%
12	12	60	0.390	57%
13	11	130	0.431	62%

female-biased sibships were completely absent.

Inbreeding depression seemed evident when I began observing this colony at about the eleventh generation. In addition to a general lack of vigor, dental malocclusion and maternal infanticide seemed frequent. A few outbred lemmings kept simultaneously and under the same conditions, had no such problems. Though change in litter size is hardly perceptible (see Table 7), it showed a slight, but significant, negative correlation with inbreeding coefficients in 324 litters ($r = -0.1575$, $p < 0.01$).

Technicians attempted to avoid crossing close relatives; nonetheless such crosses occurred. Offspring from parent/offspring and sib/sib crosses did poorly without exception, never producing F_2 progeny. This low fertility of the most inbred individuals was important in keeping the colony as outbred as it was.

The male bias was eliminated by outbreeding. Eight of the last females from this colony (generations 14 and 15) were mated to two new wild-caught males. The total sex ratio resulting from these crosses (39M:39F) was not biased. This ratio is significantly different from the 2:1 ratio in the preceding generations ($X^2 = 9.75$, $p < 0.005$). The mothers of these eight females, all mated to males from the colony, had produced a total sex ratio of 101M:62F,

Table 7. Litter sizes in the inbred colony.

Generation number	Mean	N	S.D.
1	3.167	6	0.753
2	2.756	41	1.655
3	3.538	26	1.679
4	3.130	23	1.392
5	3.348	23	1.301
6	3.400	20	1.789
7	3.000	29	1.813
8	2.462	13	1.266
9	2.450	20	1.317
10	2.714	28	1.243
11	2.500	28	1.319
12	2.389	18	1.092
13	3.082	49	1.351
Total:	2.929	324	1.478

significantly different from 1:1 ($X^2 = 9.33$, $p < 0.005$), and not significantly different from 2:1 ($X^2 = 1.62$).

Karyology

Forty-four lemmings karyotyped from this colony had chromosomes similar to the 2n=30 karyotypes described in Chapter II. One of these lacked one of the smallest chromosomes (2n=29), also as described in Chapter II. The 15 males had sex chromosomes similar to those in Figure 2. All of the 29 females had two X chromosomes, though X*Y females do occur in the Prudhoe Bay region (Chapter II). Also, because the colony's sex ratio was originally female-biased, the X* chromosome is assumed to have occurred in the founders. The mothers of five male-biased sibships (5M:1F, 13M:7F, 11M:4F, 11M:6F, and 8M:3F) were 2n=30, XX.

The important feature of the karyotype of these lemmings is the homology between the short arm of the X chromosome and the long arm of the Y chromosome (Fig. 2). This arrangement is analogous to the arrangement in *Dicrostonyx torquatus chionopaes* from Yakutia (Gileva & Chebotar, 1979; Gileva, 1980). In that race, however, the autosome fused to the sex chromosomes ("A5" of Fig. 2, Gileva & Chebotar, also Fig. 2, Gileva, 1980) is homologous to chromosome arm 1 in Figures 2, 3, and 4.

Discussion

In early generations of this laboratory colony, the sex ratio was consistent with the expectation for collared lemmings carrying the male-repressor. The change to an even sex ratio in generations six through eight is consistent with two concurrent factors: (1) a mixture of both male-biased and female-biased sibships; and (2) loss of the male-repressor, that is, a return to the normal mammalian condition.

The 2:1 sex ratio in the later generations suggests that half of the XX zygotes were inviable. In a mammal with normal sex chromosomes, where males are hemizygous for X-linked genes, an X-linked recessive gene should affect males twice as often as females, but quite the opposite seems to have occurred here. If a lethal was located on the "autosomal" short arm of the X chromosome and males were not affected because they had the dominant allele on the homologous long arm of the Y chromosome, it would produce the observed result; that is, a sex ratio of 2:1.

