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UNIVERSITY OF ALBERTA

SERUM PROTEIN VARIATION AND SELECTION IN FLUCTUATING POPULATIONS OF CRICETID RODENTS

by

© Raymond P. Canham

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled 'Serum Protein Variation and Selection in Fluctuating Populations of Cricetid Rodents' submitted by Raymond P. Canham, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Intraspecific variation among the serum proteins of the deer mouse, Peromyscus maniculatus, and two species of red-backed mice, Clethrionomys rutilus and C. gapperi, was investigated by means of starch gel electrophoresis. Loci controlling the transferrins and albumins in each species and the alpha-2 globulins in red-backed mice were found to be polymorphic.

Populations of each species near Great Slave Lake were studied from 1966 to 1968. Relative "fitness" values were calculated for the transferrin and albumin phenotypes in each generation of P. maniculatus and C. gapperi sampled except the first. These values were obtained by comparing the observed phenotypic frequency with that expected on the basis of random mating in the previous generation. The "fitness" of the various phenotypes changed from one generation to the next.

"Fitness" changes related closely to changes in the density of the study populations. When survival was good and the population density increased, homozygotes appeared to be favoured. When survival was poor and the population density declined, the "fitness" of heterozygotes was higher. An intermediate situation prevailed in stationary populations at high or low density, when survival was moderate. It was concluded that survival is a selective process as far as the transferrins and albumins of these two species are concerned.

A model was put forward to account for the observed changes in "fitness" and density. It was proposed that inbreeding was responsible for the apparent homozygous advantage in increasing populations, and that inferior phenotypes were eliminated during the decline by normal environmental conditions.

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"The ecological problem of populations has to do with the numbers of animals and what determines these numbers. The genetical problem of populations has to do with the kind or kinds of animals and what determines kind. These two disciplines meet when the questions are asked, how does the kind of animal (i.e., genotype) influence the numbers and how does the number of animals influence the kind, i.e., the genetical composition of the population? These questions are as much ecological as they are genetical."

The Genetic Factor in Population Ecology. Birch, 1960.

Opposite. Aspen poplar and white spruce near Fort Providence, N.W.T.

INTRODUCTION

Fluctuations in population size

Few problems in ecology have received as much attention in the past 50 years as have the fairly regular fluctuations in the size of animal populations known as "population cycles". Of particular interest are the three- to four-year fluctuations in the number of small rodents and the nine- to ten-year fluctuations of snowshoe hares, grouse and ptarmigan. A variety of hypotheses, based on both theoretical considerations and the results of practical studies, has been put forward to account for these cyclic fluctuations.

Theories involving such factors as climatic change (Elton, 1929), the occurrence of epidemic disease (Dymond, 1947), variation in the level of predation (Thompson, 1955) and variation in the quality or quantity of the food supply (Braestrup, 1940; Pitelka, 1958) have generally been dismissed as incorrect or of limited application. No single factor or combination of factors has been universally implicated in the control of fluctuating populations.

Palmgren (1949) and Cole (1954) suggested that population cycles are the result of random fluctuations in environmental conditions. This theory was criticised by Rowan (1954), Siivonen (1954) and others on the grounds that many of the characteristics of population fluctuations are not indicative of randomness. The nine- to ten-year cycle, in particular, shows a degree of regularity and synchrony over large areas most unlikely to occur by chance (Butler, 1953), although the same may not always be true of short-term fluctuations.

Among the most recent hypotheses on cycle causes have been those concerning the self-regulation of population density. Christian (1950)

proposed that the stresses induced by intraspecific strife in dense populations, especially in late winter, coupled with the demands of the beginning of the breeding season, brought about the exhaustion of the adreno-pituitary system. The physiological derangement so induced was said to result in reduced reproductive success and increased mortality through infection, particularly among subordinate animals (Christian, 1961).

Criticisms of this theory were made on the grounds that many of the results in its support came from laboratory experiments involving populations of abnormally high density, and that studies involving natural populations often failed to show indications of intraspecific strife, but these points were resolved by Christian and Davis (1964). Although subsequent studies had resulted in some modification of the theory as originally proposed, Christian, Lloyd and Davis (1965) were able to review an impressive body of evidence in favour of a behavioural-endocrine feedback system able to regulate the size of mammalian populations, at least when other factors failed to do so.

An alternative theory involving the self-regulation of population density was put forward by Chitty (1960). It was proposed that indefinite increase in density might be prevented by a deterioration in the quality of a population resulting from a change in the nature and frequency of behavioural interactions and a subsequent increase in susceptibility to normal mortality factors such as bad weather and the onset of the breeding season.

An earlier proposal that the qualitative change in the population might involve an increase in the prevalence of hereditary haemolytic anaemia (Chitty, 1958) was rejected by Newson and Chitty (1962) in a study of declining populations of the field vole, Microtus agrestis. No evidence was found of an abnormal physiological condition sufficient to account for

the poor survival, growth and reproduction observed in the populations.

A change in the frequency of certain genotypes was predicted in a population undergoing a cyclic fluctuation, because selection in the initial stages of expansion would favour genotypes best fitted to local conditions, whereas in dense populations the selective advantage would be with those genotypes which suffered least from intraspecific contacts (Chitty, 1965). Some consequences of the hypothesis, and some evidence in its favour, were discussed by Chitty (1967).

One of the major differences between the hypotheses of Christian and Chitty is based upon the belief of the former that phenotypic changes alone are adequate to explain a population decline, whereas the latter asserts that the genetic make-up of a population must change throughout a fluctuation in numbers. Williamson (1958) claimed that only two studies had provided any satisfactory evidence that selection in natural populations changed with change in population size: those of Ford and Ford (1930) on the marsh fritillary butterfly, Melitaea aurinia, and Gershenson (1945) on the hamster, Cricetus cricetus. Subsequently, Krebs (1964) found annual changes in skull/body regressions in fluctuating populations of the brown lemming, Lemmus trimucronatus, but in this and other studies which demonstrated qualitative changes in such populations, it was not shown that the changes were definitely genetic in origin.

Before an adequate assessment can be made of the hypothesis put forward by Chitty (1960), further research into the behavioural and genetic aspects of population fluctuations will be required. As Birch (1960) and Ayala (1969) have pointed out, genetic constitution has too often been ignored in ecological studies, and it may be for this reason that little evidence has been found of an association between density and selection in natural populations.

Genetic variation in natural populations.

Ecological genetics has been defined by Ford (1964) as the study of "the adjustments and adaptations of wild populations to their environment". Although this field has a history of almost 50 years, almost all investigations of evolution in progress in natural populations have been concerned with an invertebrate species, and generally an insect species. Among the most notable studies have been those of Cain and Sheppard (1954) on banding in Cepaea nemoralis, Kettlewell (1958) on melanism in Biston betularia, and Dobzhansky (1961) on chromosomal inversions in Drosophila pseudoobscura. The few studies performed on a mammalian species other than man include those of Lewontin and Dunn (1960) on the T locus in Mus musculus, and Rasmussen (1964) on a blood group system in Peromyscus maniculatus.

All such studies have depended upon the existence of genetic polymorphism, "the occurrence together in the same habitat of two or more discontinuous forms of a species in such proportion that the rarest of them cannot be maintained merely by recurrent mutation" (Ford, 1940). The phenomenon has received a great deal of attention on both the theoretical and the practical level, and much of this work has been reviewed by Ford (1965). In a discussion of earlier research on enzyme polymorphisms in Drosophila pseudoobscura (Lewontin and Hubby, 1966), Lewontin (1967) concluded that virtually every locus in that species was polymorphic. The results of a similar study by Harris (1969) indicate that the same is probably true in man.

The introduction of starch gel electrophoresis (Smithies, 1955) and the use of appropriate histochemical techniques (Hunter and Markert, 1957) made possible the routine separation and comparison of enzymes and other proteins controlled by different loci and by different alleles at the same locus. Improved procedures which gave starch gel electrophoresis an increased resolving power (Poulik, 1957; Smithies, 1959a) and the development of poly-

acrylamide disc and slab electrophoresis (Ornstein, 1964; Raymond, 1964), encouraged a great proliferation of studies concerned with genetic polymorphism at the biochemical level, particularly in mammals and other vertebrates.

Despite the degree of intraspecific variation revealed by the technique, electrophoresis has not been extensively applied to the study of natural populations. Results of considerable interest have come from a number of population studies in which electrophoresis has been employed, however, including those of Lewontin and Hubby (1966) and Harris (1969) mentioned above. Others have indicated effective reproductive isolation in adjacent populations of the eider duck, Somateria mollissima (Milne and Robertson, 1965), and subdivision of the population into small breeding units in the house mouse, Mus musculus (Petras, 1967). In contrast a high degree of similarity has been demonstrated between widely separated populations of harp seal, Phoca groenlandica (Naevdal, 1965) and skipjack and yellowfin tunas, Katsuwonus pelamis and Thunnus albacares (Fujino and Kang, 1967, 1968). The value of such studies leaves little doubt that electrophoresis will become one of the most important techniques available to the ecological geneticist.

Selection in fluctuating populations.

Chitty (1965) postulated the existence of a genetically-controlled behavioural polymorphism in fluctuating populations which formed the basis of variation in the ability to survive and multiply despite intraspecific contacts. This concept was given some support by the finding of changes in aggressive behaviour in adult Peromyscus maniculatus which affected the survival and recruitment of juveniles during the breeding season (Sadleir, 1965). But a behavioural polymorphism would not appear a necessary pre-

requisite for a control mechanism of the type envisioned by Chitty. All genetic polymorphisms have a biochemical basis, but a biochemical polymorphism with an effect upon physiology rather than behaviour could perhaps be involved in population control, since it is the ability to tolerate social interactions rather than the ability to behave in an intolerable way which must be variable. However, no polymorphic locus could be regarded as part of a control mechanism for the cyclic fluctuation in a natural population until it was shown that intraspecific interactions brought about selection at that locus of sufficient magnitude to cause a typical decline from peak density and that genotypes selected against at high population density were favoured when the density was low.

This is not the aim of the present study. Rather, its object is the more humble one of testing the null hypothesis that the selective forces acting upon polymorphic loci do not change during the course of a population fluctuation. Naturally, rejection of the null hypothesis would not necessarily indicate that varying selection was a cause of density changes in a population.

The results of two recent studies of a similar nature (Semeonoff and Robertson, 1968; Tamarin and Krebs, 1969) will be considered in due course. The three studies share the distinction of using the technique of electrophoresis to examine polymorphic systems in natural fluctuating populations.

MATERIALS AND METHODS

Trapping locations and species.

Mice were trapped at 18 locations in western Canada (Figures 1-3) and two in the U.S.A. Apart from the major study area near Great Slave Lake, Northwest Territories, and those in British Columbia, the trapping locations have been given the name of the nearest town or village.

Three species were collected during the course of this study: the red-backed mice, Clethrionomys rutilus and C. gapperi, and the deer mouse, Peromyscus maniculatus. All three are rodents of the family Cricetidae, but Clethrionomys spp. belong to the subfamily Microtinae, whereas Peromyscus spp. belong to the Cricetinae (Hall and Kelson, 1959). The subspecies of the deer mouse and red-backed mice within whose range of distribution each trapping location is situated, according to Hall and Kelson (1959), are given in Table 1. Other species, including Microtus pennsylvanicus, Zapus hudsonius and Mus musculus, were occasionally captured but were not used in this study.

1. GREAT SLAVE LAKE, N.W.T. The study area is situated to the south-west of the lake, close to the Mackenzie River (Figure 1). The physiography of the region has been described by Fuller (1969), who conducted one of a number of concurrent studies in the area. Most of the trapping was performed within 5 miles of the Heart Lake Laboratory and within 2 miles of each bank of the Mackenzie River (in the forest adjacent to the highway), and on two islands in the river. Providence Island, opposite the village of Fort Providence, and Green Island, 1½ miles downstream, are both about 1 mile long with a fusiform shape and are separated from other land by at least 400 yards of fast-flowing river. In the vicinity of the laboratory, where the shallow soil barely covers a Devonian coral reef, the predominant tree is jack pine, Pinus banksiana. On the south bank of the Mackenzie River and on the islands the overstory is dominated by white spruce, Picea glauca, and aspen poplar, Populus tremuloides, the latter occurring chiefly in isolated

stands. Black spruce, Picea mariana, is common in some areas. On the north bank are found balsam poplar, Populus balsamifera, aspen poplar and young white spruce.

Two species of red-backed mice are found in the area, but they are not sympatric. C. gapperi is found to the southeast of the Kakisa River, which is about 100 yards wide, whereas C. rutilus is found to the northwest, on Providence Island and Green Island, and on the north bank of the Mackenzie River. The two species can be distinguished by dorsal coat colour (C. rutilus is rufous, C. gapperi is brown) and other pelage differences, and by certain skull characteristics (Hall and Kelson, 1959). P. maniculatus is found throughout the study area.

Trapping was carried out from the beginning of June until the first week in September in 1966 and 1967, and during the final six weeks of that period in 1968.

2. FORT SMITH, N.W.T. Trapping was performed 6 miles southeast of the town, at Mountain Portage, in a white spruce and aspen poplar forest during August, 1967.

3. MANNING, Alberta. Trapping was performed about 40 miles north of the town near Twin Lakes campsite in a white spruce forest in June 1967.

4. STEAMBOAT MOUNTAIN, B.C. Trapping was performed in June 1968 near Kledo Creek (mile 335, Alaska Highway) and Mill Creek (mile 363) in a forest of black and white spruce. These areas fall within range of distribution of C. gapperi, but are close to the boundary between C. gapperi and C. rutilus, near Summit Lake (mile 393).

5. TOAD RIVER, B.C. Trapping was performed in June 1968 at 115 Creek (mile 404, Alaska Highway), beside Muncho Lake (mile 462) and near Liard River (mile 496). These areas are close to the boundary between C. gapperi

and C. rutilus but within the range of distribution of C. rutilus. The forest in these locations is white spruce and aspen poplar, together with black spruce at 115 Creek.

6. WATINO, Alberta. Trapping was performed adjacent to the campsite near the village in a woodlot of aspen and balsam poplar in July 1967, and on three occasions during the summer of 1968.

7. HIGH PRAIRIE, Alberta. Trapping was performed near the campsite on the eastern edge of the town in a woodlot of balsam poplar in July 1967.

8. CALLING LAKE, Alberta. Trapping was performed in a white spruce and aspen forest 5 miles south of the town in November 1967. Traps were left in place during daylight hours only, and no specimens of P. maniculatus were captured.

9. FOX CREEK, Alberta. Trapping was performed 10 miles northeast of the town, near Iosegun Lake, in a white spruce forest in June 1967.

10. ST. ALBERT, Alberta. Trapping was performed in two woodlots of balsam poplar and young white spruce 5 miles east of the town in May and September 1968.

11. ELLERSLIE, Alberta. Woodlots of white spruce and balsam poplar west of the village were trapped during the summer of 1967. Trapping was not performed by the author.

12. LINDBROOK, Alberta. Trapping was performed in woodlots of aspen and balsam poplar beside Ministik Lake, 10 miles southwest of the village, in October 1966.

13. INLAND, Alberta. Trapping was performed in two woodlots of balsam poplar and white spruce 5 miles southeast of the village in May and July 1968.

14. WAINWRIGHT, Alberta. Trapping was performed in a woodlot of balsam poplar 7 miles west of the village in May 1968.

15. HINTON, Alberta. A white spruce forest 10 miles southwest of the

town was trapped in July 1967. Trapping was not performed by the author.

16. NORDEGG, Alberta. Trapping was performed in coniferous forest 15 miles southwest of the village, near Windy Point, in August 1967.

17. TURNER VALLEY, Alberta. Coniferous forest near the R.B. Miller Biological Station, 15 miles west of the town, was trapped in May 1968. Trapping was not performed by the author.

18. ELKWATER, Alberta. Trapping was performed in the Cypress Hills in a white spruce forest 15 miles east of the town, near Graburn Creek, in July 1968.

19. CASCADE, Montana. Deciduous woods 20 miles southwest of the town were trapped in August 1968. Trapping was not performed by the author.

20. GOTHIC, Colorado. Coniferous forest near the Rocky Mountain Biological Station at Gothic was trapped in August 1968. Trapping was not performed by the author.

Population density and survival of young.

Fuller (1969) made a detailed study of the density changes which occurred in the populations of deer mice and red-backed mice in the study area near Great Slave Lake from 1964 to 1967, and concluded that all three species showed evidence of undergoing cyclic fluctuations, although *Peromyscus* spp. are not usually considered to do so (Jameson, 1955; Terman, 1966). Populations of each species on sampling plots in the area increased from very low levels in 1964 to peak levels in 1966, with little summer mortality in 1965 or 1966. In 1967, after a late spring, populations of *P. maniculatus* and *C. gapperi* increased until the end of July and then declined to levels lower than those at the beginning of the breeding season. The proximate causes of the decline in population density were a decreased production of

young because of the shorter breeding season, and an increased mortality rate in the young, particularly among those born late in the summer. Overwintered animals survived about as well as in the previous year. Instead of declining in 1967, populations of C. rutilus continued to increase in density. However, by the spring of 1968 populations of this species had also declined, and during the following summer those of all three species increased little from low spring levels (Fuller, pers. comm.).

The populations studied by Fuller (1969) occupied plots situated between the Heart Lake Laboratory and the south bank of the Mackenzie River, adjacent to the highway. Trapping in this area in the present study, which was not designed to measure differences in population levels, essentially agreed with these results. The population decline in C. gapperi in 1967 appeared to be largely caused by mortality among the males born in that year. Less than a third of the C. gapperi born in 1967 and captured as young or overwintered animals were males, whereas in samples of those born in the previous two years, males constituted from half to two-thirds of the total. In 1968 a further decline in the population was indicated by the capture of twice as many overwintered animals as young of the year during the six-week trapping period at the end of the summer.

Trapping on Green Island revealed population changes in P. maniculatus and C. rutilus similar to those south of the Mackenzie River, except that trap success for P. maniculatus on the island before the population decline in 1967 (20.9% in traps set for three nights) was about three times as high as it had been during the same period in the previous year. But the populations on Providence Island and the north bank of the Mackenzie were out of phase with those on Green Island and south of the river. Too small a sample was collected prior to 1968 to give any indication of changes in population density, although trap success for both species was lower than in the other

areas before the population decline. In 1968, a high trap success indicated that no serious decline in the population had occurred in the previous year. Trap success was particularly high for C. rutilus on Providence Island (10.3% in traps set for three nights) and on both the island and the north bank of the river a large proportion of the animals captured were young of the year. In contrast, the survival of young P. maniculatus in these areas was probably only moderate, and the increase in population density small, since the proportion of young animals captured during the period of trapping in 1968 (73.0%) was similar to that in the same year in the other trapping areas (68.9%), and intermediate between the proportions in those areas in the corresponding periods of 1966 and 1967 (82.1% and 61.2% respectively.)

Because all populations in the Great Slave Lake area did not fluctuate in synchrony, the region was divided into two trapping zones. In zone A (south of the Mackenzie River and Green Island) populations of P. maniculatus and C. gapperi declined in the summer of 1967, and those of C. rutilus declined by the following spring. In zone B (Providence Island and the north bank of the river) populations of P. maniculatus and C. rutilus did not decline, but reached high densities in 1968. The changes in population density and survival of the young in the major study area are summarized in Table 2.

Only those deer mice and red-backed mice born at the beginning of the breeding season become mature in the year of their birth in the Great Slave Lake area, and very few mice survive two winters. Little difficulty was encountered in categorizing a captured animal as overwintered or young of the year when body length, weight, maturity and condition of the pelage were taken into consideration, and this was also true at most other trapping locations. But at St. Albert, where the breeding season began early in 1968, a large proportion of the young P. maniculatus became mature in their first summer and were almost indistinguishable from overwintered animals by autumn.

The population density of deer mice was high (26.7% trap success in three nights of trapping) in one woodlot in early May, by which time the breeding season was well under way. Trap success was similar in two woodlots in September, despite the fact that breeding was still in progress. Survival of the young born during the summer could have been only moderate.

At Watino in early July 1967, the population of deer mice was exceptionally dense. In one night 80 live-traps set over an area of less than 400 sq yards captured 46 P. maniculatus and 4 C. gapperi, a total trap success of 62.5% (Canham, 1969a). For other areas of central and northern Alberta in 1967, the mean trap success was about 4%.

Of the 26 young of the year captured at Watino, none weighed less than 12.0 g, although mice of less than 7.0 g were frequently captured in the traps, and none became mature during two months in captivity. Four overwintered males were autopsied within 3 days of their capture, and all had the flaccid, darkened testes typically found after the end of the breeding season. Testicular smears revealed no spermatozoa. Nine overwintered females autopsied a month later all had placental scars, but none were pregnant, and none produced a litter while in captivity, although breeding normally extends to the end of August in central Alberta. Reproduction had ceased, and the population had entered a declining phase. Trapping in the same and adjacent areas at Watino on three occasions in the summer of 1968 resulted in an overall trap success of 3.7%. Of the 24 mice captured, 23 were deer mice, of which ten had overwintered.

Deer mice were generally more common than red-backed mice among captured animals. However, only C. gapperi were captured at Calling Lake. Large numbers of red-backed mice had been seen in the area in late October, but snow had since fallen and no mice were seen on the day on which trapping was performed. Although the trap success (4.7%) was quite high for daytime

trapping, it was concluded that population density had declined in the previous two weeks.

At no other trapping location was an exceptionally high trap success recorded or an indication of the direction of change in population density obtained.

Trapping methods.

Sherman live-traps (H. B. Sherman, De Land, Florida), and occasionally Longworth live-traps (Longworth Scientific Instrument Co. Ltd., Abingdon, England), were set in the forest in late afternoon or evening, with 5-10 yards between traps. Each trap was baited with peanut butter, and a pellet of laboratory mouse food was added. From 50 to 250 traps were set at one time, in parallel rows of 20 to 25 traps, when conditions permitted, and one row was usually placed along the edge of the forest. The trap success for deer mice was particularly high within a forest but close to a grass verge, perhaps because such edges are preferred habitat, or perhaps because deer mice from the forest move onto verges at night to feed. Red-backed mice were seldom captured at the forest edge, except among piles of felled trees in cut-lines, but were frequently found in damp and shaded regions of the forest.

Traps were checked as early as possible in the morning, to avoid unnecessary deaths among the captured mice. Red-backed mice suffered a greater degree of mortality in the traps than deer mice, partly because of their greater water requirement, and partly because their activity pattern made them more liable to capture during daylight hours, and therefore to confinement for an entire night. Whenever possible trapping was suspended during periods of wet or cold weather, when trap-deaths were more frequent.

Captured mice were removed from the traps during the checking procedure and placed in cages for transportation to the laboratory or camp. Mice in a weakened condition were given water as soon as possible after removal from the traps. Unless all of the traps were to be taken up, the traps in which mice had been captured were generally rebaited and reset in their original position.

Traps were left in place for one, two or three nights before being rebaited and set elsewhere, and were not checked in the evenings of the second or third day unless trap success was relatively high in the preceeding morning. Once they had been taken up, traps were not reset in their original position until at least 4 months had elapsed.

Consequences of population sampling.

The removal of a sample of mice from a population of finite size must have an effect upon the density and make-up of the population, and therefore upon the size and make-up of subsequent samples taken from it. These effects are likely to be minimal if the original sample size is small in comparison to the size of the population, and if sufficient time elapses before subsequent sampling takes place.

When traps are left in place for a few days in a continuous forest, the effect of trapping on population density is probably negligible. Mice resident in neighbouring areas expand or modify their home ranges to repopulate the area trapped (Stickel, 1946) and neither the density nor make-up of the population is much modified for very long. The population in such a situation is, in effect, infinite in size. This can hardly be the case in a small woodlot, however. Removal of a sample may appreciably reduce population density, and allow mice which were previously vagrants to settle in

the area, and thus to change the make-up of the population.

At only two locations, Watino and St. Albert, were woodlots trapped on more than one occasion. In both cases the woodlots covered an area of several acres and trapping was performed on only a portion of them. Trap success in one St. Albert woodlot which had also been trapped 4 months earlier was almost identical to that in another nearby which was trapped simultaneously and for the first time.

There is some evidence that live-traps capture a larger proportion of the female mice present in a population than of the male mice (Stickel, 1946; Van Vleck, 1968), and there is no doubt that they sometimes fail to capture the very young mice which enter them. This need be of no concern in the present study. Of more importance is the fact that the genetic make-up of each sex or age category in the sample may not be the same as that in the population from which it was taken. Trap-shyness is a widely recognized phenomenon, and may allow a large proportion of the population under study to remain uncaptured, especially if trapping is performed for only a short period. As Bailey (1968) has pointed out, if the trapped animals are dominant, the properties ascribed to them may not apply to the rest of the population. Trap-deaths may also affect one group of animals more than another. Little can be done to remedy this situation, and it can only be hoped that errors introduced in this way are consistent from sample to sample.

Blood collection and treatment.

A blood sample was taken from each mouse, usually within two days of its capture. Following an intraperitoneal injection of 1 grain of pentobarbital ('Nembutal', Abbott Laboratories Ltd., Montreal) dissolved in 0.2 ml of buffered saline ('Bacto' hemagglutination buffer, Difco Laboratories,

Detroit), the mouse was sexed, weighed, and measured (total length and tail length) and classified as young of the year or overwintered. About 0.5 ml of blood (less from a small animal) was then taken from the right suborbital canthal sinus (Rasmussen and Koehn, 1966) by means of a heparinised blood collecting tube (Fisher Scientific Co., Montreal), as shown in Figure 4. At the end of this procedure, the eyelids were pulled together so that a clot did not form on the eyeball, and the mouse was toe-clipped for future identification if it was to be kept in captivity. Mice not required for breeding or other purposes were released at a distance from the study area after they had recovered from the effects of the drug, or were destroyed. It was frequently possible to obtain a blood sample from an animal which had died in a trap, or after removal from a trap, by opening the thoracic cavity and inserting the tip of a disposable pipette into the heart.

Cells and serum were separated within 30 min of collection by centrifuging the blood at 5000 g for 2 min and removing the serum with a pipette. The cells were discarded and the serum, in which there was seldom an indication of haemolysis, was stored in small plastic tubes ('Microfuge' tubes, Beckman Instruments Inc., Toronto) in a chest freezer at -40 C until needed for electrophoresis. When bleeding took place in a field camp or laboratory, serum samples were temporarily stored in a food freezer. Later the samples were transported frozen in a 7 litre Dewar flask ('Isotherm', Karlsruher Glastechnisches Werk, Mainz, Germany, available from Canadian Laboratories Supplies Ltd., Toronto) partly filled with carbon dioxide "snow" produced by inverting a cylinder of liquid CO_2 over the flask and opening the pressure valve. This procedure was repeated at intervals of about 12 hr so that the samples remained frozen continuously.

Electrophoretic techniques.

Electrophoresis is the means by which direct current and a suitable buffer are used to separate proteins with different net electrical charges. These molecular charges result from the charges on the individual amino acids of which the proteins are composed. All amino acids have both acidic (COO^-) and basic (NH_3^+) groups in their structure, and the net electrical charge on a protein depends on the proportions of these two types present and the proportions of each not neutralized. The latter depends upon the pH of the buffer in which the protein is dissolved. When the pH of the buffer equals the isoelectric point (pI) of the protein, the number of acidic and basic charges is equal, and the protein is electrically neutral. A buffer with a higher pH tends to neutralize the basic groups so that acidic groups predominate, giving the protein a net negative charge and causing the migration of the protein towards the anode in an electrical field. A buffer with a lower pH has the opposite effect. The rate of migration depends largely upon the size of the net charge, but some electrophoretic media, including starch and polyacrylamide gels, mechanically assist the separation of proteins by slowing down larger molecules relative to smaller ones.

Different forms of a polymorphic protein can be distinguished by electrophoresis, but only if their net electrical charges differ. A polymorphism is the result of an amino acid substitution in the protein molecule due to the mutation of a codon at the locus concerned. Most amino acids possess one acidic and one basic group, but some (aspartic acid and glutamic acid) have one basic and two acidic groups, while others (histidine, lysine and argenine) have one acidic and two basic groups. Because the majority of amino acids are similarly charged, only about 26% of amino acid substitutions result in a change in the net electrical charge on the molecule (Lewontin, 1967), and only these can be detected by electrophoresis. Therefore, a single

phenotype demonstrated by the process may represent more than one genotype.

In this study vertical starch gel electrophoresis (Smithies, 1959a) was used to examine the serum proteins of captured mice. The starch gel apparatus (Otto Hiller, Madison, Wisconsin), shown in operation in Figure 5, included a 32 cm x 12 cm x 6 mm starch gel tray with a cooling chamber on the lower surface, and a plastic cover with two slot-formers, 14 cm apart. Each slot-former produced 16 slots in the starch gel, and thus up to 32 samples could be examined on a single gel.

The buffer system used to examine the serum proteins was based upon the discontinuous system of Poulik (1957). The electrode buffer, with a pH of 8.6, was made up as follows:

Boric acid	11.80 g
Lithium hydroxide	2.40 g
Distilled water to 1000 ml	

The gel buffer, also at pH 8.6, was composed of 10% electrode buffer and 90% of the following:

Tris (hydroxymethyl) aminomethane	10.67 g
Citric acid	0.92 g
Distilled water to 1000 ml	

Before making a starch gel, the inside of the gel tray and the cover, including the slot formers, were lightly greased with mineral oil. The gel tray was placed horizontally, with its end plates in position. An appropriate amount (40-50 g, depending upon the batch) of 'Starch-Hydrolysed' (Connaught Medical Research Laboratories, Toronto) was mixed with 400 ml of gel buffer and heated on a 1500 w hot-plate in a 2 litre Pyrex conical flask with a side-arm until the viscosity of the fluid had fallen well below its initial maximum (Smithies, 1959b) and the first minute bubbles indicative of boiling appeared. The flask was shaken continuously during this operation so that the fluid remained homogeneous. A vacuum was then applied at the side-arm for 60 sec to remove air bubbles. The starch was poured into the gel tray,

the cover was lowered gently into position without trapping air bubbles, and weights were placed on top of the cover.

After the gel had been allowed to set for 2-3 hr, the cover was gently removed, and serum samples were inserted into the slots with a 1 ml syringe and number 27 needle. Molten petroleum jelly was then poured over each row of slots, and the surface of the gel was covered with 'Saran Wrap' plastic film to prevent dehydration of the gel. The end plates were removed and, with the aid of a plumb line, the gel tray was placed in a vertical position in one side of the lower electrode chamber, orientated so that one row of slots was near the top edge of the gel. Electrode buffer was poured into the same side of the lower chamber and into both sides of the upper chamber to a depth of 2 cm, and the same amount of 10% sodium chloride solution was poured into the empty side of the lower chamber. Wicks of chromatographic paper were placed in position as shown in Figure 5, the cathode was placed in the side of the upper electrode chamber farthest from the gel tray, and the anode was placed in the side of the lower chamber which contained sodium chloride solution.

Direct current of 400 v from a constant-voltage power supply ('Heathkit IP-17', Heath Co., Mississauga, Ontario) was applied to the gel, which was prevented from overheating by coolant at 2 C circulated through the gel tray by a refrigerated bath (Forma Scientific Co., Marietta, Ohio). The current passing through the system decreased from about 75 to 50 ma during the following 3½ hr, at the end of which time the power supply and refrigerated bath were turned off, and the starch gel tray was returned to the horizontal position. The electrode buffer was discarded, and the silver/silver chloride electrodes were interchanged in preparation for subsequent operation of the apparatus.

The 14 cm lengths of starch gel which had been anodal to each row of slots were removed from the tray, turned over so that the sides which had been

in contact with the cooling chamber were uppermost, and immersed for 4 minutes in a saturated and filtered solution of amido black 10B in methanol/water/glacial acetic acid (50/50/1 by volume). After staining in this manner, they were washed in several changes of the same solvent mixture throughout the following 12-24 hours. At the end of this period, bands of stained protein were clearly visible. A written record of the results of electrophoresis was made, and the portions of gel were labelled and photographed on 35 mm Kodak 'High Contrast Copy' film while immersed in the solvent mixture. They were then covered in 'Saran Wrap' and stored until the film had been successfully developed.

It was found necessary to dilute the serum of red-backed mice with an equal amount of distilled water before electrophoresis, because many of the serum proteins, and particularly the albumins, stained too heavily if this was not done. The albumins of deer mice were not always adequately resolved by mere dilution of the serum, and to distinguish between them it was found necessary to use the buffer system of Brown and Welser (1968). The electrode and gel buffer, which was found to have a pH of 7.0 rather than 6.7 as stated by the authors, was made up as follows:

Tris (hydroxymethyl) aminomethane	3.63 g
Boric acid	16.70 g
Tetrasodium ethylene diamine tetraacetic acid	1.23 g
Distilled water to 1000 ml	

A new technique was developed for examining the albumins in the sera of a large number of deer mice on a single starch gel (Canham, 1969b). Rather than applying undiluted serum to a single row of cuts made in the gel after it had set (Brown and Welser, 1968), the samples were applied to a series of 12 or more rows of cuts made at intervals of about 1 cm at the cathodal end of the gel. The rows of cuts were made one row at a time with a cutter consisting of a 12 cm blade which had been ground to form 16 teeth, 4.5 mm

wide and 3.0 mm apart. Undiluted serum was applied to the cut made by each tooth with a 1 ml syringe and number 27 needle, and any surplus was removed from the surface of the gel with the syringe. In this way, about 200 serum samples could be applied to a single starch gel. The application of so many samples took a considerable time, and regions of the gel other than the row to which samples were being applied at a given moment were covered by 'Saran Wrap' to prevent dehydration of the gel. Each row was sealed with molten petroleum jelly once the cuts in it had been filled with serum.

After loading the gel with serum samples, a direct current of 400 v was applied for 3½ hr in the normal manner. During electrophoresis, the albumins from the samples in each row of cuts passed through the cuts lying anodally to them without adverse effects. The anodal portion of the gel was sliced longitudinally with a gel slicer (Buchler Instruments, Fort Lee, New Jersey) before staining, because the clearest pattern of bands was usually obtained at the centre of the gel. Only the albumin bands were visible, because other proteins were present in such relatively small amounts. The position on the gel of the rows of cuts and of the stained albumin bands is shown in Figure 6.

Polymorphic proteins chosen for study.

Examination of starch gels on which had been separated the serum proteins of deer mice and red-backed mice captured at the trapping location near Great Slave Lake revealed a considerable amount of interspecific and intraspecific variation. Although many serum proteins in each species were obviously polymorphic, many stained faintly, and could not invariably be distinguished from the background stain. The transferrins and albumins of all three species and the alpha-2 globulins of red-backed mice were chosen for study because their high intensity of staining made them quite distinct from both the background and neighbouring proteins.

The transferrins were initially identified by the iron stain developed by Ornstein (no date). Immediately before use the following three solutions were mixed in the proportion 1/1/20 and poured over a starch gel on which serum proteins had been separated:

(a)	2,4-Dinitroso-1,3-napthalenediol (Eastman #9503)	50 mg
	Absolute ethanol to 20 ml	
(b)	Hydroquinone	2 g
	Absolute ethanol to 20 ml	
(c)	Sodium acetate trihydrate	64 g
	Glacial acetic acid	28 ml
	Distilled water to 400 ml	

Light green bands which appeared within a few minutes indicated the position of the transferrins. The albumins were identified by their anodal position on the starch gel and great intensity of staining relative to other serum proteins, and by the yellow colouration produced by reaction with hydroquinone after immersion of the gel in the iron stain for about an hour. The alpha-2 globulins were not identified, but their failure to stain with benzidine or o-dianisidine indicated that they were not haptoglobins (Smithies, 1959a). The name given to them implies only that their position on the starch gel after electrophoresis was the same as that of the similarly named proteins in human serum -- between the transferrins and albumins (Smithies, 1955).

According to recent research, transferrin has a molecular weight of about 76,000 in man and contains a single polypeptide chain composed of two similar halves, each with one binding site for ferric iron (Greene and Feeney, 1968). Transferrin is the iron-transporting protein, to which virtually all plasma iron is bound, and forms the link between storage tissue (in the liver and elsewhere) and immature red blood cells (Bearn and Parker, 1966). Iron transported by transferrin becomes a component not only of haemoglobin and

myoglobin, but also of enzymes such as catalase, succinic dehydrogenase and xanthine oxidase (Giblett, 1962). The transferrin molecule is thought to determine the fate of the iron it transports, since iron receptors on the surface of cells are specific for the protein (Fletcher and Huehns, 1968). Transferrin has been found to have the property of inhibiting viral synthesis in vitro, and in rats and mice a weak anti-bacterial effect has been demonstrated (Martin and Jandl, 1959).

Albumin is believed to have a molecular weight of between 65,000 and 69,000 in man and to contain a single polypeptide chain (Putnam, 1965). Albumin has a strong affinity for ions, particularly anions, and even nonionic substances, particularly those with a hydrophobic character. The protein may be able to reduce the concentration and buffer the activity of such substances by combining with them, and to transport both undesirable and desirable materials to sites of elimination and need. Albumin also plays an important part in the regulation of plasma volume and tissue fluid balance, being responsible for about 75% of the total colloid osmotic pressure of plasma (Foster, 1960).

The transferrin and albumin loci will be represented by the symbols Tf and Al respectively in this study. Braend (1965) proposed that two letters characterize each locus, and Ashton et al. (1967) suggested that they be italicised, except when referring to a particular phenotype. The symbol Trf has been used to represent the transferrin locus in a number of species, but is probably best restricted to use in Mus musculus, for which it was originally proposed by Cohen (1960) to prevent confusion with the tufted (tf) locus.

Matings and births in captivity.

In order to discover the modes of inheritance of the proteins chosen for study, adult mice of each species were kept paired in captivity, some-

times for more than a year, and were allowed to raise their litters. Pairings were generally made without regard to serum protein phenotype, and often involved mice of the same species from different trapping locations. Each pair was kept in a plastic cage (11½" x 7" x 5"), and the male was usually not removed after the birth of a litter. In many cases a pair produced a second litter about a month after the first. None of six pairings made between one individual from each of the Clethrionomys species captured near Great Slave Lake resulted in the production of a litter.

Young produced by pairs which mated in captivity, as well as by females pregnant at capture, were bled after they had reached the age of one month, and their serum was subjected to electrophoresis.

Throughout the summer of 1967, young born to deer mice from Great Slave Lake which became pregnant before capture or in captivity were weighed at intervals of from two to four days from birth until an age of 15 days. During this period each litter was kept with its mother in one of two lightproof enclosures at the Heart Lake Laboratory, each of which contained two 40 watt 'daylight' fluorescent tubes under the control of a timer. The two enclosures were illuminated for 20 hours and 4 hours per day respectively.

Growth rate in young rodents is dependent upon the season, and even the month, of birth (Schwarz et al., 1964), and might therefore be influenced by the relative lengths of the day and night during the period of growth. One of the aims of the experiment was to test the null hypothesis that rate of growth in young deer mice is not related to the light regime in which they develop. However, other aims, more closely related to the rest of the study, were to test the null hypotheses that the rate of growth in young deer mice is related to neither the serum protein phenotype of the mother, nor that of the young themselves.

RESULTS

Qualitative variations in serum proteins.

Transferrins of deer mice.

Six forms of transferrin, each producing a band with a different migration rate during starch gel electrophoresis, were identified in P. maniculatus and named G, H, J, L, M and Q, in order of decreasing rate of migration (Figure 7). The ten combinations of transferrin bands produced after electrophoresis of the sera of captured deer mice are shown on the starch gel in Figure 8. Each serum sample gave rise to either one or two transferrin bands. When two bands were present, the intensity of staining of each was about half that of a solitary band. Bands J and M were the only ones which ever occurred alone.

From two to four forms of transferrin were found in samples from each of 19 trapping locations at which deer mice were captured. The geographical distribution and relative frequency of the transferrins are given in Table 3. Only one form, J, was common to samples from all 19 locations, but another, M, was common to all samples of P. m. borealis, (locations 1-7 and 9-17), and P. m. osgoodi, (locations 18 and 19). Forms other than J and M were found only in southern and central locations, and were invariably present in a relatively low frequency. It is notable that L, the least frequent form of transferrin in P. m. osgoodi at Cascade, was found in P. m. borealis only at Turner Valley, the nearest trapping location within the range of distribution of the subspecies. Although this could be coincidental, it probably indicates that breeding has taken place between the two subspecies at the common border of their ranges in the foothills of the Rocky Mountains.

Whether any of the transferrins identified in deer mice in this study are identical in migration rate to those found by Rasmussen and Koehn (1966) in deer mice from northern Arizona is not known, because it has not been possible to obtain serum samples with which to make a comparison.

Albumins of deer mice.

Four forms of albumin, each producing a band with a different migration rate during starch gel electrophoresis, were identified in P. maniculatus and named I, J, M and P, in order of decreasing rate of migration (Figure 7). After prolonged storage of the serum, a faint, diffuse band was sometimes present in a position anodal to each original band, and was presumably indicative of molecular breakdown in the protein. A similar storage effect is seen in the albumins of cattle, Bos taurus and B. indicus (Ashton, 1964). The five combinations of albumin bands produced after electrophoresis of the sera of captured deer mice are shown on the starch gel in Figure 9. Each serum sample gave rise to either one or two albumin bands. When two bands were present, the intensity of staining of each was about half that of a solitary band. Bands J and M were the only ones which ever occurred alone.

From one to three forms of albumin were found in samples from each of the 19 trapping locations at which deer mice were captured. The geographical distribution and relative frequency of the albumins are given in Table 3. Only one form, M, was common to samples from all 19 locations, and was the most frequent in each. Form J was widespread in its occurrence, but was invariably present in a relatively low frequency.

From their rate of migration during starch gel electrophoresis and their frequency of occurrence the albumin bands named J and M appear to be idential to those found in other subspecies of P. maniculatus and named A and C respectively by Welser et al. (1965), and re-named 100 and 96 respect-

ively by Brown and Welser (1968). No other bands were identified in P. maniculatus by those authors, and Brown and Welser (1968) found that samples from forest-inhabiting populations from northern woodlands were monomorphic for Albumin 96, in contrast to the findings of the present study.

Transferrins of red-backed mice.

Four forms of transferrin, each producing a major band with a different migration rate during starch gel electrophoresis, were identified in C. gapperi and named J, K, M and P in order of decreasing rate of migration (Figure 7). Two of these forms, K and M, were the only ones identified in C. rutilus. Each major band usually had associated with it a minor band which migrated more rapidly. The minor band was present in both fresh and previously frozen sera. Occasionally a second minor band could be seen, stained more weakly than the first, and situated anodally to it. When forms K and M were both present in the serum, the minor band associated with band M was hidden by band K, which migrated to the same position and stained more heavily than usual.

Transferrin 'shadow' bands, migrating either more slowly or more quickly than the major band, have been previously reported in other species, including primates (Boyer and Young, 1960; Harris, Penington and Robson, 1960; Parker and Bearn, 1962b), cervids (Gahne and Rendel, 1961; McDougall and Lowe, 1968), three species of Microtus (Maurer, 1967), and the laboratory mouse (Cohen, 1960; Shreffler, 1960). In most species the significance of shadow bands is unknown. In man the transferrin shadow band slower than the major band represents that portion of transferrin which is combined with iron, whereas the major band is iron free (Yoshioka, Fujii and Ito, 1966). The addition of ferrous ammonium sulphate to serum causes the relative density

of staining of the two bands to change, the shadow band becoming more dense at the expense of the major band, until the latter disappears. The addition of ferrous ammonium sulphate to the serum of red-backed mice did not cause a change in the relative intensity of staining of the major and minor bands, and the presence of the latter is probably not related to the degree of saturation of the serum with iron.

Some of the combinations of transferrin bands produced after electrophoresis of the sera of captured red-backed mice are shown on the starch gel in Figure 10. Each serum sample gave rise to either one or two major transferrin bands. When two major bands were present, the intensity of staining of each was about half that of a solitary band. Major bands P and K in C. gapperi did not occur alone.

Two or three forms of transferrin were found in samples from each of 13 trapping locations at which C. gapperi was captured, and two forms were found in samples from both locations at which C. rutilus was taken. The geographical distribution and relative frequency of the transferrins are given in Table 3. Only one form, M, was common to samples of C. gapperi taken at all 13 trapping locations, but another, J, was common to all samples of C. g. athabascae, (locations 1-4 and 6-13). It is notable that K, the less frequent form of transferrin found in C. g. loringi in the Cypress Hills, (Elkwater), was found in C. g. athabascae only at Inland, the nearest trapping location to the Cypress Hills within the range of distribution of the subspecies. Although this could be coincidental, as presumably is the finding of a transferrin in the same position in C. rutilus, it probably indicates that breeding has taken place between the two subspecies, despite the doubts of Soper (1964) that they intergrade. A comparable situation was found among the transferrins of P. maniculatus.

Albumins of red-backed mice.

Four forms of albumin, each producing a major band with a different migration rate during starch gel electrophoresis, were identified in C. gapperi and named G, M, R and S in order of decreasing rate of migration (Figure 7). One of these forms, G, and one other, P, were the only forms identified in C. rutilus. Each major band invariably had associated with it a minor band which migrated less rapidly. The minor band was present in both fresh and previously frozen sera. When forms G and M were both present in the serum, the minor band associated with band G was hidden by band M, which migrated to the same position and stained more heavily than usual. Similarly, when forms M and S were present together, the minor band associated with band M was hidden by band S. Albumin shadow bands have been previously reported in the fowl, Gallus domesticus (McIndoe, 1962), and in cattle (Ashton, 1964), although in both cases the minor band was faster than the major.

The various combinations of albumin bands produced after electrophoresis of the sera of captured red-backed mice are shown on the starch gel in Figure 11. Each serum sample gave rise to either one or two major albumin bands. When two major bands were present, the intensity of staining of each was about half that of a solitary band. Major bands R and S did not occur alone.

From one to three forms of albumin were found in samples from each of the 13 trapping locations at which C. gapperi was captured, and two forms were found in samples from both of the locations at which C. rutilus was taken. The geographical distribution and relative frequency of the albumins are given in Table 3. Only one form, G, was common to samples C. gapperi taken at all 13 trapping locations, and other forms were generally present in a relatively low frequency.

Alpha-2 globulins of red-backed mice.

Seventeen alpha-2 globulins, each represented by a band which migrated to a position between the transferrins and the albumins during starch gel electrophoresis, were identified in C. gapperi and C. rutilus, and named with the letters E-L, N-T, V and X (Figure 7). Ten types were found only in C. gapperi, two were found only in C. rutilus and five were found in both species. Fourteen of the alpha-2 globulins present in C. gapperi sera are shown on the starch gel in Figure 12. Each serum sample produced from one to eight bands in the alpha-2 globulin region of the starch gel. There was a considerable variation in the intensity of staining of the alpha-2 globulin bands, both from band to band in the serum of a given individual, and for a given band in different sera. In several instances, serum was taken from an individual on more than one occasion. Although no new alpha-2 globulins were ever found in the second sample, the relative intensity of staining of those present was not always the same as in the first sample.

From three to 14 alpha-2 globulins were found in samples from each of the 14 trapping locations at which red-back mice were captured. The geographical distribution and relative frequency of the alpha-2 globulins are given in Table 4. Only one alpha-2 globulin, N, was common to samples of C. gapperi taken at each of the 13 trapping locations, but two others, I and K, were common to all samples of C. g. athabascae. It is apparent from Table 2 that there is a fairly sharp discontinuity in the distribution of alpha-2 globulins, samples from southern locations showing a greater variety of types than those from the north. In addition, the frequency of both types I and N differs appreciably between northern and southern locations, the former being more common in the north than in the south, and the latter showing the opposite tendency. The Fox Creek and Calling Lake trapping locations seem close to the region of change with respect to the alpha-2 globulins, and the only obvious

feature of the environment with which such changes might be correlated is the transition from predominantly coniferous forest in northern Alberta to predominantly deciduous forest in central and southern regions.

A considerable variation exists in the mean number of alpha-2 globulins possessed by individuals from the various trapping locations, and in the variance of the mean. Some of the cases of significant differences in the mean and in the variance, as shown by Student's t test and the F ratio respectively, are indicated in Table 2. In several instances there are significant differences between the mean values in adjacent trapping locations in southern regions, whereas the mean varies little over a wide area in the north. This may be a result of the continuity of the boreal forest and the discontinuity of southern woodlots, and of the mouse populations therein, or may reflect a greater change in environmental conditions per unit of distance in southern areas. Also of interest is the significant difference in the variance of the mean number of alpha-2 globulins per individual between samples of C. rutilus from Toad River and from Great Slave Lake, and between samples of C. gapperi from northern and central regions (as represented by the Fox Creek sample) and those from most southern regions. The apparent limitation on the number of alpha-2 globulins possessed by individuals from certain areas may indicate the existence of distinctive environmental conditions in those areas.

There is a remarkable similarity between the types of alpha-2 globulins found in the two species of red-backed mice from Great Slave Lake, and in their relative frequencies. The same five forms are present in both species. Because there is little contact between the two species, separated as they are by the Kakisa River, a probable explanation is that natural selection has acted in a similar manner on both, due to the similarity in their habitats and in their modes of existence. In contrast to the situation at the Kakisa

River border, the alpha-2 globulins in the two species at the border near Summit Lake, B.C. on the Alaska Highway, (trapping locations 4 and 5), differ appreciably, with only one form common to both. Although there is probably even less opportunity for contact between the two species at the Summit Lake border, the differences may be due to the different conditions to the east of the Rocky Mountains, where C. gapperi was sampled, and in the mountain valleys occupied by C. rutilus. The similarity of the alpha-2 globulin types found in C. gapperi to the east of Summit Lake and in both species near the Kakisa River may be a reflection of the environmental similarities of the two areas.

Variation in the alpha-2 globulins to the extent observed in red-backed mice does not appear to have been reported for other species.

Genetic control of the serum proteins.

Transferrins and albumins of deer mice and red-backed mice.

The phenotypic frequencies of the transferrins and albumins in litters are consistent with the hypothesis that each system is under the control of co-dominant alleles at a single autosomal locus in all three species (Table 5). Not all forms of transferrin and albumin in the three species are represented in these crosses.

One type of mating, that between deer mice both of the Tf JM phenotype, produced offspring whose phenotypic frequencies differed significantly in a chi-square test from those expected based on the above hypothesis, due to a deficiency of Tf JM offspring. There is no obvious explanation for this deficiency, especially since other matings involving Tf JM females did not

result in a significant deficiency of such offspring. This situation is not comparable to that in cattle in which antagonism between the mother and the embryo, when both possess a particular form of transferrin, causes a dearth of offspring with that form through early foetal mortality (Ashton, 1959).

The proposed mode of inheritance of transferrins and albumins is supported by the absence of individuals whose serum contained less than one or more than two forms of one of the proteins. In addition, a mixture of equal amounts of two serum samples which each contained a different single form of transferrin or albumin produced upon electrophoresis two less intensely stained bands, indistinguishable from those produced by serum which contained both forms of the protein. Furthermore, in litters of which only the phenotype of the mother was known, the offspring invariably possessed one form of transferrin and one albumin also possessed by the mother.

Under the proposed mechanism of inheritance, an individual whose serum gives rise to a single major transferrin band upon electrophoresis is homozygous at the locus controlling that protein, while a sample which produces two major bands indicates a heterozygous individual. The phenotype Tf J in the deer mouse, with a single transferrin, represents the presumed genotype $\underline{Tf^{J}}/\underline{Tf^{J}}$, with two similar alleles, while phenotype Tf JM, with two forms of transferrin, represents presumed genotype $\underline{Tf^{J}}/\underline{Tf^{M}}$, with dissimilar alleles. In the same way, albumin phenotype Al M denotes genotype $\underline{Al^{M}}/\underline{Al^{M}}$, one type of homozygote, and phenotype Al JM denotes genotype $\underline{Al^{J}}/\underline{Al^{M}}$, one of the heterozygotes. The same system operates at the transferrin and albumin loci in the red-backed mice. It should be noted again at this point that not all variation in protein structure is revealed by electrophoresis, and that any single phenotype may represent more than one genotype. Alleles at a given locus which result in the production of different forms of a protein with the same charge and electrophoretic mobility must be considered as one

in a study such as this.

Control of the transferrins by co-dominant alleles at a single autosomal locus has been indicated in all other species in which breeding data have been obtained, including man (Harris, Robson and Siniscalco, 1958; Smithies and Hiller, 1959), cattle (Ashton, 1958b), the red kangaroo, Megaleia rufa (Cooper, 1964), Microtus spp. (Maurer, 1967), and the laboratory mouse (Cohen, 1960; Shreffler, 1960), as well as in P. maniculatus from northern Arizona (Rasmussen and Koehn, 1966). This mode of inheritance has also been proposed for the transferrins of numerous other vertebrate species for which breeding data were not available. Control of the albumins by the same means has been indicated by breeding data in man (Melartin and Blumberg, 1966), cattle (Ashton, 1964), and Peromyscus spp. (Welser et al., 1965), and has been proposed for the albumins of several other species.