I propose that, given a karyotype with autosomal chromatin fused to the X chromosome, a sex ratio favoring the heterogametic sex can be expected to result from intense inbreeding. Inbreeding reduces heterozygosity, exposing recessive alleles; lethals decline in frequency as

they are selectively eliminated. "X-linked autosomal" lethals should persist longer than true autosomal lethals because they can be eliminated by homozygosity only in the females. Their lethality is restricted to XX zygotes, so at least half of the lethal-carrying eggs will become male carriers when fertilized by Y sperm. In contrast, given a true autosomal lethal, some lethal eggs will be eliminated because they will be fertilized by lethal Y sperm, thus reducing more rapidly the frequency of the lethal allele in successive generations. With an "X-linked autosomal" lethal, there are only nonlethal Y sperm.

Deleterious alleles are eliminated more slowly when borne on "X-linked autosomal" chromatin than when borne on true autosomes, and thus lethals should tend to be more concentrated in "X-linked autosomal" chromatin. Either by the accumulation of individually sublethal but deleterious alleles, or by the tendency to retain a single lethal, X-linked autosomes can cause inbreeding depression to affect sex ratio.

If, in meiosis, the lethal crosses over from the autosomal arm of the X to the homologous arm of the Y chromosome, then the situation is analogous to a normal autosomal lethal; sex ratio is not affected and the allele

becomes detectable only as reduced fertility. But a high rate of crossover would be necessary to mask the linkage effect.

If the autosome fused to the X chromosome is large, then the number of loci available for deleterious alleles is also large. But, the effect of greater autosome size would be countered to some degree by the greater probability of crossover at distal loci.

Thus, given an X/autosome fusion, probability of a detectable bias of sex ratio should depend on the proportion of the euchromatic genome that is attached to the X chromosome, on the intensity of inbreeding, and on the frequency of crossover between the autosomal segments of the X and Y chromosomes. If the fused autosome is large, meiotic recombination is low, and inbreeding is intense, then sex ratios favoring the heterogametic sex may be inevitable.

Though the male-bias observed here certainly seems related to captive inbreeding, some observations suggest that male-biased subpopulations of collared lemmings might occur in nature. For example, Hantzsch (1912, cited in Manning, 1954) reported that 29 of 30 collared lemmings from Baffin Island were males, though it is unclear how he secured the specimens. Manning (1954; 1976; Manning &

MacPherson, 1958) collected and examined series of specimens that were significantly male-biased and other series that approximated the now-expected female-bias. Of course, populations of small mammals are notoriously difficult to sample randomly and, presumably, under some circumstances males are more catchable.

Evidence is scant that male-biased subpopulations occur naturally, but Fisher's (1930) balancing selection argument gives grounds in theory to suppose that they could occur. For example, Bull & Bulmer (1981) pointed out that a male could increase his fitness in a female-biased population by producing more than half Y sperm and hence more sons. If such males had been present in this colony and the X^* was lost in the ninth generation, this could have caused a male-biased sex ratio. A side effect of such a mechanism is that, in nature, the overall frequency of males would normally decrease because the increased proportion of Y sperm increases the frequency of X^*Y females so that fewer normal X^o-ova are available. The attractive aspect of Bull and Bulmer's hypothesis is that it explains the lower-than-expected sex ratios in some colonies and the higher-than-expected proportions of XY females.

In light of Bull & Bulmer's (1981) work, Gileva (1987) has reanalyzed data from her colonies and now hypothesizes that drive for the Y chromosome in male meiosis caused an excess of males from XX females and an excess of XY daughters from XY females. She does not propose an explicit meiotic mechanism, and her excellent cytological work shows no distortion of the numbers of X and Y secondary spermatocytes and oocytes in males and XY females.