Alpha-2 globulins of red-backed mice.

Limited breeding data involving four of the alpha-2 globulins common to both species of red-backed mice indicates that each type is probably under the control of a different autosomal locus with two alleles, one of which results in the presence of the protein while the other results in its absence (Table 6). Thus the + phenotype, possessing a particular alpha-2 globulin, represents both the homozygous genotype +/+ and the heterozygote +/-, whereas the - phenotype, without the alpha-2 globulin, represents only the other homozygote, -/-. It seems probable that the other alpha-2 globulins are controlled in the same manner. That the alpha-2 globulins are not controlled by a number of alleles at a single locus is supported by the occurrence of more than two unrelated forms in the serum of an individual, and by variation in the intensity of staining of the bands resulting from those forms.

Control by co-dominant alleles at a single locus has been proposed for certain of the alpha globulins in man (Smithies and Walker, 1955; Fagerhol and Braend, 1965), domestic swine, Sus scrofa (Kristjansson, 1961), cattle (Ashton, 1963; Gahne, 1963), and horses, Equus caballus (Ashton, 1958c), although other alpha globulins in cattle and horses are probably each under the control of a locus with two alleles, one of which results in the absence of the protein (Ashton, 1958a, c).

The mode of inheritance of the alpha-2 globulins in red-backed mice does not permit these proteins to be used satisfactorily as biochemical markers in a study concerned primarily with changes in fitness at certain loci. Two of the three presumed genotypes at each locus could not be distinguished by electrophoresis. In addition, the change in relative frequency of the two phenotypes at each locus in two or more successive generations of red-backed mice at a single trapping location did not approach significance in any instance. Accordingly, the remainder of this study will be concerned only with the loci controlling the transferrins and albumins in deer mice and red-backed mice.

Treatment with neuraminidase.

The enzyme neuraminidase causes hydrolytic cleavage of the glycosidic bond joining the keto group of a sialic or neuraminic acid molecule to one of a number of sugars (Gottschalk, 1957). Stepwise removal of terminal sialic acid residues from a transferrin molecule results in new components with decreased electrophoretic mobilities, and the number of new bands produced during electrophoresis is indicative of the number of residues present on each molecule. Many of the transferrin variants in man have been resolved

by the action of neuraminidase into four additional slower-moving components whose relative intensities depend upon the concentration of the enzyme (Parker and Bearn, 1962a). Variations in sialic acid content are therefore not involved in the genetic variation of human transferrin.

The results of incubation with neuraminidase of serum from mice of known phenotype can be seen in Figure 13. Upon electrophoresis following incubation, each major transferrin band was replaced by three equally-spaced bands, one with the same migration rate as the original, and two with slower migration rates. This result was obtained with serum from both homozygous and heterozygous individuals of all three species. From the results of electrophoresis performed upon aliquots removed at six hour intervals, it was clear that the most rapid change occurred during the first 12 hours of incubation, and that little or no change occurred after 48 hours. The experiment was ended at 72 hours. Transferrins in control serum incubated for an equal period with only acetate buffer did not give rise to new components.

These results indicate that each transferrin molecule in deer mice and red-backed mice probably possesses two sialic acid residues, as do the transferrins of the chimpanzee, Pan sp., and other primates (Parker and Bearn, 1962a) and the domestic fowl (Williams, 1962). Although the experiment was not repeated with an increased concentration of neuraminidase, it is not likely that this would have resulted in the appearance of additional bands, indicative of a greater number of sialic acid residues per transferrin molecule. All new components produced appeared within 18 hours, and in the majority of cases the slowest migrating became the most intensely staining before the experiment had ended.

Because each transferrin gave rise to two new components, and was not reduced to one or more common forms, the basis of the transferrin polymorphism

in deer mice and red-backed mice cannot involve variations in the sialic acid content of a molecule identical in other respects. In all probability, the various forms of transferrin in each of the species are each the result of an amino acid substitution in the molecule due to the mutation of a codon at the transferrin locus, as appears to be the case in man (Howard, Wang and Sutton, 1968; Wang, Sutton and Riggs, 1968). If so, the forms might be expected to differ from each other by one or more units of charge, and the corresponding bands to be equidistant from each other. That this is not the case can be seen from Figures 7, 8 and 10. However, each sialic acid residue on the transferrin molecule represents one unit of charge, due to its single carboxyl group (Gottschalk, 1957), and from their distance apart in Figure 13 relative to the new components it appears that deer mouse transferrins G and M must differ by three charge units. The same applies to transferrins J and Q. Other forms, which appear to vary by other than a whole number of units, are presumably dissimilar in some other way. In the red-backed mice, bands K and M differ by a single unit of charge, and so do each major and minor band (Figure 13).

It is not possible to conclude with certainty whether or not the transferrin shadow bands in red-backed mice possess one more sialic acid residue than the major bands. If each new band seen after incubation with neuraminidase was accompanied by a shadow band, as would be expected if there were no sialic acid differences, the shadow bands would be obscured by the other bands present. However, the original shadow band could usually still be seen after neuraminidase treatment, and the intensity of staining relative to that of the major band appeared about the same as before incubation. It therefore seems probable that, as in cattle (Chen and Sutton, 1967), the shadow bands do not differ from the major bands with regard to sialic acid content. In the rabbit, Oryctolagus cuniculus, the shadow band

migrates more slowly than the major band in serum transferrin and possesses a single sialic acid residue, whereas the major band has two (Baker, Shaw and Morgan, 1968).

The basis of the albumin polymorphism in deer mice and red-backed mice has not been investigated, but there seems no reason to doubt that variant forms of albumin are each the result of an amino acid substitution in the albumin molecule.

Variations in phenotypic frequency and departures from Hardy-Weinberg equilibrium.

The observed phenotypic frequencies of the transferrins and albumins in samples of deer mice and red-backed mice of more than 50 individuals are presented in Table 7. It has not been considered necessary to note the many instances in which the phenotypic frequencies in samples from two trapping locations differ significantly. In order to simplify the situation, all major forms of a protein other than the most frequent in a sample have been considered the same as the form second most frequent. Thus the number of phenotypes and presumed genotypes at each locus has been reduced in the table to three. As can be seen from Table 1, the proportion of individuals involved in this adjustment is small in the samples concerned. Pooling in this manner merely imitates that which inevitably occrs when two alleles at a locus control the production of different forms of a protein with the same net charge.

The frequency of the allele, q, controlling the more slowly migrating form of protein, and the standard error, $(pq/2N)^{\frac{1}{2}}$, where p is the frequency of the other allele and N is the number of individuals in the sample, are given for each entry in the table. The allelic frequency of the transferrins

and albumins in each species indicates that these polymorphisms are balanced (Ford, 1965).

Phenotypic equilibrium values expected from the observed allelic frequencies on the basis of the Hardy-Weinberg Law (Hardy, 1908; Stern, 1943) were calculated by the exact method of Levene (Dobzhansky and Levene, 1948). This method gives the expected values

$$\frac{2pN(2pN-1)}{4N-2}, \qquad \frac{4pqN^2}{2N-1} \qquad \text{and} \qquad \frac{2qN(2qN-1)}{4N-2}$$

for one homozygote, the heterozygote and the other homozygote respectively. The observed and expected values are given in Table 5 as decimal fractions of the total.

The method of Dobzhansky and Levene (1948) has been used to test the agreement of the observed phenotypic frequencies with those expected from the Hardy-Weinberg Law. In this test, the hypothesis that the sample is from a population in Hardy-Weinberg equilibrium is rejected when t has a significantly small probability of occurring where

$$t = \frac{\text{Observed number of homozygotes - Expected number.}}{\text{Variance}^{\frac{1}{2}}}$$

$$\text{Variance} = \frac{1}{4N^2}\left\{(N+2)(A^2+B^2) + \frac{(2N+5)}{8N^2}(A^2+B^2)^2 - \frac{(N+2)}{2}(A^3+B^3)\right\} - \tfrac{1}{2},$$

where A = 2pN and B = 2qN.

A positive value of t indicates that more homozygotes were observed than were expected, whereas the opposite is true if the value of t is negative. The probability of the t value may be obtained from a table of the area in two tails of a normal curve if no prior expectation is made as to the outcome of the test (c.f. Dobzhansky and Levene, 1948).

It can be seen from Table 7 that the value of t usually falls between zero and -1.96, indicating an insignificant heterozygote excess ($P>0.05$) in the observed frequency of the phenotypes in comparison to the expected frequency.

An excess of heterozygotes, brought about by their greater fitness, might have been anticipated, since heterozygote advantage is the mechanism usually considered to operate most frequently in the maintenance of a polymorphism (Fisher, 1922; Wright, 1931; Ford, 1965). However, in one sample, that of P. maniculatus from Great Slave Lake, there is a significant deficiency of transferrin heterozygotes.

Each sample of mice represented in Table 7 is a mixture of two sexes and of at least two generations. Although most of the sample are too small to provide meaningful information when subdivided, some are worthy of further examination. These include the samples of each species taken at Great Slave Lake, and the samples of deer mice from St. Albert and Watino. Despite its small size, the Watino sample shows a heterozygote excess in the transferrins bordering on significance, and is the only sample other than that from Fort Providence composed of more than two generations.

In every instance in the following in which a sample is composed of animals taken from two or more distinct areas, or from the same area at different times, it may be assumed that the difference between the observed phenotypic and allelic frequencies in the subsamples is not significant, nor close to significance.

Transferrins and albumins of deer mice from Great Slave Lake.

The observed and expected phenotypic frequencies and the allelic frequencies at the transferrin and albumin loci in the samples of P. maniculatus from Great Slave Lake are subdivided on the basis of sex and age, and zone and year of capture, in Table 8.

The observed frequency of the transferrin phenotypes in the young deer mice of 1967 differs significantly from that in the overwintered animals trapped in the same year ($0.002<P<0.004$). In addition, the observed frequency

for all deer mice in the samples born before 1967 differs significantly from that of mice from the same zone born during 1967 and the following year ($0.0003<P<0.0005$). The difference is due to a large increase in the proportion of heterozygotes in the young of 1967 in comparison to the overwintered generation trapped in the same year and to both generations trapped in the previous year. In the juvenile females of 1967 the heterozygote excess is significant and the allelic frequency differs significantly from that in the overwintered females trapped in the same year. Only the overwintered males do not show an excess of heterozygotes in 1967, but instead show a significant heterozygote deficiency. In 1968 the proportion of heterozygotes is somewhat reduced in the overwintered animals in comparison with the young trapped in the previous year.

The observed phenotypic frequency at the transferrin locus in the sample of deer mice from zone A (Green Island and the region south of the Mackenzie River and Great Slave Lake) in 1968 differs significantly ($0.005<P<0.007$) from that in the sample from zone B (Providence Island and the region north of the Mackenzie River). A significantly different allelic frequency in the two zones, rather than a difference in the proportion of heterozygotes, accounts largely for this, although the juvenile females from zone B do show a significant heterozygote deficiency.

At the albumin locus phenotypic and allelic frequency differences were not of sufficient magnitude to be significant in the samples obtained.

Transferrins and albumins of red-backed mice from Great Slave Lake.

In Table 9 the entire C. rutilus sample captured at Great Slave Lake in each year has been pooled because of the number of sex and age categories which consist of only a single homozygous transferrin or albumin phenotype. The observed phenotypic frequencies in successive years do not differ sign-

ificantly from each other. The large sample collected in 1968 came almost entirely from zone B.

There is a significant difference ($0.01<P<0.03$) between the observed phenotypic frequencies of C. gapperi transferrins in 1966 and in 1968 (Table 9). This is due partly to an increase in the proportion of transferrin heterozygotes throughout the three years of the study, but mainly to a change in the allelic frequency over the same period, particularly in overwintered females.

Transferrins of deer mice from Watino and St. Albert.

The frequencies of the transferrins in deer mice from Watino and St. Albert are presented in Table 10. The phenotypic frequency of the Watino sample taken in 1967 differs significantly from that of the 1968 sample ($0.01<P<0.02$), despite the small size of the latter, due largely to the difference in the proportion of heterozygotes. There is a significant heterozygote excess in the young males from Watino in 1967, and in the overwintered females of the same year the excess is almost significant. In contrast, each category in the St. Albert sample shows an insignificant deficiency of heterozygotes, in one case bordering on significance.

The albumins in deer mice from Watino and St. Albert are not worthy of further consideration, because of the low frequency of one albumin allele in the sample from each location and the corresponding absence of this allele in a number of age and sex categories.

Conclusions drawn from a Hardy-Weinberg analysis.

To this point, it has been possible to show that observed phenotypic frequencies may differ significantly between successive samples, or between

categories within a sample, and that the frequencies observed are not always those which would be expected on the basis of the Hardy-Weinberg Law. It must now be acknowledged that a significant difference between the observed and the expected phenotypic frequencies in a sample, or in an entire population, does not allow any conclusions to be drawn concerning the selective events, if any, which brought about the observed frequency. As Wallace (1958) first pointed out, deviations between observed and expected frequencies give no indication of the survival values of the various phenotypes. The less fit of two homozygotes can appear to have the greater fitness, and heterozygotes can appear superior when there is actually strong selection against them. It is not difficult to see why this can occur. The proportions of the alleles present in a population at a given moment, and used to calculate an expected frequency, can give no indication of the proportions at any moment in the past. Instead, the expected frequency provides a prediction of the make-up of the next generation, should random and equally successful mating occur in the population before selection resulting in a change in the frequency of the alleles.

When observed and expected frequencies are compared, the product of the adaptive values of the homozygotes is tested against the square of the heterozygote fitness (Lewontin and Cockerham, 1959). An excess of heterozygotes will appear whenever the geometric mean of the fitness values of the two types of homozygote is less than the fitness of the heterozygote, and not only in the case of heterozygote advantage. However, in the absence of non-random mating, a significant difference between the observed and expected phenotypic frequencies is indicative of change in the population, and thus of the operation of natural selection. Furthermore, if the allelic frequencies in the population are at an equilibrium, deviations from the Hardy-Weinberg equilibrium allow the estimation of phenotypic fitness values.

Of particular interest in the results presented is the fact that there are cases of significant and nearly significant heterozygote deficiencies as well as excesses at the transferrin locus in P. maniculatus and C. gapperi. Selection appears to have varied in successive generations and, in some cases, at different periods in a single generation.

The nature of the changes that have occured in successive generations of deer mice and red-backed mice will be examined in more detail. Unfortunately, the data obtained for C. rutilus from Great Slave Lake are not suitable for the type of analysis to be employed, because of the low frequency of one allele at both the transferrin and albumin loci and the corresponding absence of these alleles in many age and sex categories. The remainder of this study will therefore deal only with the transferrin and albumin loci of P. maniculatus and C. gapperi.

Relative "fitness" of transferrin and albumin phenotypes.

In successive generations, relative "fitness" values have been calculated for the three transferrin and two albumin phenotypes commonly found in P. maniculatus and C. gapperi. These values provide a measure of the relative success of each phenotype in surviving, from conception until able to take part in reproduction in the case of overwintered animals and until the end of the breeding season in the case of the young, if certain assumptions are made. These assumptions will be discussed later. Values for fitness in the Darwinian sense -- success in leaving breeding progeny -- cannot be obtained in a study such as this, because selection may be only partially complete at any particular stage of development (Prout, 1965). The "fitness" values calculated for a given generation in fact involve a component of the Darwin-

ian fitness of the preceding generation. "Fitness" (or fitness, with quotation marks understood) will not imply Darwinian fitness when used in this study.

Relative "fitness" values have been found for the sex and age categories in each generation other than the first sampled at a trapping location by comparing the observed frequency of a phenotype with the expected phenotypic frequency calculated from the allelic frequency in each sex in the adult (overwintered) stage of the previous, parental generation. If p_m and p_f represent the frequency of the allele controlling the more rapidly migrating transferrin or albumin in the males and females of the parental generation respectively, and q_m and q_f represent the frequency of the other allele in the two sexes, then the expansion of $(p_m + q_m)(p_f + q_f)$ gives the expected frequency of the phenotypes in the following generation. Thus

$$p_m p_f, \qquad p_m q_f + p_f q_m \qquad \text{and} \qquad q_m q_f$$

are the expected proportions of homozygotes with the more rapidly migrating form of transferrin or albumin, heterozygotes and homozygotes with the other form of the protein, respectively.

In this calculation, taking into account the allelic frequency of males and females in the parental generation separately, rather than using the overall allelic frequency, avoids a bias equal to $\frac{1}{2}(q_m - q_f)^2$ towards underestimation of the proportion of heterozygotes expected in the young, if the frequency difference in the sample represents an actual population difference (Robertson, 1965). However, an equal bias in the opposite direction will result if the observed allelic frequency difference is due entirely to sampling error.

If the fitness of the most fit phenotype, in which (observed frequency/expected frequency) is greatest, is put equal to 1.0, as recommended by Crow

(1958), then the relative fitness of each of the other phenotypes equals

$$\frac{\text{Observed frequency}}{\text{Expected frequency}} \times \frac{\text{Expected frequency of most fit phenotype}}{\text{Observed frequency of most fit phenotype}}.$$

This value is invariably less than 1.0, and represents the fitness of a phenotype as a fraction of that of the most fit.

The minimum degree of inbreeding required to occur in a population for the heterozygote to be at least as fit as the more fit homozygote has also been calculated for each set of fitness values. Inbreeding reduces the apparent heterozygote fitness because fewer heterozygotes are produced than expected from the allelic frequency in the parental generation. Since the expected ratio of phenotypes with inbreeding is

$$p^2 + pqF \quad : \quad 2pq - 2pqF \quad : \quad q^2 + pqF,$$

where F is the inbreeding coefficient, it follows that

$$R = \frac{2pq - 2pqF}{q^2 + pqF} \quad \text{and} \quad F = \frac{2pq - Rq^2}{2pq + Rpq}$$

where R is (observed frequency of the heterozygote/observed frequency of the more fit homozygote).

Transferrins and albumins of P. maniculatus from Great Slave Lake.

Relative "fitness" values for the transferrin and albumin phenotypes in each sex and age category in P. maniculatus from Great Slave Lake are presented in Table 11 and in Figures 14 and 15.

The most outstanding feature of Figure 14 is the generally high fitness of the heterozygote, Tf JM, relative to the other phenotypes, in 1967 and its low relative fitness in other years. In the overwintered males of 1967, however, the fitness of the heterozygote is low, as in the young males of the previous year. In the overwinterd females of 1967 the high fitness of the heterozygote appears to be due to the poor winter survival of

homozygous phenotype Tf J. The other homozygous phenotype, Tf M, has a very low relative fitness in the young females of 1967 and in the overwintered females of 1968, a decrease in the fitness of the heterzygote being the only major change. In the males of the same generation, phenotypes Tf J and Tf JM both show a decrease in fitness over the winter. There is a great similarity between the young in zone A and those in zone B in 1968, as well as between the sexes in each zone, with regard to the relative fitness values of the various phenotypes.

There is a considerable difference between the relative fitness values of the albumin phenotypes in the generation born in 1966, in which the homozygote Al M is the more fit, and in those born in succeeding years, in which the heterozygote Al JM is generally superior (Figure 15).

These results must be regarded with caution, because in very few categories do the observed and expected phenotypic frequencies differ significantly (Table 11). Fitness values at the albumin locus are particularly subject to error, because small variations in the observed frequency of the phenotypes can cause large differences in their apparent relative fitness as a result of the very low frequency of one allele. At the expense of differences which almost certainly occur between the sexes and age-classes, it appears necessary to pool all samples in each generation. The effect of such pooling can be seen in Table 12 and Figure 16. In all but two instances (in the albumins) the observed and expected phenotypic frequencies differ significantly, or nearly so. In addition, among the transferrins the observed phenotypic frequency of the generation born in 1966 differs significantly from those of each of the following generations in zone A ($P<0.05$), and the phenotypic frequencies in 1968 in the two zones also differ significantly from each other.

In each generation, the homozygous phenotype Tf J appears the most

fit (Figure 16). Only in the generation born in 1967 is the fitness of the heterozygote high, and it is this generation which appears most different from the rest when fitness values of the transferrins are considered. In contrast, only in the previous generation is the fitness of A1 JM low, and there is little difference between the relative fitness values in the other generations. The fitness values of the transferrin phenotypes in the two zones in 1968 appear very similar despite the significant difference between the observed phenotypic frequencies.

The transferrin and albumin loci have also been considered together. The expected frequency of the six combinations of transferrin and albumin phenotypes regularly present has been calculated on the basis of the observed frequency of the phenotypes of each (Table 13). The close agreement between the observed and expected frequencies in every case indicates that there is little or no interaction between the two loci. Nothing new can therefore be expected to appear in a comparison of the observed frequency of the six phenotypes with that expected on the basis of the observed allelic frequency in the parental generation. This comparison has been made, however, and the result gives a more striking indication of the changes in relative fitness which occurred throughout the period of the study (Table 13 and Figure 17).

Both double homozygotes are more fit than the other phenotypes in the generation born in 1966, but in the following generations their relative fitness is greatly reduced. In the generation born in 1967, the double heterozygote and one other phenotype, Tf J/A1 JM, are most fit. In the following generation, in both zone A and zone B, the double heterozygote is less fit, whereas Tf J/A1 JM is more fit, relative to the other phenotypes. In both zones, one of the double homozygotes is the second most fit phenotype. The relative fitness values of the various phenotypes in the generation born in 1968 are similar in the two zones, and appear intermediate between the

extreme patterns of fitness in the generations born in 1966 and 1967.

Transferrins and albumins of C. gapperi from Great Slave Lake.

Relative "fitness" values for the transferrin and albumin phenotypes in each sex and age category in C. gapperi from Great Slave Lake are presented in Table 14 and Figures 18 and 19. Because of the small number of young captured in 1967, the young males and females of that year have been pooled with the sample of overwintered animals of the same sex taken in 1968.

In both transferrins and albumins, there is a general tendency for the heterozygote to become more fit relative to other phenotypes in successive generations (Figures 18 and 19). The relative fitness of the transferrin phenotypes in the two sexes differs considerably in the generations born in 1967 and in 1968. In the former, there appears to be little selection at the transferrin locus in males, whereas in females, there is strong selection against homozygote Tf J and the heterozygote. In the latter generation, although the fitness of each phenotype is again quite similar in males, the heterozygote in females is by far the most fit phenotype.

In the majority of cases in both transferrins and albumins the observed and expected phenotypic frequencies do not differ significantly (Table 14), and as in deer mice the albumin fitness values are particularly liable to error because of the very low frequency of one allele. The result of pooling within each generation can be seen in Table 15 and Figure 20. Despite pooling, only in the transferrins do the observed and expected phenotypic frequencies differ significantly in the majority of cases.

The increase in relative fitness of the heterozygote in both transferrins and albumins in successive generations is more clearly seen after pooling (Figure 20). Unfortunately, the deviations in the sex ratio in the

generations born in 1967 and 1968 cause the fitness values of females to dominate in one year, and the fitness values of males to dominate in the other.

The expected frequency of the six combinations of transferrin and albumin phenotypes regularly present has been calculated on the basis of the observed frequency of the phenotypes of each (Table 16). As in the deer mouse, no interaction between the transferrin and albumin loci is apparent. The observed frequency of the six phenotypes has also been compared to the frequency expected on the basis of the observed allelic frequency in the parental generation, and again the differences between successive generations aremore clearly revealed (Table 16 and Figure 21).

The relative fitness of the double heterozygote and of the Tf J/Al GM phenotype increases in successive generations. The most fit phenotype in the generations born in 1966 and 1967, one of the double homozygotes, is the least fit in the generation born in 1968. The relative fitness values of the phenotypes in the generations born in 1966 and 1967 appear somewhat similar, although those in the latter generation are intermediate in certain respects between the extreme patterns of fitness in the generations born in 1966 and 1968. This situation contrasts with that in the deer mouse, in which the generation born in 1968 is intermediate.

Transferrins of P. maniculatus from Watino and St. Albert.

Relative "fitness" values for the transferrin phenotypes in P. maniculatus from Watino and St. Albert are presented in Table 17. The sexes have been pooled in each age group from Watino, because of the small sample size. In only one instance does the difference between the observed and expected frequency approach significance.

At Watino, the heterozygote is the most fit phenotype in both age

categories of the generation born in 1967, and the homozygote Tf J is the least fit. In the following generation Tf J is the most fit phenotype.

At St. Albert in 1968, little selection is apparent at the transferrin locus. However, in both sexes homozygote Tf M is the most fit phenotype and the heterozygote is the least fit.

Variations in growth rate of deer mice.

An approximately linear growth rate was found in deer mice during the first two weeks after birth. The coefficient of regression of weight (in grams) with respect to age (in days) was calculated for each individual in each litter, and a mean value was found for the litter. Student's t test for the significance of the difference between sample means was used to test the regression coefficients of litters in between-litter comparisons, and the same test for the significance of the difference between paired samples was used to test the means of individual coefficients of regression in within-litter comparisons. The results of these tests are given in Table 18. In the between-litter tests, the difference in mean litter size was not significant in any instance other than the test involving small and large litters. Not all litters took part in tests involving the transferrin phenotype of the mother, because in a few instances this was not known. Tests involving the albumin phenotypes were not performed because of the small number of mothers and offspring which had a phenotype other than Al M.

The two light regimes in which litters were raised did not have a significantly different effect upon the growth rate of the young in the relatively small sample used in this experiment. Small litters, with from three to five young, were found to have a significantly higher growth rate than large litters, with six or seven young. However, most of this difference

was due to the difference between large and small litters born to mothers with the Tf JM phenotype, which was itself significant. Small litters from mothers with this phenotype had a growth rate almost significantly greater than small litters from mothers with the Tf M phenotype.

In within-litter comparisons, neither growth rates of male and female young nor those of young with the same and with a different transferrin phenotype from that of the mother were found to differ significantly. However, young with the Tf M phenotype were found to grow significantly faster than young with the Tf JM phenotype, whichever the phenotype of the mother.

DISCUSSION

Validity of the calculated "fitness" values.

The "fitness" values calculated for the various phenotypes in successive generations were said to provide a measure of the relative success of the phenotypes in surviving, from conception until able to breed in the case of overwintered animals, and until the end of the breeding season in the case of young of the year. In ascribing these values, the following assumptions were made:

1) The samples of overwintered and young of each sex collected in any year were representative of those categories in the population at the beginning and end of the breeding season respectively.

This is probably a close approximation to the truth, at least as far as the Great Slave Lake and St. Albert trapping locations are concerned, in that the majority of overwintered animals in the samples were taken early in the breeding season (except at Great Slave Lake in 1968) and the majority of young animals were taken near the end. But as previously pointed out, it is by no means certain that trapping yields a random sample of the population present at the moment of sampling.

2) The number of embryos conceived was not dependent upon the phenotype of the parents.

There were no significant differences between the mean sizes of litters born in captivity to parents of different phenotypes, or between the phenotypic frequencies of pregnant and non-pregnant females in the samples collected. It is therefore improbable that the sizes of litters at conception or the number of litters conceived depended upon the phenotype of the parents.

3) Mutations were random with respect to phenotype.

There is no reason to doubt that this was so, but even if it was not, a mutation rate similar to that in Mus musculus -- 0.8×10^{-5} mutations per locus per gamete (Russell, 1965) -- would be of little importance in a study such as this.

4) All mice categorized as young of the year were the offspring of overwintered animals.

Although the majority of mice in the Great Slave Lake region do not mature until the spring following their birth, a certain proportion of those born at the beginning of the breeding season mature towards the end of their first summer. This proportion is very small in deer mice, but larger in red-backed mice, in which young born in early June may mature and produce a litter in early or mid-August (Fuller, 1969). Their young are likely to become active and able to be trapped by the end of August or early September, and thus may have contributed to the young of the year taken during this period. The overall effect on the sample of young red-backed mice taken each year was undoubtedly slight.

None of the young deer mice captured at Watino in 1967 were mature at the time of capture, and none had become mature two months later. An autopsy performed at that time on a few of the larger individuals revealed minute testes or uteri typical of juvenile animals. Although no mature young were captured in 1968 at Watino, the sample collected was small.

The autumn sample of deer mice from St. Albert probably contained a large proportion of young whose parents were born in the same year, since many young born in the spring of 1968 became mature by the middle of the summer. If the allelic frequencies in the mature young differed from those in the overwintered animals, the inclusion of the offspring of the former

in the sample of young of the year might have resulted in the assignment of incorrect "fitness" values to the various phenotypes. Differences between the allelic and phenotypic frequencies in samples of mature and immature deer mice born in 1968 at St. Albert were very small, and thus the effect of overlapping generations was probably negligible in this instance.

5) Inbreeding did not occur in the populations under study.

This assumption is unquestionably false, and as a result, a major error may have been introduced into the calculations of "fitness" values. Inbreeding can involve both matings between related individuals, and subdivision of the population into separate breeding units with allelic frequency differences brought about by genetic drift (Wright, 1943). Either would cause an underestimation of the "fitness" of heterozygous phenotypes at the various loci, since the actual proportion of heterozygotes expected would be lower than that calculated (Li, 1955a).

In practice, a certain amount of inbreeding is bound to occur in a mouse population. The chances are higher that an individual will meet and mate with a relative than with an unrelated mouse, simply because the individual is unlikely to migrate an infinite distance away from its place of birth before mating. Furthermore, in this study the populations in each trapping zone at Great Slave Lake were composed of two or more subpopulations physically separated by either distance or the Mackenzie River, across which exchange of genetic material was undoubtedly negligible. However, the amount of inbreeding due to subdivision of the populations and subsequent genetic drift was probably quite small, since the allelic frequency of adults captured in each of the areas which were together regarded as a trapping zone did not differ appreciably. For instance, in overwintered deer mice the frequency of the allele responsible for the

slower transferrin band in the three major areas which constituted zone A (Heart Lake, the south bank of the Mackenzie River and Green Island) were 0.757, 0.739 and 0.633 respectively in 1967, the only year in which 15 or more overwintered animals were collected from each of these areas. This situation is in marked contrast to that found in woodlots around the northern outskirts of Edmonton, Alberta by D. A. Birdsall (pers. comm.). In many cases the frequency of alleles at loci controlling proteins in the serum of deer mice differed markedly in woodlots separated from each other by only a meadow or grain-field, or even a road.

The difference between the findings in the two studies may have been due to a difference in the intensity and type of selection operating in the two areas. In populations of deer mice at Great Slave Lake, selection may have overcome the effects of genetic drift, whereas near Edmonton it may not have done so. A comparison of the "fitness" values calculated for the transferrin phenotypes of young deer mice from Great Slave Lake and St. Albert (Tables 11 and 17) indicates that this may well have been the case. There appears to have been strong selection operating in the Great Slave Lake populations, and the less frequent homozygote was usually favoured over the more frequent. It is also possible that genetic drift is sufficiently small in populations which occupy a continuous forest, as a result of more extensive migration than is found between adjacent but separate woodlots, that isolation between subpopulations tends to break down. But although migration could explain the similar phenotypic and allelic frequencies found in populations of deer mice south of the Mackenzie River, it could hardly account for the similarity between the frequencies north of the river and on Providence Island in 1968 (Table 19).

An estimate of the coefficient of inbreeding in a population may

be obtained from the phenotypic frequency at a suitable polymorphic locus (Li and Horvitz, 1953), but only if there is an apparent heterozygote deficiency when the observed frequency is compared with the frequency expected on the basis of random association of gametes, and if it is assumed that selection for or against heterozygotes has not occurred at the locus concerned in the generation under study. By making this assumption, Rasmussen (1964) explained a significant heterozygous deficiency at a blood group locus in natural populations of P. m. gracilis. Selection against heterozygotes was ruled out as a possible explanation on the grounds that an unstable equilibrium at the locus would have resulted (Li, 1955b). Since this would be true only if the polymorphisms were maintained by heterozygous advantage, it seems unreasonable to dismiss the possibility of such selection so lightly. On the other hand, it is equally unreasonable to ignore inbreeding.

The effect of assuming that the study populations were panmictic has been to cause an underestimation of the "fitness" of heterozygous phenotypes. But the results may nevertheless be used comparatively if the error introduced into the calculations is a consistent one. It is therefore necessary to discover whether the inbreeding coefficient remained constant from generation to generation in the populations studied at Great Slave Lake.

Fuller (1969, per. comm.) found that the population density of overwintered C. gapperi at the beginning of the breeding season was higher in 1967 than in 1966, and lower in 1968 than in either of the previous two years. In P. maniculatus the density of overwintered mice was lower in 1967 than in 1966, and lower still in 1968. Since an individual mouse is likely to come into contact with more mice in years of high population density

than when density is low, the inbreeding coefficient is presumably inversely related to spring population levels.

From an examination of Figures 16 and 20, it can be seen that changes in the coefficient of inbreeding are not adequate to explain the observed changes in fitness at the various loci. A considerable decrease in the inbreeding coefficient (F) from 1966 to 1967, rather than the slight increase which probably occurred, would have been required to account for the observed increase in relative "fitness" of the transferrin and albumin heterozygotes in populations of P. maniculatus (Table 12). If the inbreeding coefficient did increase to some extent, the actual increase in fitness of each of the heterozygous phenotypes was correspondingly greater than it appeared. Similarly, an overall decrease rather than an increase in the inbreeding coefficient would have been required to account for the increase in relative "fitness" of the transferrin and albumin heterozygotes in C. gapperi during the course of the study (Table 15). It must therefore be concluded that the observed increases in the fitness of heterozygous phenotypes in the populations at Great Slave Lake cannot be explained on the basis of changes in the level of inbreeding.

Maintenance of the polymorphisms.

If permanent heterozygous advantage is assumed to be the mechanism by which the transferrin and albumin polymorphisms are maintained in populations of deer mice and red-backed mice, it must also be assumed that inbreeding is of a sufficient magnitude to counter those cases of apparent homozygous advantage found in this study. But there are many other ways by which a polymorphism can be maintained in a population (Williamson, 1958). One of these is frequency-dependent selection (Wright, 1948; Lew-

ontin, 1958) in which selective values depend upon the frequency of the alleles involved. Frequency-dependent selection is able to maintain a balanced polymorphism even in the face of frequency-independent selection against the heterozygote (Clarke and O'Donald, 1964).

Tobari and Kojima (1967) presented convincing evidence that frequency-dependent selection is responsible for the maintenance of three polymorphisms involving chromosomal inversions in Drosophila ananassae. When the frequency of an inversion homozygote in an experimental population was smaller than its equilibrium value, that homozygote was found to have a selective advantage over the other two inversion karyotypes. Selective differences among karyotypes diminished as frequencies of the inversions approached their equilibrium values. Similarly, Kojima and Yarbrough (1967) and Kojima and Tobari (1969) found that frequency-dependent selection is involved in the maintenance of polymorphisms at the alcohol dehydrogenase locus and an esterase locus in Drosophila melanogaster. When a homozygote at one of these loci was present in low frequency, its viability was enhanced, but when its frequency was high, viability was reduced. At equilibrium, selection was approximately neutral. In view of the very small segregational load imposed upon a population at or near the point of allelic equilibrium, the authors suggested that frequency-dependent selection may be part of the solution to the dilemma of explaining the observed degree of genic variability in natural populations without invoking intolerably large genetic loads to accompany maintenance of the polymorphisms by heterozygous advantage (Lewontin and Hubby, 1966).

There is some evidence that frequency-dependent selection was involved in the maintenance of the transferrin polymorphism in P. maniculatus populations at Great Slave Lake. Selection was not only variable, but also appeared to favour the less-frequent homozygous phenotype in each generation (Table 12).

Mechanism of selection for transferrin phenotypes.

Although the biochemical consequences of variations in the molecular structure of transferrins and albumins are unknown, it can be assumed that functional differences exist between the various forms of each protein, and result in the selective differences between phenotypes demonstrated in P. maniculatus and C. gapperi. In certain other species, the transferrin polymorphism is known to be responsible for population variation at the physiological level. Fertility in skipjack tuna (Fujino and Kang, 1967) and, in cattle, fertility, milk production and rate of gain in the young (Ashton, 1961; Ashton, Fallon and Sutherland, 1964; Fowle et al., 1967) are significantly influenced by the transferrin phenotype.

Between-litter and within-litter comparisons of growth rate regressions in deer mice (Table 18) have revealed that rate of growth in the young during the two week period following birth is dependent upon the size of the litter, the transferrin phenotype of the mother and the transferrin phenotype of the young themselves. Under the conditions of the experiment, the highest growth rate was found in Tf M young from small litters with Tf JM mothers. It may be speculated that in natural populations a high postnatal rate of growth is an advantage in certain years but not in others, or that relative growth rates of the transferrin phenotypes vary from year to year in response to changes in the environment. In the absence of experimental evidence, no firm conclusions can be drawn in this regard, but it is conceivable that differences in growth rate of the young form a basis for the observed changes in selection at the transferrin locus.

Density changes, survival and selection.

An examination of the population density changes in P. maniculatus

and C. gapperi at Great Slave Lake (Table 2) and the corresponding changes in selection at the transferrin and albumin loci (Figures 16 and 20) reveals a strong correlation between the level of survival in the population and the relative "fitness" values of the various phenotypes. In an increasing population, with good survival (both species, 1966), one or both of the homozygous phenotypes at each locus are favoured over the heterozygous phenotype. In a declining population, with poor survival (both species, 1967; C. gapperi, 1968), the relative "fitness" of heterozygotes is higher than during a period of increase. When survival is moderate, at either low or high population density (P. maniculatus, 1968, zones A and B respectively) the "fitness" values for the heterozygote and more frequent homozygote at the transferrin locus are about equal. When the decline essentially involves only one sex (males in C. gapperi, 1967), only in that sex are transferrin heterozygotes favoured (Figure 18). "Fitness" values in overwintered animals seem unaffected by density changes (Figures 14, 15, 18 and 19), although at the transferrin locus in P. maniculatus this applies only to males.

A change in the frequency of the transferrin phenotypes in P. maniculatus during the summer of 1967 coincides with the decline in the density of the population. The phenotypic frequency of the transferrins in the entire sample of deer mice captured before the end of July differs significantly from the frequency in the sample captured after the beginning of August (Table 19). This difference is not entirely due to a change in the proportion of overwintered animals to young of the year in the two samples. Furthermore, no such difference is apparent in the samples taken during the summer of 1966.

Selection at the albumin locus appears to relate less exactly to survival than that at the transferrin locus, at least in P. maniculatus,

although there is still a clear distinction between selection in an increasing population (1966) and that in declining or stationary populations (1967 and 1968). But as previously mentioned, the large difference between the frequency of the two albumin alleles in each species causes the "fitness" values calculated for the albumin phenotypes to be less reliable than those for the transferrins.

The correlation between survival and selection is particularly clear when the transferrin and albumin loci in each species are considered together (Figures 17 and 21). In P. maniculatus, the double homozygotes are the most "fit" in an expanding population (1966) and among the least "fit" during a decline (1967), when heterozygotes are favoured. An intermediate situation prevails in stationary populations (zones A and B, 1968), in which "fitness" values for the least frequent single heterozygote/single homozygote and the less frequent double homozygote are highest. In C. gapperi one of the double homozygotes is favoured in an expanding population (1966) whereas heterozygotes are favoured during a decline (1968). In a period of dissimilar survival rates in the two sexes (1967), differences between the relative "fitness" values of the phenotypes are less acute.

A similar relationship between survival and selection is also evident in deer mouse populations at Watino (Table 17). In a declining population (1967), the transferrin heterozygote is strongly favoured. Little change is apparent in the "fitness" of phenotypes among overwintered animals of the following year, but in the young, the heterozygote "fitness" is low and one of the homozygotes is favoured. In the stationary population of deer mice at St. Albert (Table 17), there is little difference between the "fitness" values of the three transferrin phenotypes.

Differences between relative "fitness" values in an increasing population may be more an illusion than a reality because of the influence

of inbreeding, which causes the "fitness" of heterozygous phenotypes to be underestimated in every generation. Selective differences between phenotypes may be quite small (and frequency-dependent) during a population increase, larger in a stationary population, and very large during a population decline, with heterozygous phenotypes favoured whenever survival is less than optimal. Changes in selection accompanying changes in survival may thus be as much quantitative as qualitative.

Results indicating that changes in allelic frequency are closely related to changes in density were also obtained in two previous studies performed on fluctuating rodent populations. Semeonoff and Robertson (1968) found that a decrease in population density in Microtus agrestis was related to an increase in the frequency of an esterase homozygote. Tamarin and Krebs (1969), in a study of frequency changes at the transferrin locus in two vole species, found that increasing density and survival was associated with an increase in the frequency of one allele in M. ochrogaster, and a decrease in the frequency of the same allele in M. pennsylvanicus. In each species there was an "increase" genotype (a homozygote in M. ochrogaster and the heterozygote in M. pennsylvanicus) which was selected for during increase and peak phases and against during the decline. It was concluded by the authors of each of these studies that the finding of frequency changes associated with density changes in the study populations lent support to the hypothesis of population control put forward by Chitty (1960).

The major conclusion of the present study is that changes in survival and population density from generation to generation in fluctuating populations of P. maniculatus and C. gapperi are accompanied by changes in selection at the transferrin and albumin loci. Survival in such populations is therefore a selective process as far as these two serum proteins are concerned.

Causes of changes in population density and survival.

Fuller (1969) found that population declines in P. maniculatus and C. gapperi at Great Slave Lake in the summer of 1967 were preceded in May by cold, wet weather and persistent snow cover. Delayed sexual maturation of overwintered animals, early cessation of breeding and poor survival in the young of the year were believed to have resulted from the adverse spring conditions. The declines in population density were thus attributed to an extrinsic factor -- weather -- acting through decreased recruitment, rather than to a density-dependent, intrinsic control mechanism.

In P. maniculatus the decline in population density (from 27 animals/hectare to 8 animals/hectare during a period of 3½ weeks) began in August, 1967, and reversed what appeared to be a typical population increase during the early summer (Fuller, 1969). If adverse spring conditions caused the decline, why should the population density have increased until August? There is some indication that the population increase in 1967 was not completely typical. Prior to the population decline, as well as after it, there was a greater proportion of transferrin heterozygotes in the sample of young P. maniculatus than in the sample of overwintered animals (Table 19). No such excess was found in samples taken in 1966. It therefore seems likely that summer survival was poorer in 1967 than in the previous year.

Populations of deer mice on Providence Island and the north bank of the Mackenzie River (zone B) did not decline in unison with those south of the river, studied by Fuller, and on Green Island (zone A). If the population decline in 1967 in zone A was brought about by adverse spring weather, why were the populations in zone B not similarly affected? It is possible that 1967 spring weather conditions were less severe on the north bank of the Mackenzie River and on Providence Island than south of the river and

on Green Island. However, in the absence of supporting evidence, it is unreasonable to assume that such a difference existed.

An alternative explanation for the anomaly is that the populations of deer mice in the two zones differed from each other in such a way that the spring weather of 1967 affected those in zone A to a much greater extent than those in zone B. But although this concept forms part of the hypothesis on the control of population density put forward by Chitty (1960), the difference in the response of populations in the two zones to adverse weather, as well as the selective changes which were observed in this study, can be explained without invoking a behavioural polymorphism.

The following model is proposed. As the population density in zone A increased from low levels in 1964, so did the number of intraspecific contacts and the amount of aggression in the population (Christian, 1950). Stresses thus induced were sufficiently aggravated by the cold, wet spring of 1967 that reproductive physiology was deranged throughout the population. Not only was the start of the breeding season delayed, but young were born and weaned in a weakened condition. Summer survival of the young was moderate, but cool autumn nights were sufficient to bring about a rapid decline in population density. Lack of intraspecific strife in the sparse populations of zone B enabled overwintered animals to reproduce successfully despite the adverse spring weather in 1967.

Inbreeding was largely or entirely responsible for the apparent superiority of transferrin and albumin homozygotes in zone A during the population increase. At this phase of the fluctuation, selection pressures were small, and less hardy phenotypes survived as well as the more hardy. During the decline, when only phenotypes highly adapted to the normal conditions of the environment survived, heterozygotes were favoured at most loci, including those controlling the transferrins and albumins, because the poss-

ession of two functionally different forms of a protein is normally more advantageous than the possession of a single form. However, at some loci homozygotes were favoured because of the inefficiency of the alternate form of the protein. Selection at the transferrin and albumin loci when survival was poor was thus part of a general phenomenon.

It is believed that in the year of the decline inferior phenotypes among the physically-weakened young were unable to withstand normal environmental conditions, and were eliminated from the population. This concept may be adequate to explain most instances of changing selection observed in fluctuating populations.

SUMMARY

1. Starch gel electrophoresis revealed a considerable amount of intraspecific variation among the serum proteins of Peromyscus maniculatus, Clethrionomys rutilus and C. gapperi captured at 20 locations in western Canada and the U.S.A. Among the transferrins and albumins of both deer mice and red-backed mice, certain forms are clearly widespread in their distribution, whereas others are limited. A great variety of alpha-2 globulins occurs in red-backed mice, especially in C. gapperi from central and southern Alberta. C. rutilus and C. gapperi from northern Canada possess only a few alpha-2 globulins, and most are common to both species.

2. Transferrins in each species are under the control of a single autosomal locus with several co-dominant alleles, each representing a different form of the protein. Albumins are controlled in a similar manner. Each alpha-2 globulin in red-backed mice appears to be controlled by a different autosomal locus with two alleles, one of which results in the absence of the protein. Neuraminidase treatment indicated that the transferrin polymorphism is not a result of variations in sialic acid content of the molecule.

3. A comparison between the observed frequencies of transferrin and albumin phenotypes in the larger samples of deer mice and red-backed mice and those expected on the basis of the Hardy-Weinberg Law, revealed that in several instances there was a significant or nearly significant excess or deficiency of heterozygotes. Observed and expected frequencies of transferrin phenotypes also differed significantly in some samples of deer mice and red-backed mice from the major study area near Great Slave Lake, N.W.T. and of deer mice from Watino and St. Albert, Alberta, subdivided on the basis of year of capture, sex and age at capture. Significant differences also occurred between the

observed frequencies in certain of these categories.

4. Relative "fitness" values were obtained for the various phenotypes in samples of P. maniculatus and C. gapperi by comparing the observed phenotypic frequencies with those expected on the basis of random mating in the overwintered animals of the previous generation. In many cases, the observed and expected frequencies, and thus the relative "fitness" of the various phenotypes differed significantly. Furthermore, the phenotypic "fitness" values changed considerably from one generation to the next. Changes in the level of inbreeding in the populations would have been inadequate to account for many of the changes in "fitness", but instead would have made them appear smaller than they actually were.

5. Differences in growth rate during the two weeks following birth in P. maniculatus indicated a possible basis for the selective differences between transferrin phenotypes.

6. Changes in relative "fitness" of the phenotypes were found to relate closely to changes in population density. In P. maniculatus and C. gapperi populations from Great Slave Lake, the "fitness" of transferrin and albumin homozygotes was high when survival was good and population density was increasing. In a declining population with poor survival, heterozygotes had a high relative "fitness". An intermediate situation prevailed in stationary populations at high or low density, when survival was moderate. It was concluded that survival is a selective process as far as the transferrins and albumins of these two species are concerned.

7. A model was put forward to account for the observed changes in relative "fitness" and density. It was proposed that inbreeding was responsible for

the apparent selective differences in increasing populations, and that in the year of the decline normal environmental conditions prevented the survival of inferior phenotypes among physically-weakened young.

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Table 1. - Subspecies of *P. maniculatus*, *C. rutilus* and *C. gapperi* at the trapping locations.

Location	*P. maniculatus*	*C. rutilus*	*C. gapperi*
5. Toad River	*borealis* Mearns	*dawsoni* (Merriam)	-
1. Gt. Slave Lake	*borealis* Mearns	*dawsoni* (Merriam)	*athabascae* (Preble)
2. Fort Smith	*borealis* Mearns	-	*athabascae* (Preble)
3. Manning	*borealis* Mearns	-	*athabascae* (Preble)
4. Steamboat Mtn.	*borealis* Mearns	-	*athabascae* (Preble)
6. Watino	*borealis* Mearns	-	*athabascae* (Preble)
7. High Prairie	*borealis* Mearns	-	*athabascae* (Preble)
8. Calling Lake	*borealis* Mearns+	-	*athabascae* (Preble)
9. Fox Creek	*borealis* Mearns	-	*athabascae* (Preble)
10. St. Albert	*borealis* Mearns	-	*athabascae* (Preble)
11. Ellerslie	*borealis* Mearns	-	*athabascae* (Preble)
12. Lindbrook	*borealis* Mearns	-	*athabascae* (Preble)
13. Inland	*borealis* Mearns	-	*athabascae* (Preble)+
14. Wainwright	*borealis* Mearns	-	*athabascae* (Preble)+
15. Hinton	*borealis* Mearns	-	*athabascae* (Preble)+
16. Nordegg	*borealis* Mearns	-	*athabascae* (Preble)+
17. Turner Valley	*borealis* Mearns	-	*loringi* (V. Bailey)
18. Elkwater	*osgoodi* Mearns	-	*loringi* (V. Bailey)+
19. Cascade	*osgoodi* Mearns	-	*galei* (Merriam)*
20. Gothic	*rufinus* (Merriam)	-	

+Not captured. *Not distinguished from other microtines (*Microtus* spp.) and not used in study.
Taxonomic information from Hall and Kelson (1959).

Table 2. - Density changes and summer survival of young *P. maniculatus*, *C. rutilus* and *C. gapperi* from Great Slave Lake.

Species	Zone A 1964	1965	1966	1967	1968	Zone B 1968
P. maniculatus						
Population density:	low	increase	increase	decline	low	high
Survival of young:	moderate	good	good	poor	moderate	moderate
C. rutilus						
Population density:	low	increase	increase	increase	low	increase
Survival of young:	moderate	good	good	good	moderate	good
C. gapperi						
Population density:	low	increase	increase	decline	decline	-
Survival of young:	moderate	good	good	poor (males only)	poor	-

Table 3. - Geographical distribution and frequency of occurrence of transferrins and albumins - P. maniculatus, C. rutilus and C. gapperi. Individuals possessing each form given as percentage of total.

Location	No.	P. maniculatus										Sp.	No.	Clethrionomys spp.								
		.....Transferrins.....						...Albumins...						..Transferrins..				.....Albumins.....				
		G	H	J	L	M	Q	I	J	M	P			J	K	M	P	G	M	P	R	S
5. Toad River	39	-	-	77	-	82	-	-	5	100	-	rut.	25	-	24	100	-	60	-	84	-	-
1. Gt. Slave L.	577	-	-	44	-	78	-	-	16	88	-	rut.	216	-	12	99	-	5	-	100	-	-
												gap.	196	78	-	73	-	99	19	-	-	1
2. Fort Smith	17	-	-	100	-	24	-	-	6	100	-	gap.	7	57	-	57	-	100	-	-	-	14
3. Manning	10	-	-	100	-	40	-	-	+	100	-	gap.	3	100	-	67	-	67	67	-	-	33
4. Steamboat M.	18	-	-	89	-	72	-	-	22	100	-	gap.	24	83	-	50	-	100	8	-	-	-
6. Watino	68	-	-	78	-	84	-	-	1	100	-	gap.	3	67	-	67	-	100	-	-	-	-
7. High Prairie	6	-	-	100	-	100	-	-	17	100	-	gap.	3	67	-	100	-	100	-	-	-	-
8. Calling Lake												gap.	7	100	-	71	-	100	71	-	-	-
9. Fox Creek	9	-	-	78	-	67	-	-	11	100	-	gap.	22	64	-	95	-	100	5	-	-	-
10. St. Albert	405	-	1	78	-	67	2	-	3	100	1	gap.	61	34	-	100	-	100	-	-	3	-
11. Ellerslie	32	-	-	88	-	66	-	-	3	100	-	gap.	34	38	-	100	-	100	9	-	3	-
12. Lindbrook	12	-	-	83	-	33	17	-	-	100	-	gap.	12	33	-	92	8	100	8	-	-	-
13. Inland	31	-	-	97	-	55	-	-	6	100	-	gap.	11	18	45	91	-	100	9	-	-	-
14. Wainwright	25	-	-	92	-	36	-	-	8	100	-											
15. Hinton	12	33	-	67	-	67	-	-	-	100	-											
16. Nordegg	20	-	-	85	-	35	-	-	5	100	-											
17. Turner Vall.	10	-	-	100	10	40	-	-	-	100	-											
18. Elkwater	54	-	-	100	-	7	-	-	9	100	-	gap.	8	-	38	100	-	100	38	-	-	-
19. Cascade	63	-	-	97	2	32	-	2	-	100	-											
20. Gothic	73	-	4	100	-	-	-	-	8	100	-											

+ = Absent in captured mice, but present in offspring from mating prior to capture.
- = Absent in captured mice and their offspring.