The effect Gileva (1987) describes is consistent with the mechanism proposed here. Inbreeding in her colony was "up to 0.25-0.30 by the last (11th) generation" (Gileva *et al.*, 1982), comparable to the inbreeding that was associated with the male-bias described here. Further, if one accepts my argument, that the probability of affecting sex ratio by inbreeding increases with the size of an autosomal attachment to the X, then the two cytotypes studied by Gileva are excellent candidates. In both races, *Dicrostonyx torquatus torquatus* and *D. t. chionopaes*, the X chromosome is attached to approximately the largest autosomal arm in the karyotype. Thus, Gileva's excess of sons from $X^{o}X^{o}$ females, and her excess of sons and $X^{*}Y$ daughters from $X^{*}X^{o}$ females, might result from reduced proportions of homozygotes ($X^{o}X^{o}$ daughters) from both

genotypes. But, the slightly under-represented (X^2 = 3.00) XX daughters of XY females in Gileva's colony should be considered heterozygous (X^*X^o) under the existing male-suppressor hypothesis. This might still be explained, under my hypothesis, by crossover between the autosomal arms of the X^o and the X^*, such that a lethal was carried on both types of X chromosome; or, by the presence of lethals at more than one locus.

Inbreeding in the colony described here seems more intense than a wild population could sustain. Also, discrepancies in presumably outbred collared lemmings, between the expected sex ratio of 0.42 and several observations of lower values, do suggest that further undescribed mechanisms affect sex determination (Bull & Bulmer, 1981; Malcolm *et al.*, 1986). Nevertheless, the effect proposed here might cause either more males or more X^*Y females than Mendelian predictions from the male-suppressor hypothesis alone.

Thus the value of these observations may be mostly cautionary: inbreeding depression can directly skew the sex ratio in organisms with autosomal chromatin fused to their sex chromosomes. But, a selective advantage for the fusion of autosomal chromatin to heterochromosomes is also

possible; heterozygosity imparted by such a karyotype is apparently adaptive under close inbreeding. This would be particularly beneficial when, as in collared lemmings, many females, as well as all males, have heterochromosomes. If inbreeding limits fitness in natural populations of collared lemmings, fusions of autosomes to the sex chromosomes might be favored by natural selection in males and in XY females, because the fusions maintain heterozygosity.

White (1957; 1973), in a model extended by Charlesworth & Charlesworth (1980), proposed that the advantage of fusions between sex chromosomes and autosomes is due to increased heterozygosity for a gene that has a higher heterotic effect in the heterogametic sex. Improved heterozygosity under inbreeding might be a less stringent model, in that it presumes no specific characteristics, such as higher heterotic effect in one sex, for loci on the fused autosome.

Alternatively, because centric fusions are a common feature of chromosomal evolution in many rodents, the sex chromosomes of collared lemmings might be involved in fusions simply by chance. In mice (*Mus*), however, where autosome/autosome fusions are profuse, X/autosome fusions are extremely rare (Gropp & Winking, 1981). In contrast,

populations of collared lemmings have at least two independent X/autosome fusions. In *D. t. chionopaes*, the fusion involves one of the largest autosomal arms and makes the X the only Robertsonian metacentric in the karyotype. An unbanded karyotype of *D. hudsonius* (Krohne, 1982) appears similar to that of *D. t. chionopaes*. These facts suggest that X/autosome fusions in collared lemmings are not perpetuated by chance alone.

Two genetic features suggest that inbreeding, hence adaptation to it, is important in the biology of collared lemmings. First, inbreeding, or "viscous gene flow" (Hamilton, 1967), is the prevailing explanation for the evolution of female-biased reproduction in opposition to frequency-dependent ("Fisherian") selection for even sex ratios (Charnov, 1982, Maynard-Smith, 1978). Though genetic structure of lemming populations has not been studied, work on numerous invertebrates supports this general model (Charnov, 1982). Secondly, collared lemmings have geographically diverse karyotypes, which contrasts with the conservative chromosomal evolution in *Lemmus*, the other holarctic genus of lemmings (Gileva, 1983). Robertsonian polymorphism occurs in many, if not all, continental populations of collared lemmings (Gileva, 1980;

Malcolm *et al.*, 1986; and observations mentioned here). Diploid numbers vary within the genus from 28 to at least 48, ignoring supernumerary (B) chromosomes that may make the diploid number as high as 86 (Chernyavskii & Kozlovskii, 1980). The karyotypic diversity of collared lemmings suggests that chromosomal mutations have a high probability of fixation; this in turn suggests that effective population sizes are small.