Table 4. Geographical distribution and frequency of occurrence of alpha-2 globulins - C. rutilus and C. gapperi. Individuals possessing each form given as percentage of total.

	Location	Sp.	No.	Alpha-2 globulins																Mean bands per animal + S.D.
				E	F	G	H	I	J	K	L	N	O	P	Q	R	S	T	V	X	
5.	Toad River	rut.	25	4	-	100	-	-	-	4	-	-	-	-	-	-	-	-	-	-	1.08^{a} 0.08^{a}
1.	Gt. Slave L.	rut.	216	-	1	-	-	98	1	93	-	6	-	-	-	-	-	-	-	-	2.00^{a} 0.14^{a}
		gap.	196	-	1	-	-	96	2	90	-	14	-	-	-	-	-	-	-	-	2.00^{b} 0.22
2.	Fort Smith	gap.	7	-	-	-	-	100	14	71	-	14	-	-	-	-	-	-	-	-	2.00 0.33
3.	Manning	gap.	3	-	-	-	-	100	-	100	-	+	-	-	-	-	-	-	-	-	2.00_{b} 0.33
4.	Steamboat M.	gap.	24	-	-	-	-	96	-	92	-	33	-	-	-	-	-	-	-	-	2.21^{b} 0.26
6.	Watino	gap.	3	-	-	-	-	100	-	100	-	33	-	-	-	-	-	-	-	-	2.33 0.33
7.	High Prairie	gap.	3	-	-	-	-	100	-	67	-	33	-	-	-	-	-	-	-	-	2.00 0.33
8.	Calling Lake	gap.	7	-	57	-	-	86	29	100	-	57	-	-	-	14	-	-	-	-	4.00^{c} 1.00_{b}
9.	Fox Creek	gap.	22	-	-	-	36	59	-	82	5	86	-	-	-	-	-	-	-	-	2.82^{c} 0.73^{b}
10.	St. Albert	gap.	61	-	-	-	20	39	3	90	-	97	11	16	5	23	-	11	15	20	3.05^{d} 1.41^{b}
11.	Ellerslie	gap.	34	-	-	-	6	29	12	68	12	85	21	68	15	47	6	15	32	18	4.29^{d} 1.71
12.	Lindbrook	gap.	12	-	-	-	-	42	17	75	8	75	17	75	-	17	-	58	67	17	4.67 1.70
13.	Inland	gap.	11	-	-	-	-	9	-	18	18	64	9	100	-	36	9	9	91	64	4.36^{e} 0.85
18.	Elkwater	gap.	8	-	-	-	-	-	-	-	13	50	-	75	-	63	25	25	-	-	2.50^{e} 1.71

+ = Absent in captured mice, but present in offspring from mating prior to capture.
- = Absent in captured mice and their offspring.
Values for 'mean bands per animal' with similar superscript differ significantly ($P<0.05$).
Squared values of standard deviations with similar superscript differ significantly ($P<0.05$).

Table 5. - Transferrin and albumin phenotypes of parents and offspring - *P. maniculatus*, *C. rutilus* and *C. gapperi*.

Parental phenotypes ♀	♂	Total litt.	Total young	Total young of each phenotype					Expected ratio*
P. maniculatus - Tf				GJ	GM	J	JM	M	
GJ	J	4	24	10	-	14	-	-	1:1
GM	JM	4	18	1	6	-	8	3	1:1:1:1
GM	M	1	5	-	1	-	-	4	1:1
J	JM	17	87	-	-	49	38	-	1:1
JM	J	11	48	-	-	20	28	-	1:1
JM	JM	17	91	-	-	24	35	32	1:2:1+
JM	M	7	41	-	-	-	24	17	1:1
M	JM	11	59	-	-	-	30	29	1:1
J	J	16	81	-	-	81	-	-	-
J	M	3	18	-	-	-	18	-	-
M	J	1	5	-	-	-	5	-	-
M	M	10	44	-	-	-	-	44	-
Total		102	521	11	7	188	186	129	-
P. maniculatus - Al				J		JM		M	
JM	M	6	30	-		12		18	1:1
M	JM	3	14	-		5		9	1:1
M	M	93	477	-		-		477	-
Total		102	521	-		17		504	-
C. rutilus - Tf				K		KM		M	
KM	M	1	4	-		2		2	1:1
M	M	3	8	-		-		8	-
Total		4	12	-		2		10	-
C. rutilus - Al				G		GP		P	
GP	G	2	7	4		3		-	1:1
GP	GP	1	4	-		2		2	1:2:1
P	G	1	1	-		1		-	-
Total		4	12	4		6		2	-
C. gapperi - Tf				J		JM		M	
JM	JM	7	37	12		18		7	1:2:1
J	M	1	6	-		6		-	-
M	J	2	9	-		9		-	-
Total		10	52	12		33		7	-
C. gapperi - Al				G		GM		M	
G	GM	3	14	9		5		-	1:1
G	G	7	38	38		-		-	-
Total		10	52	47		5		-	-

*Based on hypothesis of co-dominant alleles at a single autosomal locus.
+Observed frequency differs significantly from expected ($0.03<P<0.05$). In all other cases observed and expected frequencies do not differ significantly ($P<0.05$). Yates' correction applied where appropriate.

Table 6. - Alpha-2 globulin phenotypes of parents and offspring - C. rutilus and C. gapperi.

Band	Sp.	Parental phenotypes ♀	Parental phenotypes ♂	Total litters	Total young	Total young of each phenotype +	Total young of each phenotype -	Proposed genotype of + parent(s)*	Expected ratio*
I	rut.	+	+	4	12	12	..	+/+, and +/+ or +/-	...
I	gap.	+	+	5	26	26	..	+/+, and +/+ or +/-	...
I	gap.	+	+	2	9	7	2	+/- and +/-	3:1
I	gap.	+	-	1	6	6	..	+/+	...
I	gap.	-	+	2	11	11	..	+/+	...
J	gap.	-	+	3	14	5	9	+/-	1:1
J	gap.	-	-	7	38	..	38	...	...
K	rut.	+	+	1	4	4	..	+/+, and +/+ or +/-	...
K	rut.	+	-	3	8	8	..	+/+	...
K	gap.	+	+	5	26	26	..	+/+, and +/+ or +/-	...
K	gap.	+	-	3	14	14	..	+/+	...
K	gap.	+	-	1	6	3	3	+/-	1:1
K	gap.	-	+	1	6	3	3	+/-	1:1
N	gap.	+	+	2	12	10	2	+/- and +/-	3:1
N	gap.	+	-	4	20	10	10	+/-	1:1
N	gap.	-	-	4	20	..	20	...	...

*Based on hypothesis of two alleles at each locus, one of which results in the absence of the protein. In all cases observed and expected frequencies do not differ significantly ($P>0.05$).

Table 7. - Observed and expected phenotypic frequencies of transferrins and albumins - P. maniculatus, C. rutilus and C. gapperi.

Location	N	Observed freq.			Expected freq.#			t	q	S.E.
P. maniculatus-Tf		J	JM	M	J	JM	M			
1. Gt. Slave	508	0.112	0.386	0.502	0.093	0.424	0.483	+2.05*	0.694	0.014
6. Watino	68	0.162	0.618	0.221	0.220	0.502	0.278	-1.91	0.529	0.043
10.St. Albert	405	0.323	0.459	0.217	0.306	0.495	0.199	+1.45	0.447	0.017
18.Elkwater	54	0.926	0.074	0.000	0.928	0.071	0.002	-0.31	0.037	0.048
19.Cascade	63	0.667	0.302	0.032	0.667	0.301	0.032	-0.02	0.183	0.034
20.Gothic	73	0.959	0.041	0.000	0.959	0.041	0.000	-0.14	0.021	0.012
Others+	241	0.423	0.456	0.120	0.434	0.434	0.131	-0.80	0.349	0.022
Total+	1412	0.328	0.397	0.268	0.321	0.411	0.268	+1.28	0.474	0.009
P. Maniculatus-Al		J	JM	M	J	JM	M			
1. Gt. Slave	508	0.004	0.175	0.821	0.008	0.166	0.825	-1.19	0.908	0.009
6. Watino	68	0.000	0.015	0.985	0.000	0.015	0.985	0.00	0.993	0.007
10.St. Albert	405	0.000	0.040	0.960	0.000	0.039	0.961	-0.39	0.980	0.005
18.Elkwater	54	0.000	0.093	0.907	0.001	0.089	0.909	-0.29	0.954	0.027
19.Cascade	63	0.000	0.016	0.984	0.000	0.016	0.984	0.00	0.992	0.008
20.Gothic	73	0.000	0.082	0.918	0.002	0.079	0.919	-0.34	0.959	0.036
Others+	241	0.000	0.062	0.938	0.001	0.060	0.939	-0.39	0.969	0.008
Total+	1412	0.001	0.094	0.904	0.003	0.090	0.906	-1.36	0.951	0.004
C. rutilus - Tf		K	KM	M	K	KM	M			
1. Gt. Slave	216	0.000	0.046	0.954	0.000	0.045	0.954	-0.33	0.977	0.007
5. Toad River	25	0.000	0.240	0.760	0.009	0.221	0.769	-0.48	0.880	0.159
Total+	241	0.000	0.066	0.934	0.001	0.064	0.935	-0.58	0.967	0.008
C. rutilus - Al		G	GP	P	G	GP	P			
1. Gt. Slave	216	0.009	0.106	0.884	0.004	0.117	0.879	+1.40	0.938	0.012
5. Toad River	25	0.160	0.440	0.400	0.136	0.489	0.376	+0.51	0.620	0.217
Total+	241	0.025	0.141	0.834	0.017	0.156	0.827	+1.23	0.905	0.013
C. gapperi - Tf		J	JM	M	J	JM	M			
1. Gt. Slave	196	0.270	0.510	0.219	0.276	0.500	0.224	-0.29	0.474	0.025
10.St. Albert	61	0.000	0.344	0.656	0.029	0.287	0.684	-1.57	0.828	0.034
Others+	134	0.164	0.433	0.403	0.170	0.421	0.409	-0.33	0.619	0.030
Total+	391	0.192	0.458	0.350	0.201	0.440	0.359	-0.81	0.579	0.018
C. gapperi - Al		G	GM	M	G	GM	M			
1. Gt. Slave	196	0.801	0.194	0.005	0.806	0.184	0.010	-0.78	0.102	0.015
10.St. Albert	61	0.967	0.033	0.000	0.967	0.032	0.000	-0.09	0.016	0.012
Others+	134	0.851	0.142	0.007	0.856	0.131	0.013	-0.73	0.078	0.016
Total+	391	0.844	0.151	0.005	0.848	0.142	0.009	-1.06	0.081	0.010

#Based upon the Hardy-Weinberg Law.
+Observed and expected frequencies for samples summed.
*Value of t indicative of significant difference ($0.01<P<0.05$).

Table 8. - Observed and expected phenotypic frequencies of transferrins and albumins - P. maniculatus from Great Slave Lake.

Category	N	Observed freq.			Expected freq.#			t	q	S.E.
Transferrins		J	JM	M	J	JM	M			
Zone A										
0 ♂-1966	16	0.125	0.313	0.563	0.073	0.418	0.510	+1.04	0.719	0.079
0 ♀-1966	17	0.118	0.291	0.588	0.064	0.401	0.535	+1.14	0.735	0.076
Y ♂-1966	30	0.100	0.233	0.667	0.044	0.345	0.611	+1.82	0.783	0.053
Y ♀-1966	19	0.158	0.368	0.474	0.111	0.462	0.427	+0.90	0.658	0.077
Total+	82	0.122	0.293	0.585	0.071	0.395	0.534	+2.36*	0.732	0.035
Zone A										
0 ♂-1967	35	0.171	0.257	0.571	0.087	0.426	0.487	+2.38*	0.700	0.055
0 ♀-1967	40	0.050	0.400	0.550	0.060	0.380	0.560	-0.34	0.750	0.048
Y ♂-1967	30	0.067	0.500	0.433	0.097	0.440	0.463	-0.76	0.683	0.060
Y ♀-1967	25	0.160	0.760	0.080	0.286	0.507	0.206	-2.52*	0.460	0.070
Total+	130	0.108	0.454	0.438	0.108	0.454	0.438	-0.17	0.665	0.029
Zone A										
0 ♂-1968	23	0.000	0.391	0.609	0.035	0.322	0.643	-1.08	0.804	0.058
0 ♀-1968	15	0.267	0.400	0.333	0.209	0.515	0.276	+0.88	0.533	0.091
Y ♂-1968	40	0.150	0.400	0.450	0.120	0.461	0.420	+0.84	0.650	0.053
Y ♀-1968	44	0.205	0.523	0.273	0.214	0.503	0.283	-0.26	0.534	0.053
Total+	122	0.156	0.443	0.402	0.141	0.472	0.387	+0.68	0.623	0.031
Zone B										
0 ♂-1968	21	0.048	0.476	0.476	0.077	0.418	0.505	-0.65	0.714	0.070
0 ♀-1968	26	0.000	0.269	0.731	0.016	0.238	0.747	-0.72	0.865	0.047
Y ♂-1968	64	0.094	0.375	0.531	0.078	0.408	0.515	+0.64	0.719	0.040
Y ♀-1968	63	0.111	0.286	0.603	0.063	0.382	0.555	+2.02*	0.746	0.039
Total+	174	0.080	0.339	0.580	0.062	0.376	0.562	+1.30	0.750	0.023
Albumins		J	JM	M	J	JM	M			
Zone A										
0 ♂-1966	16	0.063	0.313	0.625	0.043	0.353	0.605	+0.48	0.781	0.073
0 ♀-1966	17	0.000	0.294	0.706	0.018	0.258	0.724	-0.61	0.853	0.061
Y ♂-1966	30	0.000	0.133	0.867	0.003	0.127	0.870	-0.33	0.933	0.032
Y ♀-1966	19	0.053	0.158	0.789	0.014	0.235	0.751	+1.54	0.868	0.054
Total+	82	0.024	0.207	0.768	0.016	0.225	0.760	+0.71	0.872	0.026
Zone A										
0 ♂-1967	35	0.000	0.171	0.829	0.006	0.159	0.835	-0.50	0.914	0.033
0 ♀-1967	40	0.000	0.125	0.875	0.003	0.119	0.878	-0.37	0.938	0.027
Y ♂-1967	30	0.000	0.200	0.800	0.008	0.183	0.808	-0.54	0.900	0.039
Y ♀-1967	25	0.000	0.240	0.760	0.012	0.216	0.772	-0.61	0.880	0.046
Total+	130	0.000	0.177	0.823	0.008	0.162	0.831	-1.08	0.912	0.018
Zone A										
0 ♂-1968	23	0.000	0.087	0.913	0.001	0.085	0.914	-0.15	0.957	0.030
0 ♀-1968	15	0.000	0.267	0.733	0.014	0.239	0.747	-0.49	0.867	0.062
Y ♂-1968	40	0.000	0.175	0.825	0.007	0.162	0.832	-0.55	0.913	0.032
Y ♀-1968	44	0.000	0.295	0.705	0.020	0.255	0.725	-1.09	0.852	0.038
Total+	122	0.000	0.213	0.787	0.011	0.191	0.798	-1.29	0.893	0.020
Zone B										
0 ♂-1968	21	0.000	0.048	0.952	0.000	0.048	0.952	0.00	0.976	0.024
0 ♀-1968	26	0.000	0.231	0.769	0.011	0.208	0.780	-0.59	0.885	0.044
Y ♂-1968	64	0.000	0.063	0.938	0.001	0.061	0.938	-0.22	0.969	0.015
Y ♀-1968	63	0.000	0.190	0.810	0.008	0.174	0.818	-0.79	0.905	0.026
Total+	174	0.000	0.132	0.868	0.004	0.124	0.872	-0.91	0.934	0.013

0 = Overwintered animals. Y = Young of the year.

#Based upon the Hardy-Weinberg Law.

+Expected frequency calculated from total observed.

*Value of t indicative of significant difference ($0.01<P<0.05$).

Table 9. - Observed and expected phenotypic frequencies of transferrins and albumins - C. rutilus and C. gapperi from Great Slave Lake. 90

Category	N	Observed freq.			Expected freq.#			t	q	S.E.
C. rutilus - Tf		K	KM	M	K	KM	M			
1966	33	0.000	0.091	0.909	0.002	0.088	0.911	-0.22	0.955	0.026
1967	32	0.000	0.031	0.969	0.000	0.031	0.969	0.00	0.984	0.016
1968	151	0.000	0.040	0.960	0.000	0.039	0.961	-0.27	0.980	0.008
C. rutilus - Al		G	GP	P	G	GP	P			
1966	33	0.000	0.061	0.939	0.000	0.060	0.940	-0.12	0.970	0.021
1967	32	0.031	0.250	0.719	0.022	0.268	0.710	+0.39	0.844	0.045
1968	151	0.007	0.086	0.907	0.002	0.095	0.903	+1.15	0.950	0.013
C. gapperi - Tf		J	JM	M	J	JM	M			
0♂-1966	7	0.429	0.286	0.286	0.307	0.527	0.164	+1.27	0.429	0.132
0♀-1966	13	0.615	0.385	0.000	0.646	0.323	0.031	-0.73	0.192	0.077
Y♂-1966	12	0.333	0.500	0.167	0.330	0.508	0.163	+0.05	0.417	0.101
Y♀-1966	15	0.267	0.467	0.267	0.241	0.517	0.241	+0.39	0.500	0.091
Total+	47	0.404	0.426	0.170	0.378	0.478	0.144	+0.75	0.383	0.050
0♂-1967	40	0.275	0.575	0.150	0.313	0.499	0.188	-0.98	0.438	0.055
0♀-1967	14	0.357	0.429	0.214	0.317	0.508	0.174	+0.60	0.429	0.094
Y♂-1967	2	0.500	0.500	0.000	0.500	0.500	0.000	0.00	0.250	0.217
Y♀-1967	6	0.167	0.500	0.333	0.152	0.530	0.318	+0.15	0.583	0.142
Total+	62	0.290	0.532	0.177	0.308	0.498	0.195	-0.55	0.444	0.045
0♂-1968	14	0.286	0.500	0.214	0.278	0.516	0.206	+0.12	0.464	0.094
0♀-1968	38	0.132	0.500	0.368	0.142	0.478	0.379	-0.28	0.618	0.056
Y♂-1968	26	0.231	0.539	0.231	0.245	0.510	0.245	-0.29	0.500	0.069
Y♀-1968	9	0.111	0.778	0.111	0.236	0.529	0.236	-1.45	0.500	0.118
Total+	87	0.184	0.540	0.276	0.205	0.499	0.297	-0.78	0.546	0.038
C. gapperi - Al		G	GM	M	G	GM	M			
0♂-1966	7	1.000	0.000	0.000	1.000	0.000	0.000	0.00	0.000	0.000
0♀-1966	13	0.615	0.308	0.077	0.585	0.369	0.046	+0.63	0.231	0.083
Y♂-1966	12	0.833	0.167	0.000	0.833	0.167	0.003	-0.20	0.083	0.056
Y♀-1966	15	0.867	0.133	0.000	0.867	0.129	0.002	-0.18	0.067	0.046
Total+	47	0.809	0.170	0.021	0.797	0.192	0.010	+0.82	0.106	0.032
0♂-1967	40	0.825	0.175	0.000	0.832	0.162	0.007	-0.47	0.088	0.032
0♀-1967	14	0.857	0.143	0.000	0.860	0.138	0.003	-0.19	0.071	0.049
Y♂-1967	2	1.000	0.000	0.000	1.000	0.000	0.000	0.00	0.000	0.000
Y♀-1967	6	0.833	0.167	0.000	0.833	0.167	0.000	0.00	0.083	0.080
Total+	62	0.839	0.161	0.000	0.845	0.150	0.006	-0.65	0.081	0.024
0♂-1968	14	0.857	0.143	0.000	0.860	0.138	0.003	-0.19	0.071	0.049
0♀-1968	38	0.789	0.211	0.000	0.799	0.191	0.010	-0.67	0.105	0.035
Y♂-1968	26	0.720	0.280	0.000	0.713	0.265	0.021	-0.85	0.154	0.050
Y♀-1968	9	0.778	0.222	0.000	0.784	0.209	0.007	-0.23	0.111	0.074
Total+	87	0.770	0.230	0.000	0.783	0.205	0.013	-1.17	0.115	0.024

0 = Overwintered animals. Y = Young of the year.
#Based upon the Hardy-Weinberg Law.
+Expected frequency calculated from total observed.
In each case, value of t is not indicative of significant difference.

Table 10. - Observed and expected phenotypic frequencies of transferrins - *P. maniculatus* from Watino and St. Albert.

Category	N	Observed freq.			Expected freq.#			t	q	S.E.
		J	JM	M	J	JM	M			
Watino										
0 ♂-1967	7	0.143	0.571	0.286	0.164	0.527	0.307	-0.23	0.571	0.132
0 ♀-1967	12	0.000	0.750	0.250	0.131	0.489	0.381	-1.90	0.625	0.099
Y ♂-1967	16	0.000	0.750	0.250	0.133	0.484	0.383	-2.25*	0.625	0.086
Y ♀-1967	10	0.200	0.600	0.200	0.237	0.526	0.237	-0.45	0.500	0.112
Total+	45	0.067	0.689	0.244	0.166	0.490	0.344	-2.75*	0.589	0.052
0 ♂-1968	4	0.000	0.750	0.250	0.108	0.535	0.358	-0.88	0.625	0.171
0 ♀-1968	6	0.333	0.500	0.167	0.318	0.530	0.152	+0.15	0.417	0.142
Y ♂-1968	7	0.429	0.429	0.143	0.396	0.494	0.110	+0.37	0.357	0.128
Y ♀-1968	6	0.500	0.333	0.167	0.425	0.485	0.092	+0.82	0.333	0.136
Total+	23	0.348	0.478	0.174	0.339	0.496	0.165	+0.17	0.413	0.073
St. Albert										
0 ♂-1968	61	0.279	0.459	0.262	0.256	0.504	0.240	+0.70	0.492	0.045
0 ♀-1968	65	0.431	0.369	0.200	0.377	0.477	0.146	+1.83	0.385	0.043
Y ♂-1968	147	0.306	0.476	0.218	0.295	0.498	0.207	+0.53	0.456	0.029
Y ♀-1968	132	0.311	0.485	0.205	0.305	0.496	0.199	+0.26	0.447	0.031

0 = Overwintered animals. Y = Young of the year.
#Based upon the Handy-Weinberg Law.
+Expected frequency calculated from total observed.
*Value of t indicative of significant difference ($0.005<P<0.05$).

Table 11. - Relative "fitness" of transferrin and albumin phenotypes - P. maniculatus from Great Slave Lake.

Category	Zone	N	Observed frequency			Expected frequency#			Relative "fitness"			P	F
Transferrins			J	JM	M	J	JM	M	J	JM	M		
Y ♂ - 1966	A	30	0.100	0.233	0.667	0.075	0.397	0.529	1.000	0.438	0.940	+	0.455
Y ♀ - 1966	A	19	0.158	0.368	0.474	0.075	0.397	0.529	1.000	0.438	0.423	-	0.260
0 ♂ - 1967	A	35	0.171	0.257	0.571	0.075	0.397	0.529	1.000	0.282	0.470	-	0.411
0 ♀ - 1967	A	40	0.050	0.400	0.550	0.075	0.397	0.529	0.645	0.968	1.000	-	0.024
Y ♂ - 1967	A	30	0.067	0.500	0.433	0.075	0.400	0.525	0.711	1.000	0.660	-	0.000
Y ♀ - 1967	A	25	0.160	0.760	0.080	0.075	0.400	0.525	1.000	0.891	0.071	***	0.032
0 ♂ - 1968	A	23	0.000	0.391	0.609	0.075	0.400	0.525	0.000	0.844	1.000	-	0.118
0 ♀ - 1968	A	15	0.267	0.400	0.333	0.075	0.400	0.525	1.000	0.281	0.179	-	0.411
Y ♂ - 1968	A	40	0.150	0.400	0.450	0.092	0.480	0.429	1.000	0.508	0.641	-	0.211
Y ♀ - 1968	A	44	0.205	0.523	0.273	0.092	0.480	0.429	1.000	0.487	0.285	-	0.225
Y ♂ - 1968	B	64	0.094	0.375	0.531	0.039	0.344	0.618	1.000	0.449	0.354	-	0.184
Y ♀ - 1968	B	63	0.111	0.286	0.603	0.039	0.344	0.618	1.000	0.289	0.339	-	0.311
Albumins			J	JM	M	J	JM	M		JM	M		
Y ♂ - 1966	A	30	0.000	0.133	0.867	0.032	0.302	0.666		0.340	1.000	-	0.613
Y ♀ - 1966	A	19	0.053	0.158	0.789	0.032	0.302	0.666		0.442	1.000	-	0.508
0 ♂ - 1967	A	35	0.000	0.171	0.829	0.032	0.302	0.666		0.457	1.000	-	0.492
0 ♀ - 1967	A	40	0.000	0.125	0.875	0.032	0.302	0.666		0.316	1.000	*	0.639
Y ♂ - 1967	A	30	0.000	0.200	0.800	0.005	0.137	0.857		1.000	0.641	-	0.000
Y ♀ - 1967	A	25	0.000	0.240	0.760	0.005	0.137	0.857		1.000	0.507	-	0.000
0 ♂ - 1968	A	23	0.000	0.087	0.913	0.005	0.137	0.857		0.595	1.000	-	0.387
0 ♀ - 1968	A	15	0.000	0.267	0.733	0.005	0.137	0.857		1.000	0.440	-	0.000
Y ♂ - 1968	A	40	0.000	0.175	0.825	0.006	0.165	0.830		1.000	0.935	-	0.000
Y ♀ - 1968	A	44	0.000	0.295	0.705	0.006	0.165	0.830		1.000	0.473	*	0.000
Y ♂ - 1968	B	64	0.000	0.063	0.938	0.003	0.133	0.864		0.431	1.000	-	0.550
Y ♀ - 1968	B	63	0.000	0.190	0.810	0.003	0.133	0.864		1.000	0.657	-	0.000

0 = Overwintered animals. Y = Young of the year.
#Based upon observed allelic frequency in overwintered animals of previous generation.
P = Probability in chi-square test between observed and expected frequencies.
- = P>0.1; + = 0.05<P<0.1; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** P<0.001.
F = Inbreeding coefficient necessary for heterozygote to be as fit as most fit homozygote.

Table 12. Relative "fitness" of transferrin and albumin phenotypes - P. maniculatus from Great Slave Lake. Pooling performed within each generation.

Category	Zone	N	Observed frequency			Expected frequency#			Relative "fitness"			P	F
			J	JM	M	J	JM	M	J	JM	M		
Transferrins													
Y-1966 + O-1967	A	124	0.113	0.315	0.573	0.075	0.397	0.529	1.000	0.523	0.715	+	0.200
Y-1967 + O-1968	A	93	0.108	0.527	0.366	0.075	0.400	0.525	1.000	0.919	0.486	**	0.024
Y - 1968	A	84	0.179	0.464	0.357	0.092	0.480	0.429	1.000	0.496	0.427	*	0.267
Y - 1968	B	127	0.102	0.331	0.567	0.039	0.344	0.618	1.000	0.363	0.346	***	0.244
			J	JM	M	J	JM	M		JM	M		
Albumins													
Y-1966 + O-1967	A	124	0.008	0.145	0.847	0.032	0.302	0.666		0.379	1.000	***	0.572
Y-1967 + O-1968	A	93	0.000	0.194	0.806	0.005	0.137	0.857		1.000	0.667	-	0.000
Y - 1968	A	84	0.000	0.238	0.762	0.006	0.165	0.830		1.000	0.635	+	0.000
Y - 1968	B	127	0.000	0.126	0.874	0.003	0.133	0.864		0.933	1.000	-	0.063

O = Overwintered animals. Y = Young of the year.
#Based upon observed allelic frequency in overwintered animals of previous generation.
P = Probability in chi-square test between observed and expected frequencies.
- = P>0.1; + = 0.05<P<0.1; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** = P<0.001.
F = Inbreeding coefficient necessary for heterozygote to be as fit as most fit homozygote.

Table 13. - Relative "fitness" of the transferrin/albumin phenotypes - P. maniculatus from Great Slave Lake. Pooling performed within each generation.

Category	Zone	N		Tf/Al phenotypes							P
				JM/JM	J/JM	M/JM	JM/M	J/M	M/M	Others	
Y-1966 + 0-1967	A	124	Observed frequency =	0.040	0.024	0.081	0.266	0.089	0.492	0.008	
			Expected freq. (1) =	0.046	0.016	0.083	0.267	0.096	0.485	0.008	-
			Expected freq. (2) =	0.120	0.023	0.159	0.265	0.050	0.352	0.032	***
			Relative "fitness"# =	0.188	0.601	0.283	0.563	1.000	0.781	0.141	
Y-1967 + 0-1968	A	93	Observed frequency =	0.097	0.022	0.075	0.430	0.086	0.290	0.000	
			Expected freq. (1) =	0.102	0.021	0.071	0.425	0.087	0.295	0.000	-
			Expected freq. (2) =	0.055	0.010	0.072	0.343	0.064	0.450	0.005	*
			Relative "fitness"# =	0.844	1.000	0.500	0.601	0.641	0.309	0.000	
Y - 1968	A	84	Observed frequency =	0.119	0.048	0.071	0.345	0.131	0.286	0.000	
			Expected freq. (1) =	0.110	0.043	0.085	0.354	0.136	0.272	0.000	-
			Expected freq. (2) =	0.079	0.015	0.071	0.398	0.076	0.356	0.006	+
			Relative "fitness"# =	0.477	1.000	0.320	0.274	0.546	0.254	0.000	
Y - 1968	B	127	Observed frequency =	0.047	0.016	0.063	0.283	0.087	0.504	0.000	
			Expected freq. (1) =	0.042	0.013	0.071	0.289	0.089	0.496	0.000	-
			Expected freq. (2) =	0.046	0.005	0.082	0.297	0.033	0.534	0.003	*
			Relative "fitness"# =	0.340	1.000	0.252	0.315	0.859	0.312	0.000	

O = Overwintered animals. Y = Young of the year.
(1) : Based upon observed phenotypic frequency at each locus.
(2) : Based upon observed allelic frequencies in overwintered animals of previous generation.
#Based upon (2).
P = Probability in chi-square test between observed and expected frequencies.
- = P>0.1; + = 0.05<P<0.1; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** = P<0.001.

Table 14. - Relative "fitness" of transferrin and albumin phenotypes - C. gapperi from Great Slave Lake.

Category	N	Observed frequency			Expected frequency#			Relative "fitness"			P	F
Transferrins		J	JM	M	J	JM	M	J	JM	M		
Y ♂ - 1966	12	0.333	0.500	0.167	0.461	0.456	0.082	0.357	0.542	1.000	-	0.183
Y ♀ - 1966	15	0.267	0.467	0.267	0.461	0.456	0.082	0.179	0.316	1.000	-	0.365
0 ♂ - 1967	40	0.275	0.575	0.150	0.461	0.456	0.082	0.327	0.692	1.000	-	0.106
0 ♀ - 1967	14	0.357	0.429	0.214	0.461	0.456	0.082	0.298	0.361	1.000	-	0.319
Y♂-1967 + 0♂-1968	16	0.313	0.500	0.188	0.321	0.491	0.188	0.957	1.000	0.980	-	0.000
Y♀-1967 + 0♀-1968	44	0.136	0.500	0.364	0.321	0.491	0.188	0.220	0.527	1.000	**	0.281
Y ♂ - 1968	26	0.231	0.539	0.231	0.205	0.508	0.287	1.000	0.940	0.714	-	0.028
Y ♀ - 1968	9	0.111	0.778	0.111	0.205	0.508	0.287	0.355	1.000	0.253	-	0.000
Albumins		G	GM	M	G	GM	M	G	GM			
Y ♂ - 1966	12	0.883	0.167	0.000	0.769	0.231	0.000	1.000	0.666		-	0.304
Y ♀ - 1966	15	0.867	0.133	0.000	0.769	0.231	0.000	1.000	0.512		-	0.453
0 ♂ - 1967	40	0.846	0.154	0.000	0.769	0.231	0.000	1.000	0.706		-	0.266
0 ♀ - 1967	14	0.857	0.143	0.000	0.769	0.231	0.000	1.000	0.555		-	0.411
Y♂-1967 + 0♂-1968	16	0.875	0.125	0.000	0.847	0.147	0.006	1.000	0.826		-	0.162
Y♀-1967 + 0♀-1968	44	0.795	0.205	0.000	0.847	0.147	0.006	0.673	1.000		-	0.000
Y ♂ - 1968	26	0.720	0.280	0.000	0.832	0.161	0.008	0.436	1.000		+	0.000
Y ♀ - 1968	9	0.778	0.222	0.000	0.832	0.161	0.008	0.678	1.000		-	0.000

0 = Overwintered animals. Y = Young of the year.
P = Probability in chi-square test between observed and expected frequencies.
- = P>0.1; + = 0.05<P<0.1; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** = P<0.001.
F = Inbreeding coefficient necessary for heterozygote to be as fit as most fit homozygote.
#Based upon observed allelic frequency in overwintered animals of previous generation.

Table 15. - Relative "fitness" of transferrin and albumin phenotypes - C. gapperi from Great Slave Lake. Pooling performed within each generation.

Category	Zone	N	Observed frequency			Expected frequency#			Relative "fitness"			P	F
Transferrins			J	JM	M	J	JM	M	J	JM	M		
Y-1966 + O-1967		81	0.296	0.519	0.185	0.461	0.456	0.082	0.286	0.506	1.000	***	0.206
Y-1967 + O-1968		60	0.183	0.500	0.317	0.321	0.491	0.188	0.339	0.605	1.000	*	0.221
Y - 1968		35	0.200	0.600	0.200	0.205	0.508	0.287	0.828	1.000	0.591	-	0.000
Albumins			G	GM	M	G	GM	M	G	GM			
Y-1966 + O-1967		81	0.840	0.160	0.000	0.769	0.231	0.000	1.000	0.636		-	0.332
Y-1967 + O-1968		60	0.817	0.183	0.000	0.847	0.147	0.006	0.770	1.000		-	0.000
Y - 1968		35	0.714	0.286	0.000	0.832	0.161	0.008	0.484	1.000		+	0.000

O = Overwintered animals. Y = Young of the year.
#Based upon observed allelic frequency in overwintered animals of previous generation.
P = Probability in chi-square test between observed and expected frequencies.
- = P>0.1; + = 0.05<P<0.1; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** = P<0.001.
F = Inbreeding coefficient necessary for heterozygote to be as fit as most fit homozygote.

Table 16. - Relative "fitness" of the transferrin / albumin phenotypes - C. gapperi from Great Slave Lake. Pooling performed within each generation.

Category	N		Tf/Al phenotypes							P
			JM/GM	J/GM	M/GM	JM/G	J/G	M/G	Others	
Y-1966 + 0-1967	81	Observed frequency =	0.099	0.049	0.012	0.420	0.247	0.173	0.000	
		Expected freq. (1) =	0.083	0.047	0.030	0.436	0.249	0.155	0.000	-
		Expected freq. (2) =	0.105	0.107	0.019	0.351	0.355	0.063	0.000	***
		Relative "fitness"# =	0.344	0.170	0.238	0.439	0.255	1.000	0.000	
Y-1966 + 0-1967	60	Observed frequency =	0.117	0.033	0.033	0.383	0.150	0.283	0.000	
		Expected freq. (1) =	0.092	0.029	0.051	0.409	0.150	0.259	0.000	-
		Expected freq. (2) =	0.072	0.047	0.028	0.416	0.272	0.159	0.006	+
		Relative "fitness"# =	0.622	0.399	0.681	0.518	0.310	1.000	0.000	
Y - 1968	35	Observed frequency =	0.143	0.086	0.057	0.457	0.114	0.143	0.000	
		Expected freq. (1) =	0.172	0.057	0.057	0.428	0.143	0.143	0.000	-
		Expected freq. (2) =	0.082	0.033	0.046	0.423	0.170	0.239	0.008	-
		Relative "fitness"# =	0.672	1.000	0.476	0.416	0.258	0.231	0.000	

0 = Overwintered animals. Y = Young of the year.
(1) : Based upon observed phenotypic frequency at each locus.
(2) : Based upon observed allelic frequencies in overwintered animals of previous generation.
#Based upon (2).
P = Probability in chi-square test between observed and expected frequencies.
- = P>0.1; + = 0.05<P<0.1; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** = P<0.001.

Table 17. - Relative "fitness" of transferrin phenotypes - P. maniculatus from Watino and St. Albert.

Category	N	Observed frequency			Expected frequency#			Relative "fitness"			P	F
		J	JM	M	J	JM	M	J	JM	M		
Watino												
Y ♂ + Y ♀ - 1967	26	0.077	0.692	0.231	0.268	0.518	0.214	0.215	1.000	0.807	+	0.000
O ♂ + O ♀ - 1968	10	0.200	0.600	0.200	0.268	0.518	0.214	0.644	1.000	0.807	-	0.000
Y ♂ + Y ♀ - 1968	13	0.462	0.385	0.154	0.250	0.500	0.250	1.000	0.417	0.333	-	0.412
St. Albert												
Y ♂ - 1968	147	0.306	0.476	0.218	0.312	0.498	0.189	0.852	0.830	1.000	-	0.081
Y ♀ - 1968	132	0.311	0.485	0.205	0.312	0.498	0.189	0.920	0.900	1.000	-	0.046

O = Overwintered animals. Y = Young of the year.
#Based upon observed allelic frequency in overwintered animals of previous generation.
P = Probability in chi-square test between observed and expected frequencies.
- = $P>0.1$; + = $0.05<P<0.1$; * = $0.01<P<0.05$; ** = $0.001<P<0.01$; *** = $P<0.001$.
F = Inbreeding coefficient necessary for heterozygote to be as fit as most fit homozygote.

Table 18. - Between-litter and within-litter comparisons of growth rate regressions in P. maniculatus from Great Slave Lake.

	N	Mean regression coefficient#	Variance	P
(a) Between-litter comparisons.				
Litters exposed to 20 hrs. light/day	14	0.444	0.007	
Litters exposed to 4 hrs. light/day	15	0.407	0.003	-
Small litters (<5 young)	17	0.448	0.007	
Large litters (>6 young)	12	0.392	0.001	*
Litters with Tf JM mother	12	0.447	0.009	
Litters with Tf M mother	13	0.405	0.002	-
Small litters with Tf JM mother	6	0.500	0.012	
Large litters with Tf JM mother	6	0.395	0.001	*
Small litters with Tf M mother	8	0.412	0.002	
Large litters with Tf M mother	5	0.393	0.002	-
Small litters with Tf JM mother	6	0.500	0.012	
Small litters with Tf M mother	8	0.412	0.002	+
Large litters with Tf JM mother	6	0.395	0.001	
Large litters with Tf M mother	5	0.393	0.002	-
(b) Within-litter comparisons.				
Males	28	0.423		
Females		0.417	0.001	-
Young with same Tf type as mother	15	0.437		
Young without same Tf type as mother		0.437	0.002	-
Tf JM young	15	0.417		
Tf M young		0.432	0.001	*
Tf JM young with Tf JM mother	11	0.426		
Tf M young with Tf JM mother		0.442	0.001	*
Tf JM young with Tf M mother	3	0.394		
Tf M young with Tf M mother		0.407	0.001	*

#Mean value of the mean coefficient of regression of weight with respect to age in each litter.
N = Number of litters.
P = Probability in Student's t test between mean regression coefficients.
- = P>0.1; + = 0.01<P<0.05; * = 0.001<P<0.01; ** = P<0.001.

Table 19. - Observed phenotypic frequencies of transferrins - P. maniculatus from Great Slave Lake. 1966 and 1967: by age and month of capture. 1968: by place of capture.

Category#		N	Observed freq.			q	S.E.
			J	JM	M		
1966							
Overwintered	June and July	22	0.136	0.318	0.545	0.705	0.069
	Aug. and Sept.	11	0.091	0.273	0.636	0.773	0.089
Young	June and July	23	0.130	0.261	0.609	0.739	0.065
	Aug. and Sept.	26	0.115	0.308	0.577	0.731	0.061
Total	June and July	45	0.133	0.289	0.578	0.722	0.047
	Aug. and Sept.	37	0.108	0.297	0.595	0.743	0.051
1967							
Overwintered	June and July	57	0.105	0.298	0.596	0.746	0.041
	Aug. and Sept.	18	0.111	0.444	0.444	0.667	0.079
Young	June and July	18	0.167	0.500	0.333	0.583	0.082
	Aug. and Sept.	37	0.081	0.676	0.243	0.581	0.057
Total	June and July (a)	75	0.120	0.347	0.533	0.707	0.037
	Aug. and Sept.(a)	55	0.091	0.600	0.309	0.609	0.047
1968							
Heart Lake Laboratory (b)		73	0.151	0.438	0.411	0.630	0.040
S. bank, Mackenzie River (c)		41	0.171	0.439	0.390	0.610	0.054
Providence Island (b,c)		101	0.050	0.317	0.634	0.792	0.029
N. bank, Mackenzie River		73	0.123	0.370	0.507	0.692	0.038

#Observed phenotypic frequencies in categories with similar superscripts (a,b,c) differ significantly; (a): $0.01 < P < 0.02$; (b) and (c): $0.005 < P < 0.01$.

Figure 1. Map of major study area near Great Slave Lake, N.W.T. (trapping location 1).

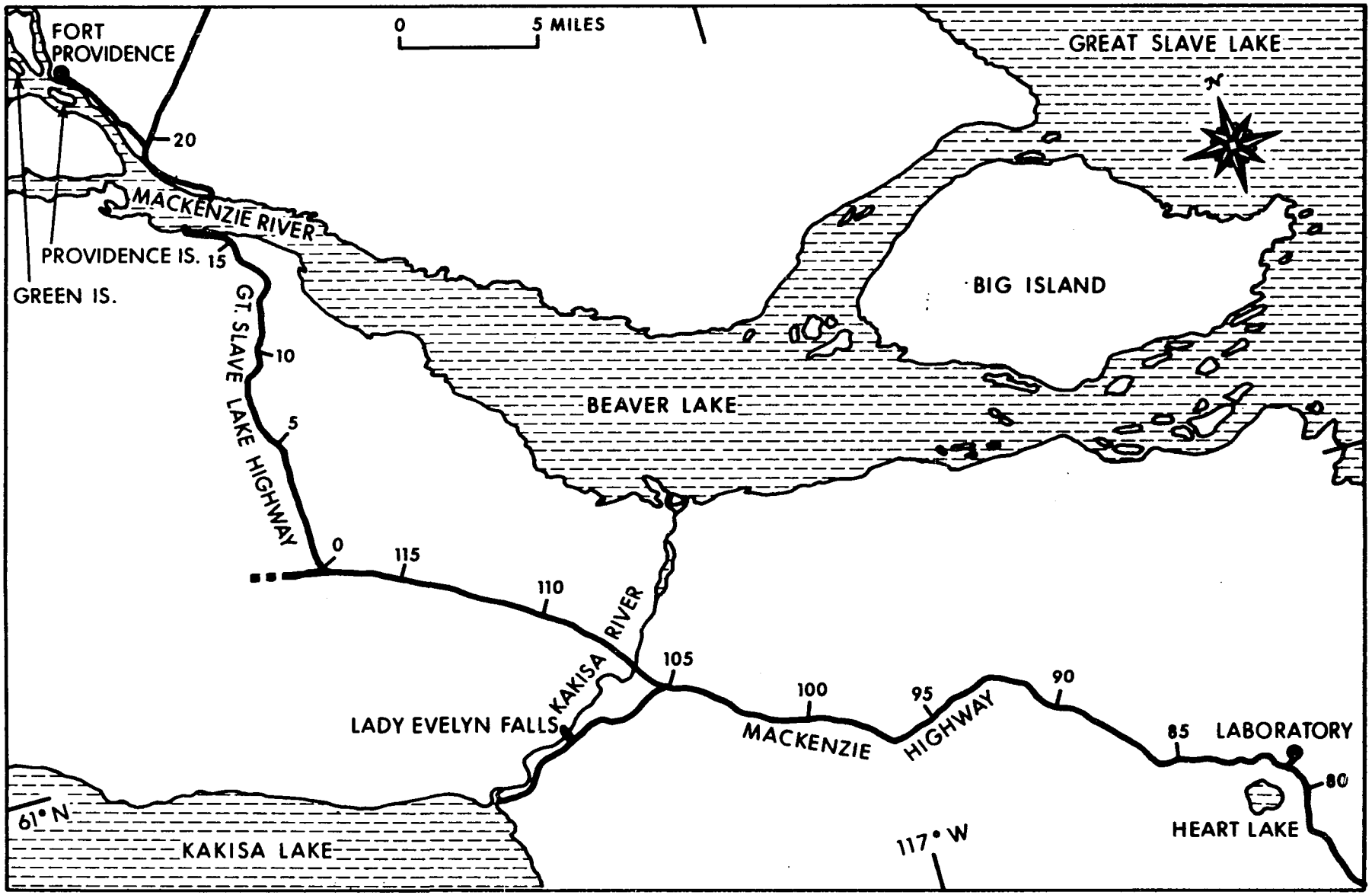

FORT PROVIDENCE
0
5 MILES
GREAT SLAVE LAKE
N
20
MACKENZIE RIVER
PROVIDENCE IS.
15
GREEN IS.
BIG ISLAND
GT. SLAVE LAKE HIGHWAY
10
5
BEAVER LAKE
0
115
110
KAKISA RIVER
105
100
95
90
LADY EVELYN FALLS
MACKENZIE HIGHWAY
85
LABORATORY
80
61° N
KAKISA LAKE
117° W
HEART LAKE

Figure 2. Map of Great Slave Lake region of the Northwest Territories, and northern Alberta and British Columbia, showing trapping locations 1 - 5. Small rectangle at west end of Great Slave Lake is the area shown in Figure 1.

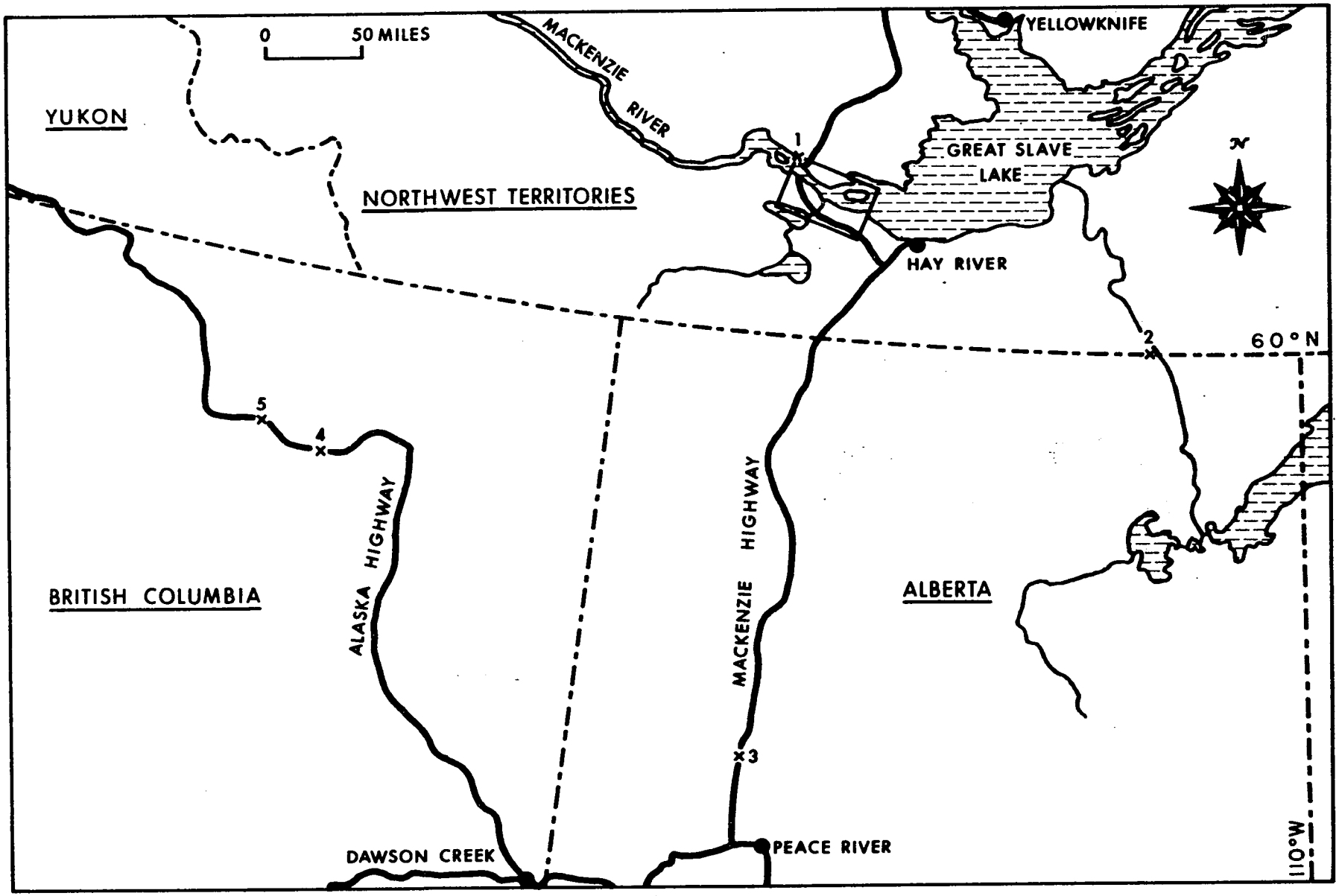

0
50 MILES
MACKENZIE RIVER
YELLOWKNIFE
YUKON
NORTHWEST TERRITORIES
GREAT SLAVE LAKE
N
HAY RIVER
60°N
1
2
3
4
5
ALASKA HIGHWAY
MACKENZIE HIGHWAY
BRITISH COLUMBIA
ALBERTA
DAWSON CREEK
PEACE RIVER
110°W

Figure 3. Map of central and southern Alberta, showing trapping locations 6 - 18.

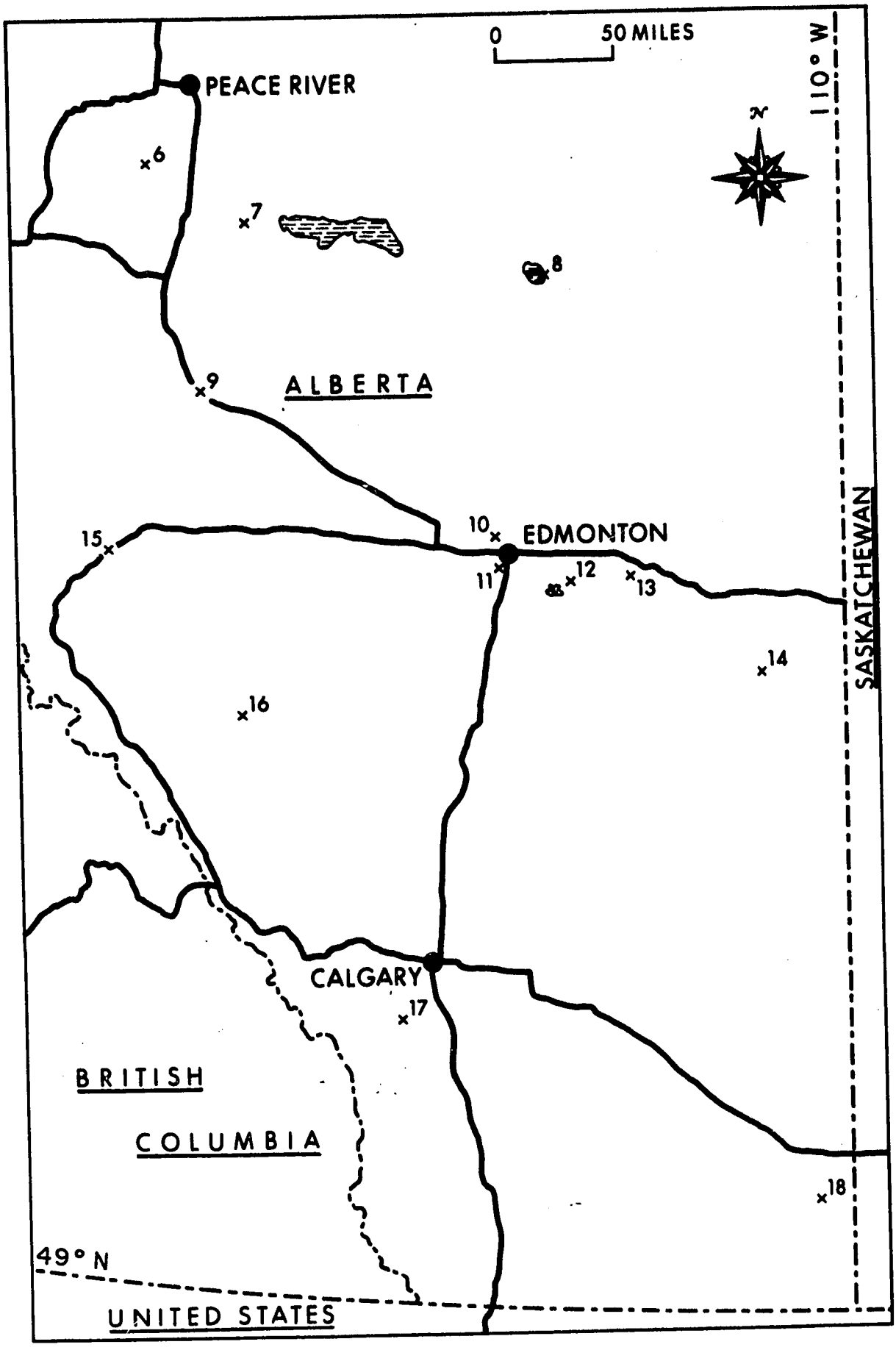

0
50 MILES
110° W
PEACE RIVER
6
7
8
9
ALBERTA
10
EDMONTON
11
12
13
14
15
16
17
18
SASKATCHEWAN
CALGARY
BRITISH
COLUMBIA
49° N
UNITED STATES

Figure 4. Removal of blood from the suborbital canthal sinus of a drugged deer mouse by means of a blood collecting tube.