Ecological or demographic causes of this inferred endogamy are discussed in the next Chapter. Regardless of the cause, if inbreeding depression does limit fitness of collared lemmings, and if, as these observations suggest, attachment of chromatin to the heterochromosomes maintains heterozygosity, then the autosomal fusions to the sex chromosomes of collared lemmings are adaptive.

Chapter IV

IS FEMALE-BIASED SEX DETERMINATION IN LEMMINGS A BY-PRODUCT OF STAYING TOGETHER FOR WARMTH?

Collared lemmings and wood lemmings, rodents of the Arctic and Subarctic, respectively, have evolved genetic modifications of sex determination that result in surpluses of daughters (Gileva & Chebotar, 1979; Fredga et al., 1976 and 1977). Female-biased sex ratios can evolve when mating occurs between neighboring individuals who are more related than if mating occurred randomly. Hamilton (1967) described such inbred populations as "viscous." Two sources of viscous gene flow have been proposed for lemmings: (1) small effective population sizes associated with low phases of cyclical changes in population density (Stenseth, 1978; Maynard-Smith & Stenseth, 1978; Carothers, 1980), and (2) mosaicism of habitat (Stenseth, 1983). Neither factor is unique to collared and wood lemmings, however, and I suggest a third possibility: cold climate favors winter aggregation and inhibits the dispersal of winter-born offspring, which mature and mate with close relatives. Dispersal and outbreeding occur during warmer months. This scenario is more parsimonious than the other explanations because (1) the necessary restriction of

population size occurs seasonally rather than at intervals of several years, and (2) it becomes unnecessary to propose that these lemmings have unusually discontinuous populations or habitat.

Large biases in the sex ratio at birth are rare in mammals (Williams, 1979); the apparent advantage to an individual of producing mostly female offspring is offset by a frequency-dependent advantage to producing the scarcer sex (Fisher, 1930; Maynard-Smith, 1978; Charnov, 1982). Collared and wood lemmings therefore appear to have overcome frequency-dependent selection for a balanced sex ratio. The XX/XY sex determining mechanism is so basic in mammals that recognizably similar X chromosomes are found among marsupials and placental mammals. Collared lemmings and wood lemmings have thus overcome an obligate mode of chromosomal sex determination, as well as selection for a balanced sex ratio.

Because the normal X chromosome must be maintained for males to occur, this system could revert to normal and thus seems fragile. Yet the male-suppressor is ubiquitous among the widespread and chromosomally diverse races of collared lemming (Gileva et al., 1982), including a nearly relict lower latitude population on Umnak Island (53° 15'N, 168°

20'W) that has lost other features of the genus, such as snow claws and the white winter pelage (Rausch & Rausch, 1972). Thus, the selective forces that maintain female-biased reproduction in these lemmings must be profound, but they are yet to be identified.

Proposed causes of female-biased reproduction

The near universality that selection favors equal parental investment in offspring of each sex, regardless of mating system (Fisher, 1930), may be overcome when inbreeding is interspersed with episodes of dispersal; groups (or "neighborhoods," Nunney, 1985a) with more females will increase more rapidly and thus will contribute more to the global pool of dispersers. This general idea was originally proposed by Hamilton (1967) and since has received theoretical and empirical embellishment. Essentially the same demographic parameters reappear in numerous independent models (see Harvey et al., 1985 for a concise overview). Stenseth (1978) and Maynard-Smith & Stenseth (1978) applied Hamilton's (1967) model to wood lemmings, proposing that inbreeding occurs in discrete small demes during the low phase of a population cycle. Carothers (1980) related the evolution of the male-repressor in lemmings to "unrestrained population growth"

during the high phase of a cycle, and also invoked changing frequencies of the gene through the course of a population cycle.

A causal relationship between these two theoretically significant phenomena, lemming cyclicity and sex ratio distortion, is attractive, but supporting evidence is scant. High amplitude population cycles are better documented in brown [*Lemmus sibiricus* Kerr, sensu lato] and Norway lemmings, which have normal sex determination. No clear relationship between density and dispersal (Cockburn, 1985), and hence between density and inbreeding, has been shown in arvicoline rodents.

If female-biased reproduction is a relatively robust strategy that serves two widespread lemmings well, why is it not a more general feature among small mammals, all of which exhibit some degree of structured subpopulations and dispersal? Stenseth (1983) contrasted the "*Microtus-Lemmus* species" and "*Dicrostonyx-Myopus* species" on the basis of the habitat types described by Getz (1978): the former species inhabit "large, relatively contiguous, stable habitats," while the latter inhabit "small, isolated, patchy, and ephemeral habitats." Collared lemmings occur in a wide range of habitats spanning about 25 degrees of latitude. It is difficult to imagine that they specialize

on some peculiarly patchy resource within the monotonous texture of tundra. If habitat mosaicism is the key factor, it is surprising that the only two mammals known to have male-repressor genes are northern rather than temperate or tropical.

An alternative explanation for maintenance of the male-repressor gene is that carriers are more fit because of greater litter-size, greater survival, or a mating advantage. This alternative has not been tested rigorously. However, Benenson (1983) proposed that differences in fecundity between the three genotypes of female lemming are necessary for maintainence of the male-repressor system. Larger litter sizes in carriers of the male-repressor were described by Gileva *et al.* (1982), but these differences, attributed to heterozygosity by the authors, might be accentuated by captive inbreeding. Also, it seems probable that in the wild, fecundity is most often nutritionally limited.

Collared lemmings versus brown lemmings

Collared lemmings and brown lemmings have been sympatric throughout much of the Arctic since the early Pleistocene (Guthrie & Matthews, 1971), yet there is a marked contrast between their rates of chromosomal

evolution (Gileva, 1983). Collared lemmings show a much greater rate of change than do brown lemmings. Like female-biased reproduction, rapid chromosomal evolution is associated with inbreeding, because the frequency of homogametic matings, hence the fixation of chromosomal mutations, is inversely related to the effective size of the gene pool. Thus, these two sympatric and superficially similar species differ drastically in the genetic structure of their populations: brown lemmings and their close relative the Norway lemming have normal sex determination and a slow rate of chromosomal and morphological evolution; collared lemmings have evolved more rapidly and maintain a female-biased system of sex determination. What ecological or behavioral characteristics can account for this contrast?

Collared lemmings are the only small over-wintering homeotherm at the highest latitudes. They are among the most morphologically specialized arvicolids (Rausch, 1980). Where they occur with brown lemmings, collared lemmings occupy high, well-drained ground, extending into rocky alpine situations, whereas brown lemmings inhabit wetter, sedge-dominated areas (Batzli et al., 1980). In winter, the higher areas inhabited by collared lemmings are wind-

swept, with dense shallow snow. Collared lemmings physiologically tolerate an ambient temperature of -40°C almost three times as long as brown lemmings (Ferguson & Folk, 1970). Fuller et al. (1975) indicate that on Banks Island, where both species are found, collared lemmings predominate in the north, whereas brown and collared lemmings are about equally abundant in the south. Possibly the distribution of brown lemmings is limited by their tolerance of cold, whereas collared lemmings are limited in their northerly distribution only by the extent of land.

Winter reproduction may be particularly crucial to collared lemmings because of the latitudes at which they occur. For example, Fuller et al. (1975) observed population declines in "at least five, and perhaps six, of seven summers" in high-arctic collared lemmings. They suggested that winter breeding "is indispensable for survival of high-arctic lemming populations." Collared lemmings are also exceptional among arvicolids in their ability to attain sexual maturity while exposed to short photoperiods (Hasler et al., 1976) and their tendency to grow larger when exposed to short photoperiods (Malcolm & Brooks, 1985).