Figure 5. Vertical starch gel electrophoresis apparatus in operation. Surface of gel to which samples are applied faces away. Pipes conduct coolant at 2 C to and from water-jacket against near surface of the gel.

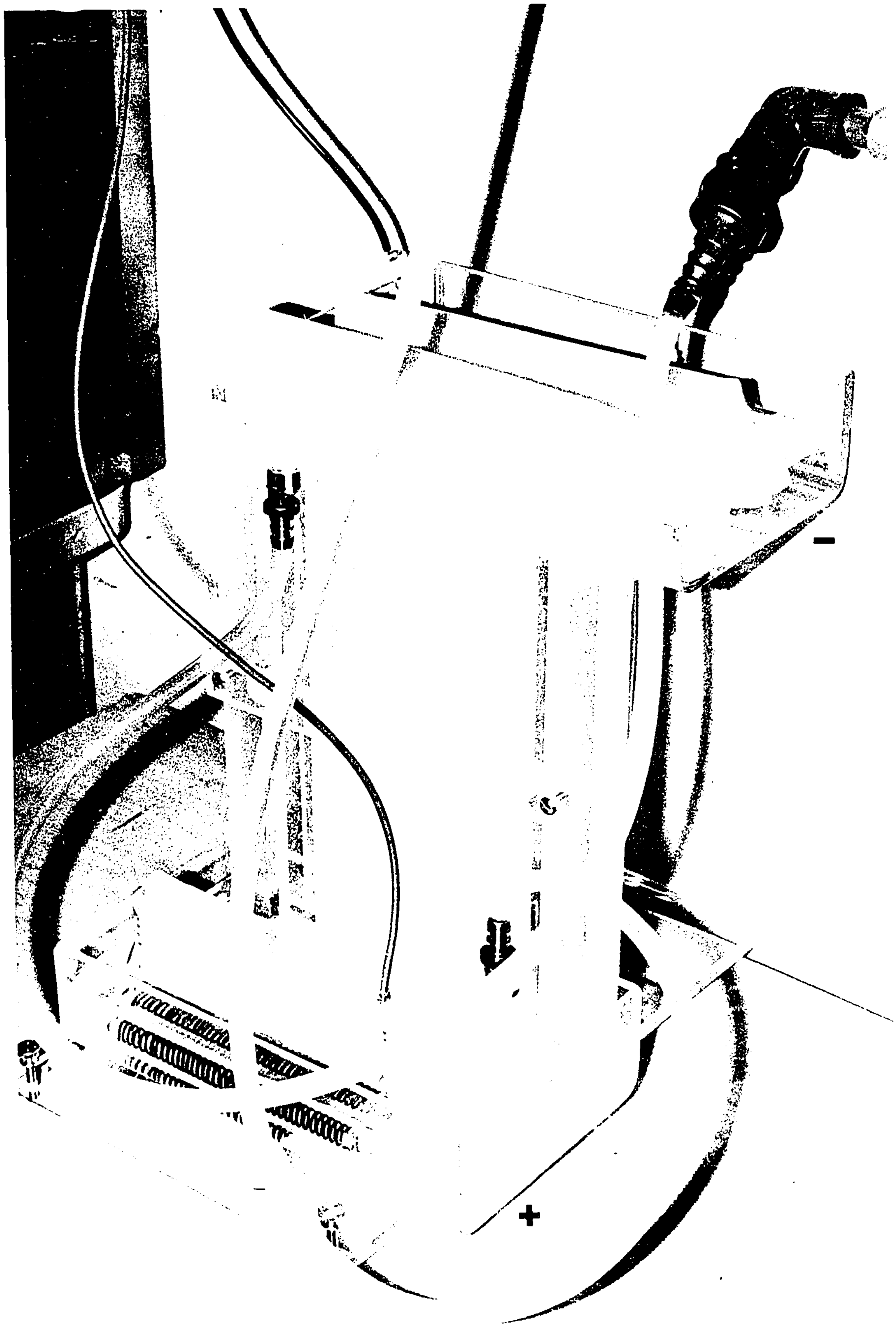


Figure 6. Diagram of starch gel (a) loaded with serum samples and (b) stained to show albumin bands. R_1 - R_n are (a) rows of serum samples in cuts, and (b) the corresponding rows of albumin bands.

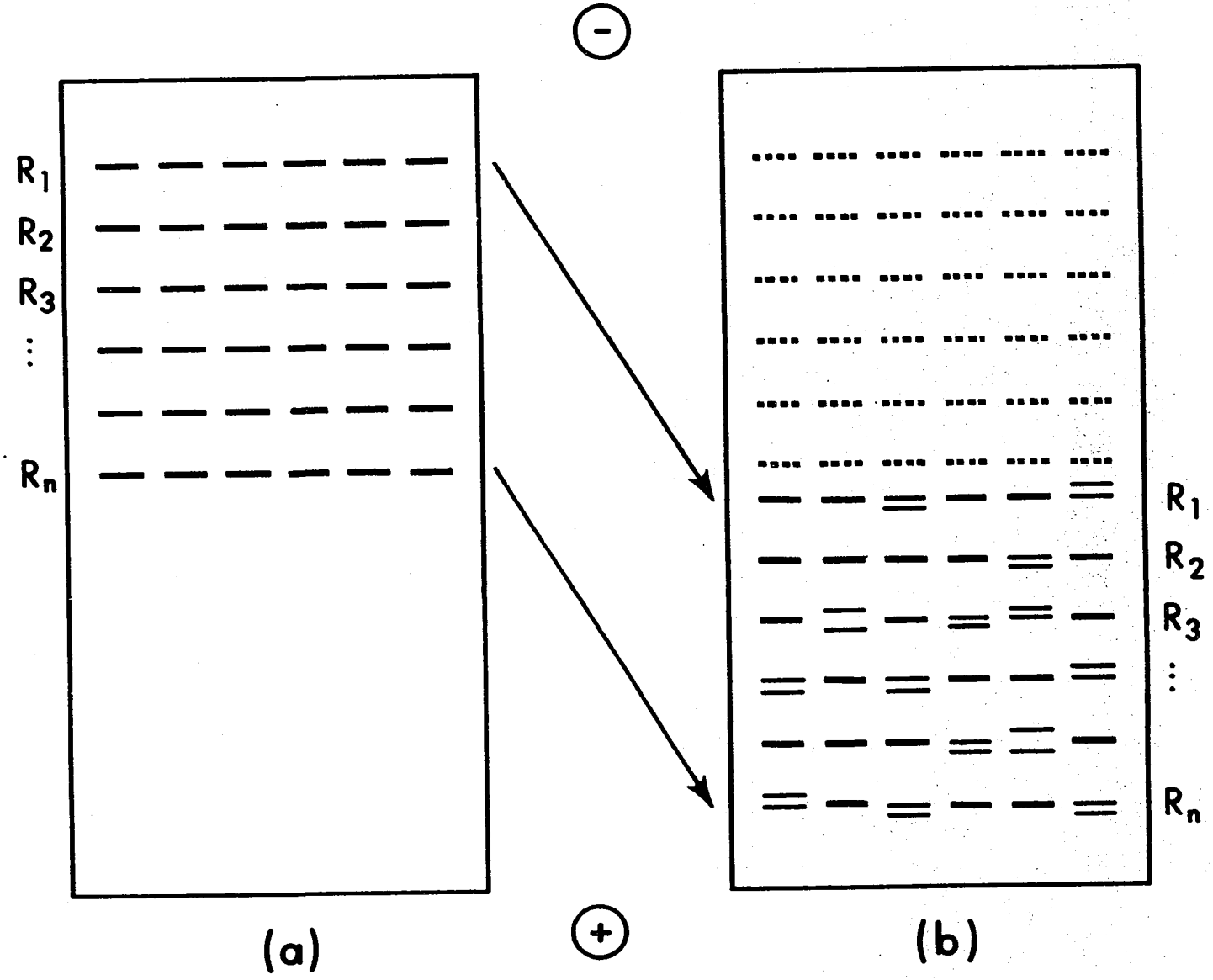

R1
R2
R3
Rn
(a)
(b)
R1
R2
R3
Rn

Figure 7. Serum protein variation in deer mice and red-backed mice, as revealed by starch gel electrophoresis. Bands are named with letters. Numbers give the position of the bands on the gel relative to the most anodal and most cathodal forms of the protein, as a percentage of the distance from the former.

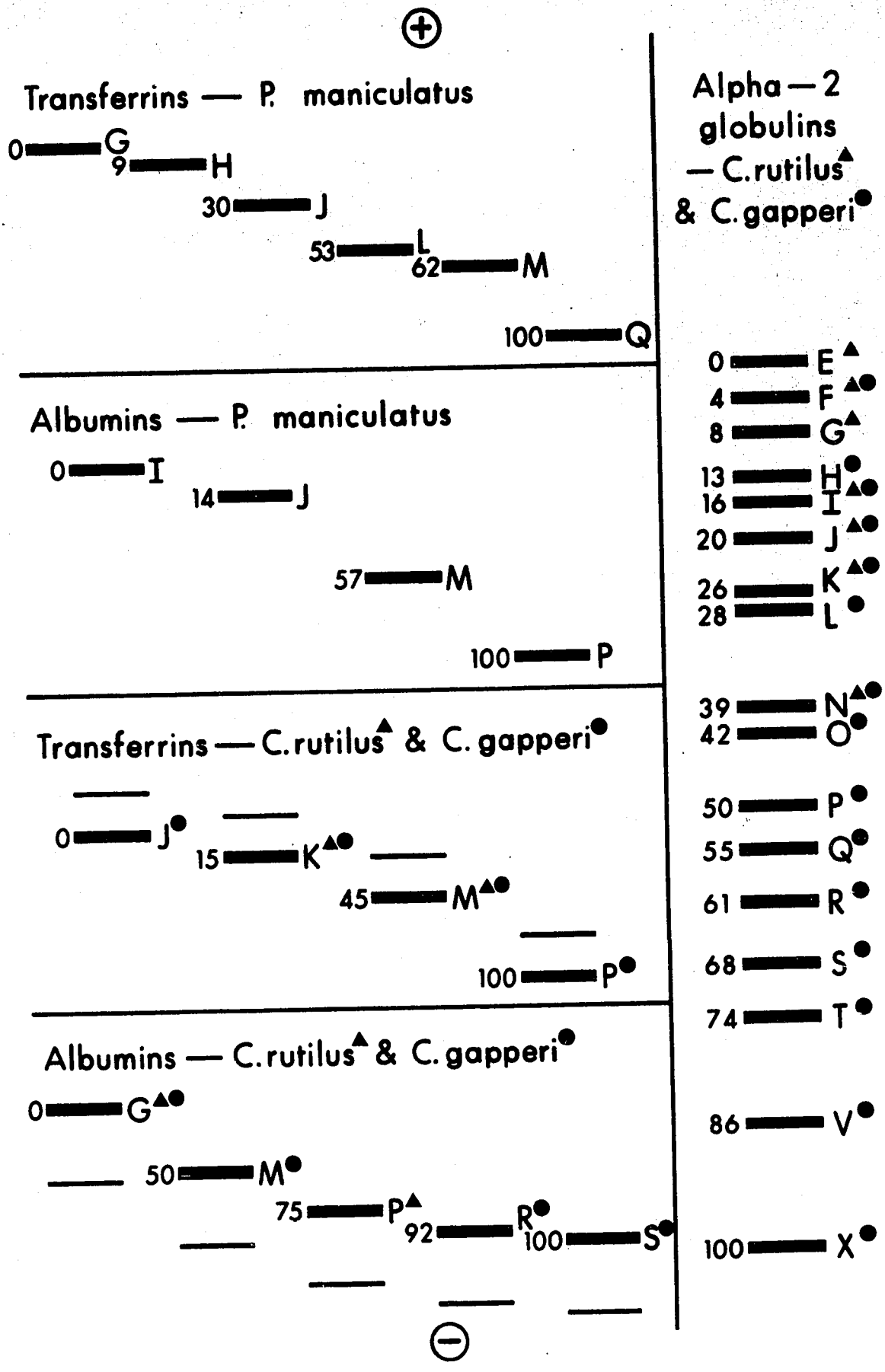

⊕
Transferrins — P. maniculatus
0 G
9 H
30 J
53 L
62 M
100 Q
Albumins — P. maniculatus
0 I
14 J
57 M
100 P
Transferrins — C. rutilus▲ & C. gapperi●
0 J●
15 K▲●
45 M▲●
100 P●
Albumins — C. rutilus▲ & C. gapperi●
0 G▲●
50 M●
75 P▲
92 R●
100 S●
⊖
Alpha — 2 globulins — C. rutilus▲ & C. gapperi●
0 E▲
4 F▲●
8 G▲
13 H●
16 I▲●
20 J▲●
26 K▲●
28 L●
39 N▲●
42 O●
50 P●
55 Q●
61 R●
68 S●
74 T●
86 V●
100 X●

Figure 8. Starch gel showing the six transferrin bands and ten phenotypes found in deer mice. Serum sample 1: Tf JQ. 2: Tf MQ. 3: Tf M. 4: Tf JM. 5: Tf JL. 6: Tf HJ. 7: Tf HM. 8: Tf GM. 9: Tf GJ. 10: Tf J.

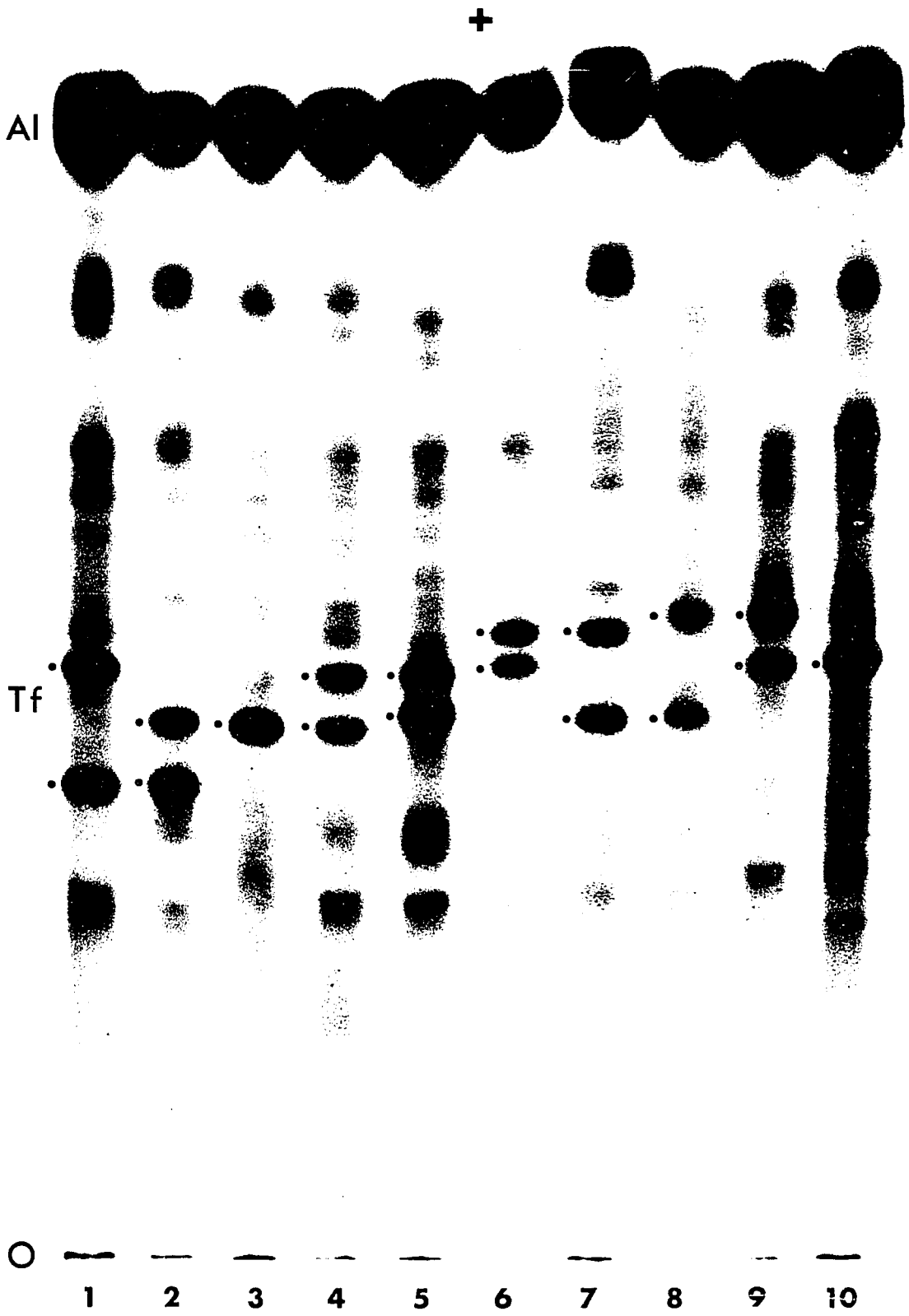

+
Al
Tf
O
1
2
3
4
5
6
7
8
9
10

Figure 9. Left: starch gel showing the four albumin bands and five phenotypes found in deer mice. Serum sample 1: Al MP. 2: Al M. 3: Al IM. 4: Al JM. 5: Al J.

Right: portion of starch gel showing deer mouse albumins separated by multiple cut method. Three phenotypes are shown: Al IM, Al M and Al JM (first column, top to bottom). Sample in middle of third column shows some deterioration through prolonged storage.

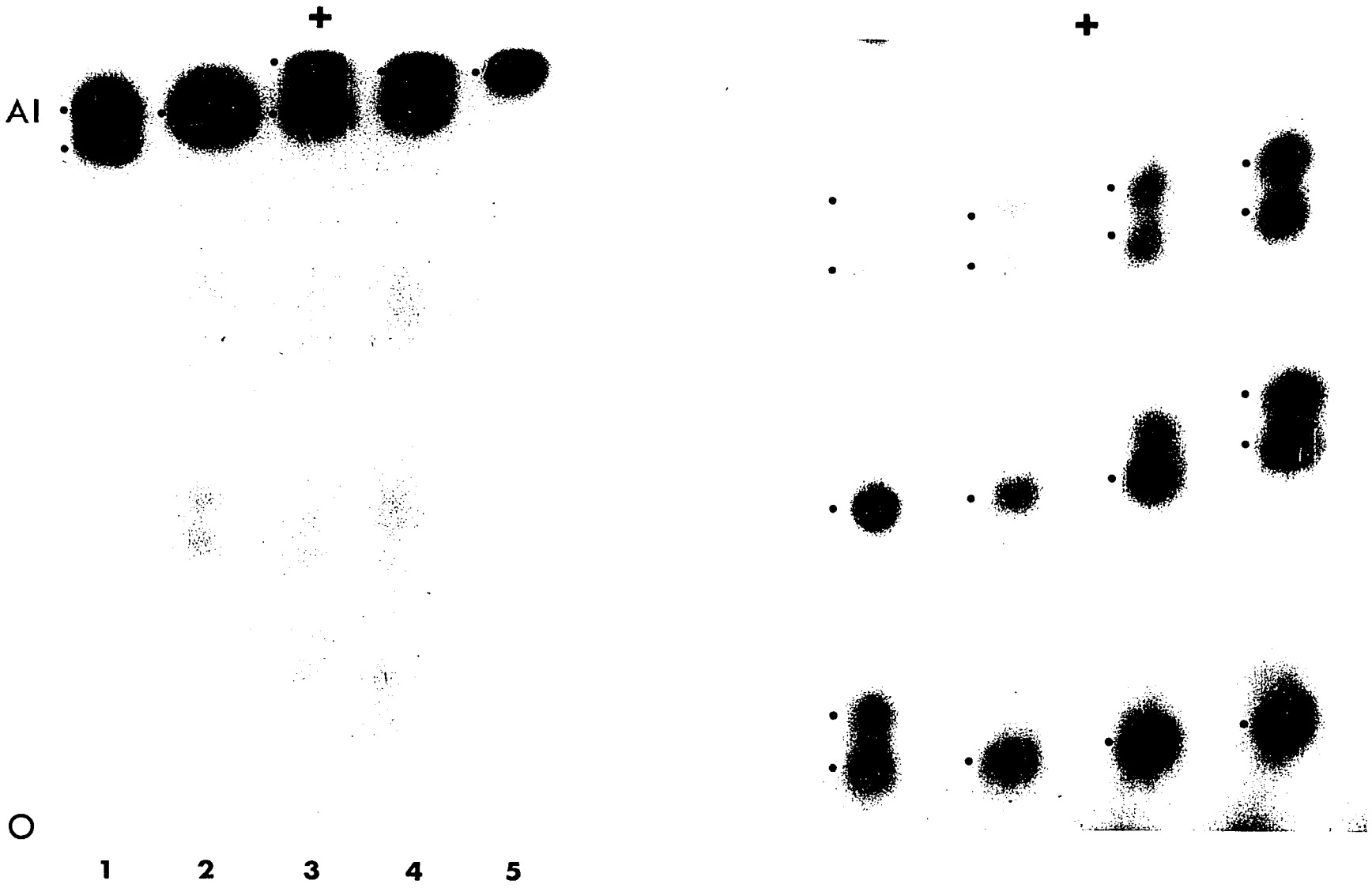

+
Al
O
1
2
3
4
5
-
+

Figure 10. Starch gel showing transferrin bands and phenotypes found in red-backed mice. Serum samples 1 - 4: C. gapperi, samples 5 and 6: C. rutilus. 1: Tf M. 2: Tf J. 3: Tf JM. 4: Tf KM. 5: Tf KM. 6: Tf M. Not shown: Tf MP (C. gapperi), and Tf K (C. rutilus). Edge samples are from deer mouse (Tf JM). Some samples were diluted with water before electrophoresis.

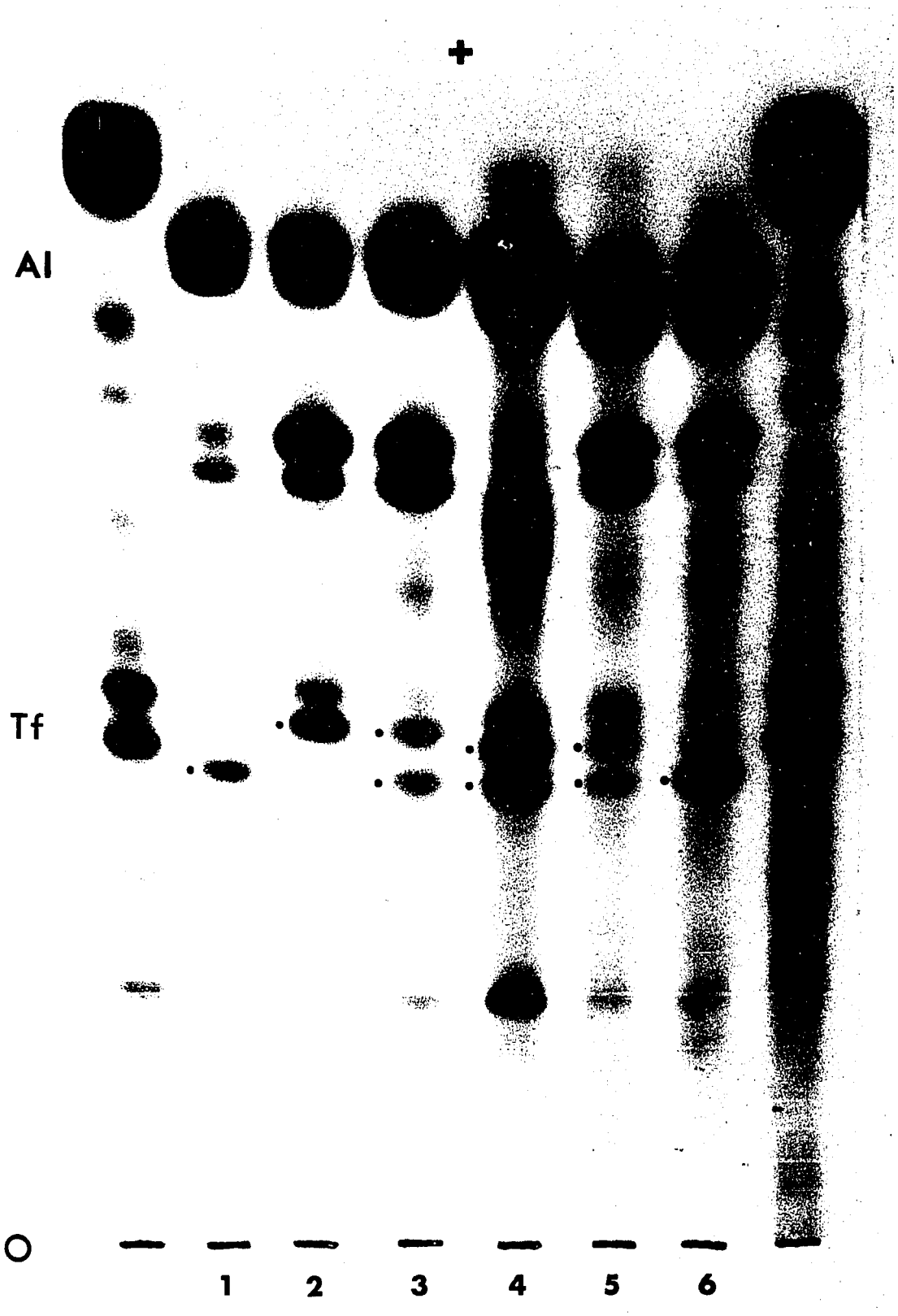

+
Al
Tf
O
1
2
3
4
5
6

Figure 11. Starch gel showing the five albumin bands and eight phenotypes found in red-backed mice. Serum samples 1 - 3: C. rutilus, samples 4 - 9: C. gapperi. 1: Al G. 2: Al P. 3: Al GP. 4: Al GS. 5: Al GR. 6: Al MS. 7: Al GM. 8: Al M. 9: Al G. Some samples were diluted with water before electrophoresis.