Winter reproduction is also important in brown lemmings but it may be a marginal prospect. Breeding

intensity at Barrow, Alaska, varies more during winter than during summer, probably depending upon snowpack, temperature, and the availability and quality of food (Batzli et al., 1980). Winter reproduction may be an essential precursor to the cyclically high densities at Barrow, but in poor years little if any winter breeding occurs (MacLean et al., 1974). Thus, for collared lemmings to reproduce in winter at latitudes as high as ten degrees north of Barrow, they must have overcome some constraints that limit winter reproduction in brown lemmings.

Staying together for warmth

Sharing a nest with conspecifics is an obvious tactic for conserving warmth and moisture; the costs and benefits for small rodents have been reviewed by Madison (1984). Often, winter reproduction and aggregation are mutually exclusive, presumably because reproductive hormones produce aggressive behavior (West & Dublin, 1984). But a rodent that tolerates this conflict could exploit habitat that would otherwise be intolerably cold. Winter aggregation may afford a further advantage when combined with reproduction. Suppose that time away from the nest, and hence foraging area, are especially limited for a solitary female with a litter of sucklings, becuase her offspring

devolop homeothermy only at 10 to 12 days of age. In this case, her potential foraging area would be greater if other lemmings of homeothermic age were available to warm the litter.

For a small homeotherm in a polar environment, the advantages of dispersal and outbreeding may be outweighed by the advantages of aggregating. Winter reproduction and winter aggregation together could produce the degree of inbreeding necessary for the evolution of female-biased reproduction.

Wood lemmings

Wood lemmings inhabit boreal taiga. Thus, when wood lemmings are contrasted with sympatric arvicolids, the support for winter aggregation as a cause of aberrant sex determination is less compelling than for collared lemmings. Yet the advantages of aggregation to any homeotherm reproducing during cold winters are similar; the range of wood lemmings adjoins the range of collared lemmings and includes the frigid taiga of central Siberia.

For the collared lemmings of Umnak Island (Rausch & Rausch, 1972), female-biased reproduction persists following relaxed environmental constraints. Once a species has evolved more social breeding and female-biased

reproduction, reversion to the normal system could be selectively disadvantageous to individuals or to individual trait groups (Harvey et al., 1985; Nunney, 1985a and 1985b), in spite of the evolutionary reversibility of these particular genetic systems. If seasonal inbreeding and its concomitant mode of sex determination is an irreversible specialization, this might explain its present occurrence in the more primitive and seemingly less cold-specialized wood lemming.

Discussion

If winter aggregation combined with winter reproduction underlies viscous gene flow, and hence female-biased reproduction, lemmings conceived in the winter should, on average, have more homozygous loci than lemmings conceived following dispersal in the summer. Study of allozymes could test this prediction and also provide evidence relevant to two other hypotheses: (1) if inbreeding is cyclical, as first proposed by Stenseth (1978), then heterozygosity should vary with density; (2) if inbreeding is due to structured habitat (Stenseth, 1983), then spatially discrete kin groups should be observed.

If, as proposed here, the unique sex determining

mechanisms in collared and wood lemmings are by-products of adaptation to cold, then their evolutionary basis will not be certain until the population structures of collared, wood, and brown lemmings are studied in winter.

Chapter V

CONCLUSIONS

In Chapter II, I describe chromosomal variation in collared lemmings from northeastern Alaska. Breeding experiments with outbred animals showed X-linkage of the male-repressor and genotypic frequencies consistent with the hypothesis proposed for collared lemmings in Siberia (Gileva & Chebotar, 1979). Because the same sex ratios could be achieved by an autosomal dominant male-repressor, X-linkage in both collared and wood lemmings suggests homologous loci, with separate solutions to the problem of YY zygotes having evolved later.

A standard nomenclature for chromosome arms in *Dicrostonyx* was developed, and details of the northeastern Alaska karyotypes are compared to data in the literature. With some complexities, chromosomal variation in *Dicrostonyx* essentially represents a centric fusion/fission complex, or "Robertsonian fan" (Matthey, 1973). In such a complex, intersterility in crosses of individuals from distant localities may not indicate discrete barriers to gene flow. Thus, the proposed taxonomy (Honaki *et al*, 1982), in which *Dicrostonyx* was split into ten species,

seems premature (Also see Jarrell & Fredga, in press.).

In Chapter III, I show that the male bias in the captive colony was related to the loss of genetic variability associated with inbreeding. As homozygosity increased, first the male-repressor would have been lost; the alternative allele cannot be lost because it is always carried by males. Secondly, the arrangement of the karyotype, with about 4% of the autosomal chromatin fused to the X and Y chromosomes, assures heterozygosity in heterogametic individuals, all of whom would now (with the male-repressor lost) be males. Thus, a lethal in the autosomal arm of the X chromosome should affect females twice as often as males. Truly autosomal lethals, revealed by inbreeding, would result in reduced fecundity without affecting the sex ratio. Also, these would be eliminated more rapidly since they are more likely to occur homozygotically. This effect could account for the distortions from random segregation in collared lemmings described by Bull & Bulmer (1981) and by Gileva (1987).

Outbreeding females from this colony caused a normal 1:1 sex ratio. This shows that, indeed, the male-repressor was lost, and that outbred collared lemmings, thus defined as homozygous X^{o}, are capable of producing an even sex ratio.

If the fitness of natural populations is limited by inbreeding, such karyotypes may be adaptive because of the heterozygosity they impart. X/autosome fusions, which have twice evolved independently in *Dicrostonyx*, could be particularly favored in a species where some females (XY females), as well as all males, are heterogametic.

In Chapter IV, I challenge published models (Maynard-Smith & Stenseth, 1978; Stenseth & Maynard-Smith, 1978; Stenseth, 1983; Carothers, 1980) on the ultimate demographic parameters that select for female-biased reproduction in lemmings. I argue that the parameters that have been proposed do not distinguish collared lemmings and wood lemmings from other lemmings, nor from arvicoline rodents generally, all of which, so far as is known, have even natal sex ratios.

As an alternative, I propose that the probable necessity of winter aggregation, when combined with winter reproduction, may create the "viscous gene flow" (Hamilton, 1967), under which natural selection can favor female-biased reproduction.

In summary, the questions that drew me into this study were answered. Collared lemmings in Alaska share a common female-biased sex determining system with their congeners

in Siberia. The male-repressor is X-linked. The attachment of autosomal chromatin to the sex chromosomes can favor heterogametic genotypes when inbreeding depression limits fertility. Depending on the presence or absence of the male-repressor, this phenomenon might skew sex ratios from expectation in either direction. Thus it might explain the inconsistencies with Mendelian predictions of the male-repressor hypothesis observed in Gileva & Chebotar's (1979) data by Bull & Bulmer (1981) and by Gileva (1987). In fact, given the large autosome that is attached to the X chromosome in Gileva's lemmings, and their high degree of inbreeding, this effect must have occurred to some degree.

The male bias observed in inbred lemmings is a phenomenon that probably does not occur in nature. Nevertheless, it demanded explanation and it is a unique by-product of a particular chromosomal arrangement, which may well be adaptive under less intense inbreeding. There are few, if any, cases among vertebrates where the adaptive significance of a particular chromosomal arrangement has been shown.

Sewall Wright showed that, "the combination of partial isolation of subgroups with intergroup selection seems to provide the most favorable condition for evolutionary

advance" (Wright, 1940). Guthrie & Matthews (1971) indicated that, indeed, evolutionary advance in the lineage of collared lemmings has been notable:

> "The most spectacular evolutionary change occurred in the *Predicrostonyx-Dicrostonyx* lineage. It is one of the more rapid directional changes documented in mammalian evolution..."

Hamilton (1967) indicated that the "viscous gene flow" associated with a strongly structured population could favor the evolution of female-biased reproduction. Female-biased reproduction, the high degree of chromosomal variability, and even the rapid rate of morphological change, all imply small effective population size. In each of these factors, collared lemmings contrast with the largely sympatric "true" (Norway and brown) lemmings of the genus *Lemmus*. Relative deme size is clearly an intriguing problem in the biology of lemmings.

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