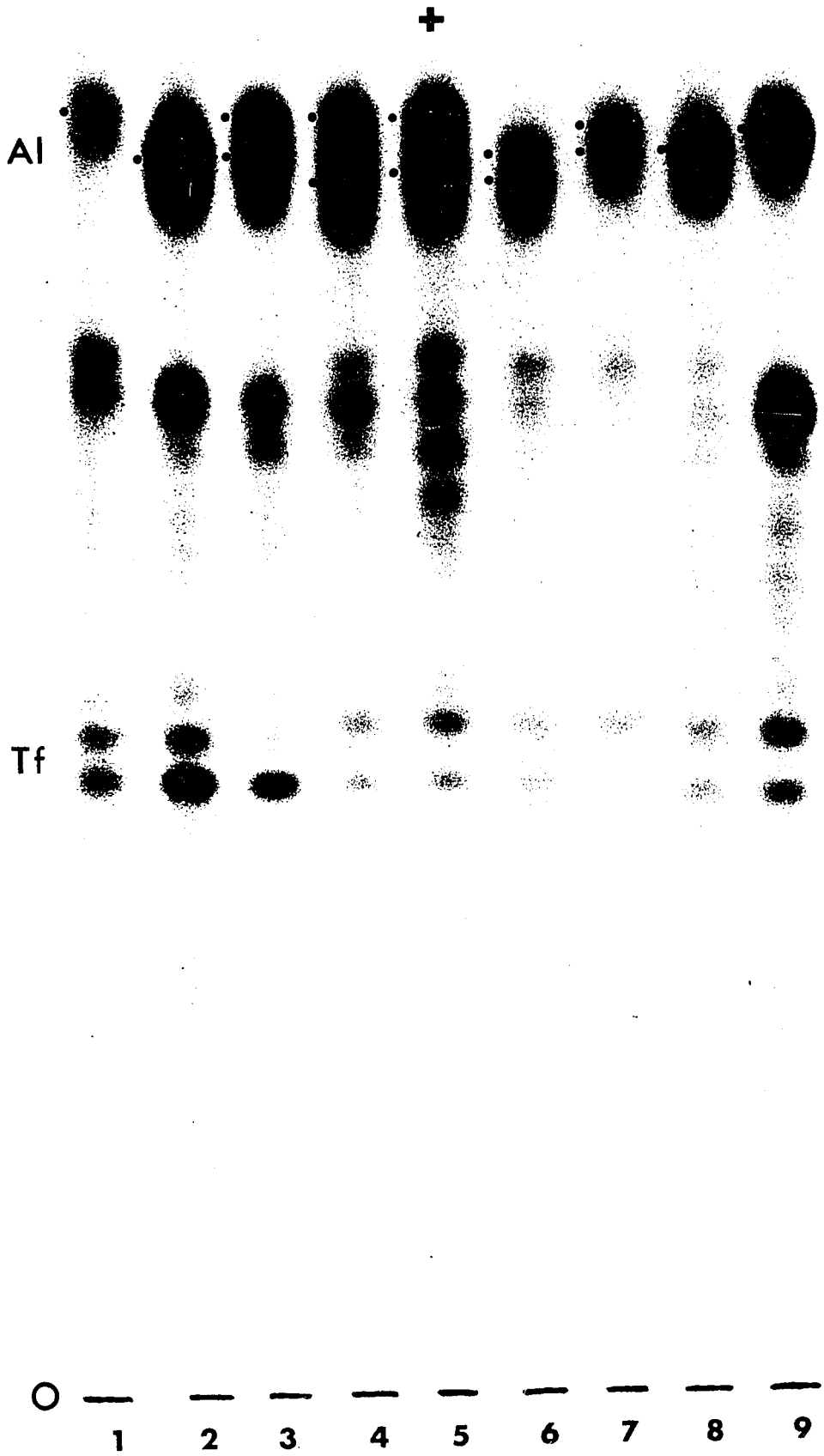

+
Al
Tf
O
1
2
3
4
5
6
7
8
9

Figure 12. Starch gel showing fourteen of the fifteen alpha-2 globulin bands found in C. gapperi. Serum sample 1: bands H, O, P, T and V. 2: K, N, Q, V and X. 3: L, N, P and S. 4: I, K, N, P, R and V. 5: F, I, K, N and R. Not shown: E and G, (present in C. rutilus only), and J. Sample 5 has two transferrin bands (Tf JM). Some samples were diluted with water before electrophoresis.

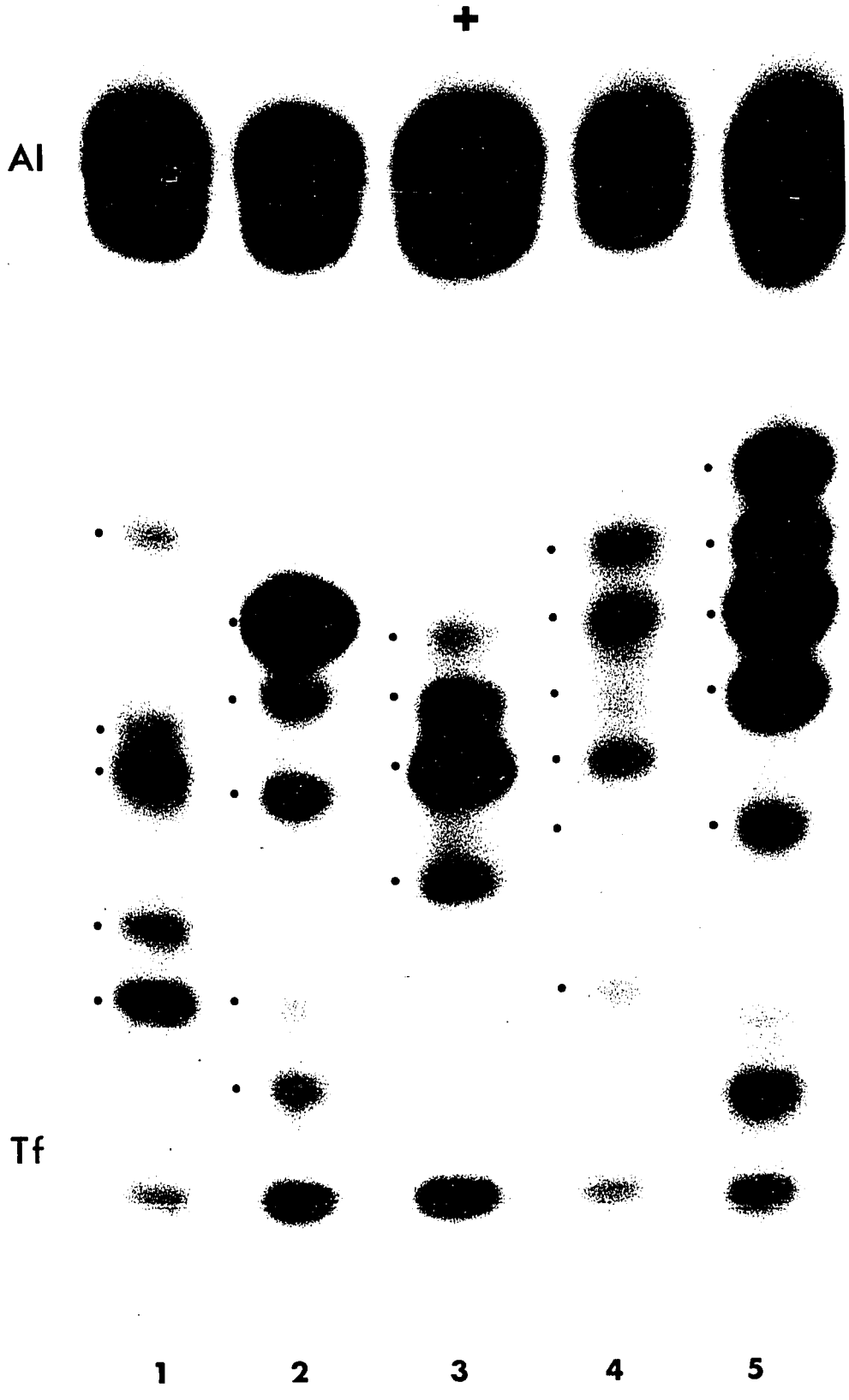
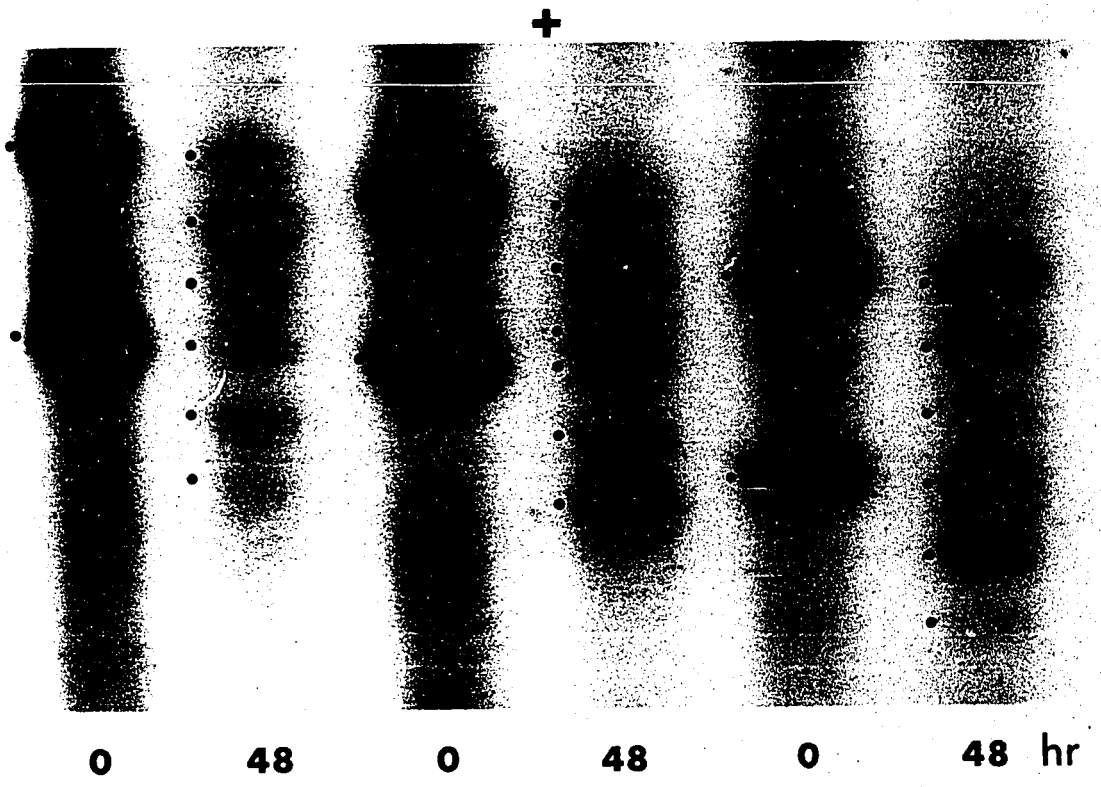

+
Al
Tf
1
2
3
4
5

Figure 13. Top: starch gel showing separation of the transferrins in serum samples from three deer mice before and after treatment of the serum with neuraminidase.
Left: Tf GM, centre: Tf HM, right: Tf JQ.
Bottom: starch gels showing separation of the transferrins in serum samples from two C. rutilus before and after treatment of the serum with neuraminidase.
Left: Tf M, right: Tf KM.


+
0
48
0
48
0
48 hr


+
0
24
48 hr

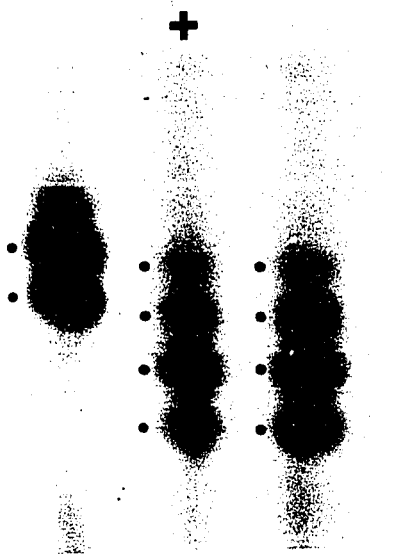

+
0
24
48 hr

Figure 14. Relative "fitness" of the transferrin phenotypes in each sex and age category - P. maniculatus from Great Slave Lake. Tf J: stipled. Tf JM: blocked. Tf M: striped. O: overwintered animals. Y: young of the year. A and B: trapping zones.

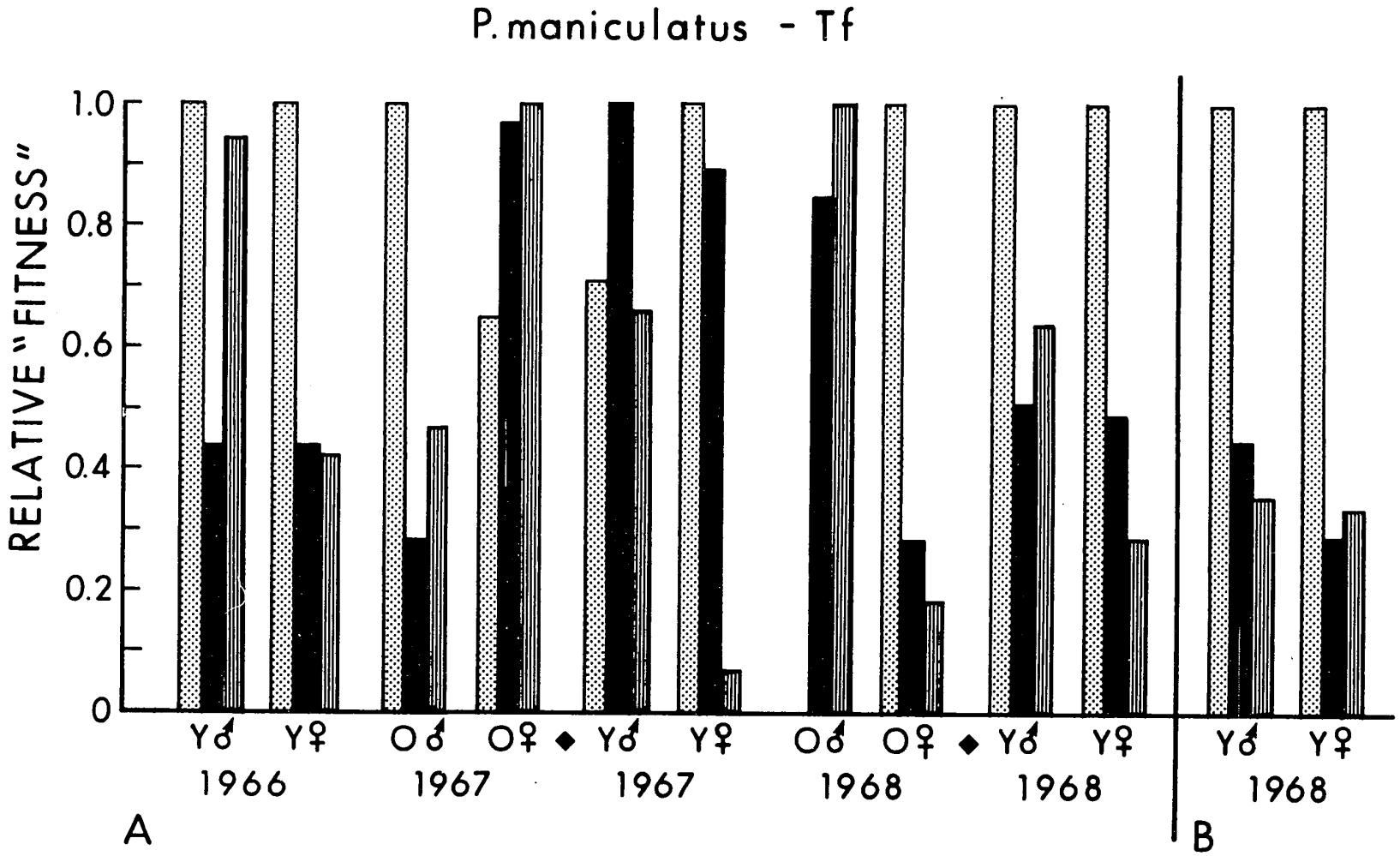

P. maniculatus - Tf
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y♂
Y♀
O♂
O♀
1966
1967
1967
1968
1968
1968
A
B

Figure 15. Relative "fitness" of the albumin phenotypes in each sex and age category - *P. maniculatus* from Great Slave Lake. Al JM: blocked. Al M: striped. O: overwintered animals. Y: young of the year. A and B: trapping zones.

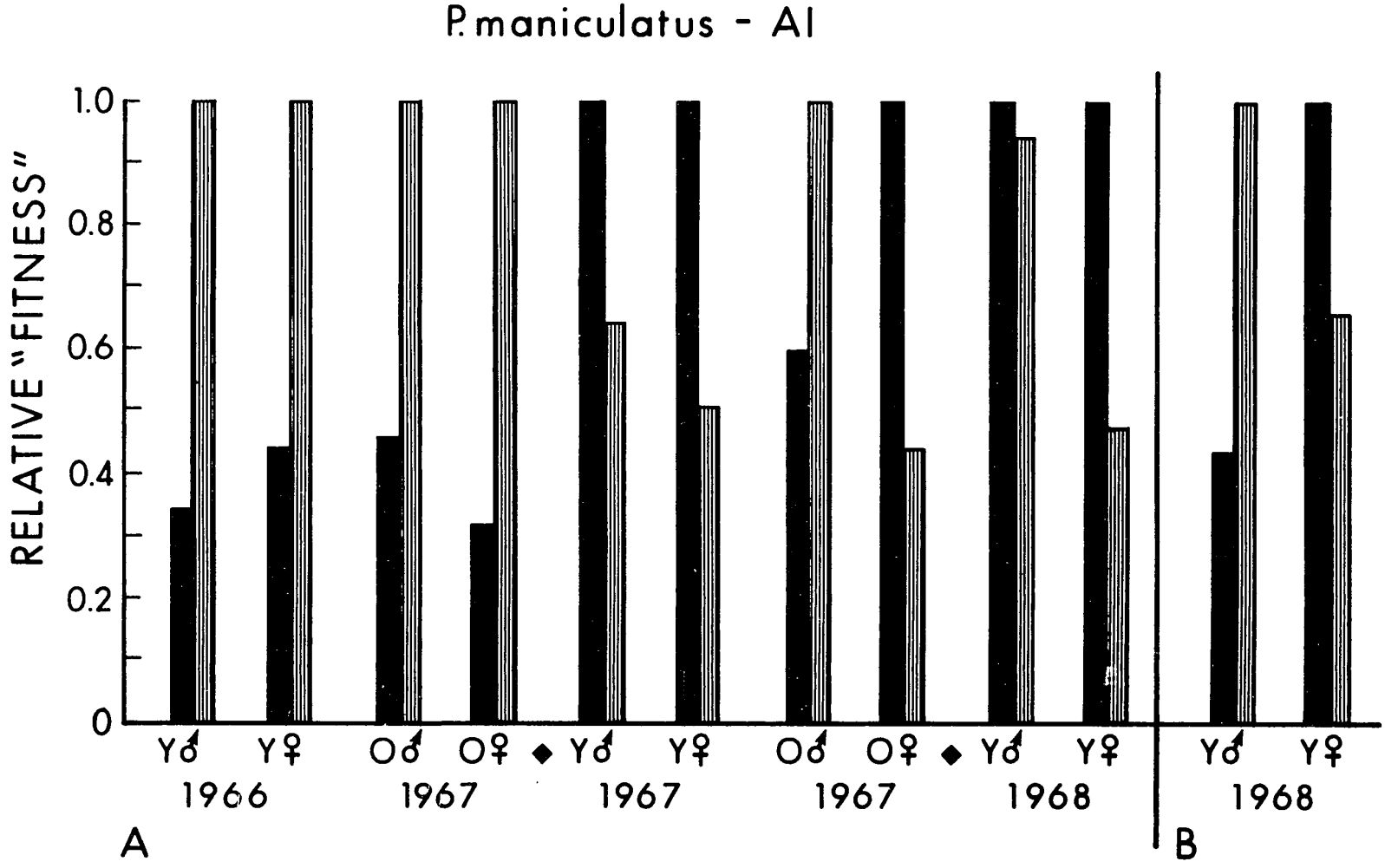

P. maniculatus - AI
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y♂
Y♀
O♂
O♀
◆
Y♂
Y♀
O♂
O♀
◆
Y♂
Y♀
Y♂
Y♀
1966
1967
1967
1967
1968
1968
A
B

Figure 16. Relative "fitness" of the transferrin and albumin phenotypes in successive generations - P. maniculatus from Great Slave Lake. Sexes and age categories pooled within each generation. Tf J: stipled. Tf JM and Al JM: blocked. Tf M and Al M: striped. O: overwintered animals. Y: young of the year. A and B: trapping zones.

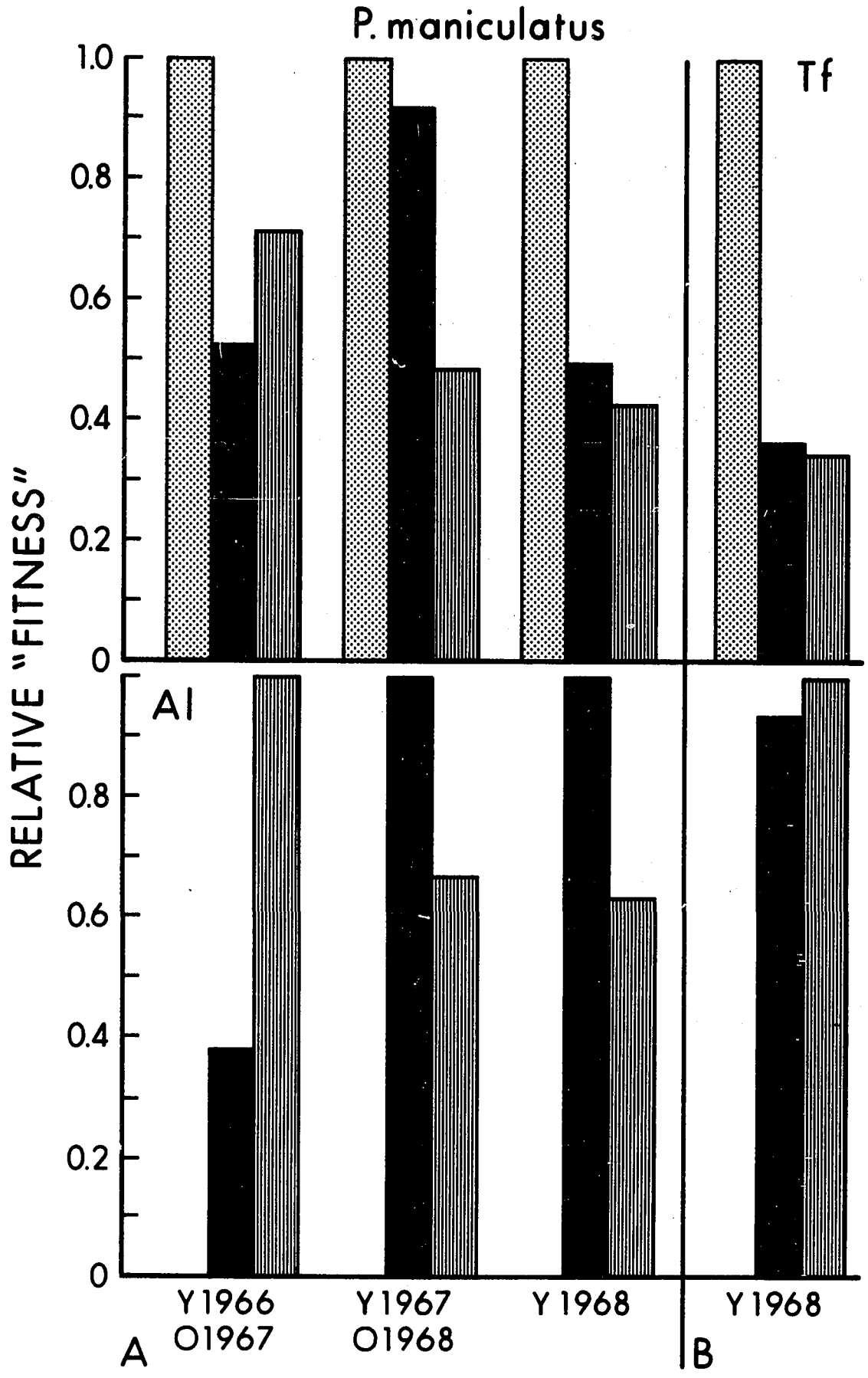

P. maniculatus
Tf
Al
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y 1966
O1967
Y 1967
O1968
Y 1968
Y 1968
A
B

Figure 17. Relative "fitness" of the transferrin/albumin phenotypes in successive generations - P. maniculatus from Great Slave Lake. Sexes and age categories pooled within each generation. Tf JM/Al JM: blocked. Tf J/Al JM, Tf M/Al JM and Tf JM/Al M: striped. Tf J/Al M and Tf M/Al M: checked. O: overwintered animals. Y: young of the year. A and B: trapping zones.

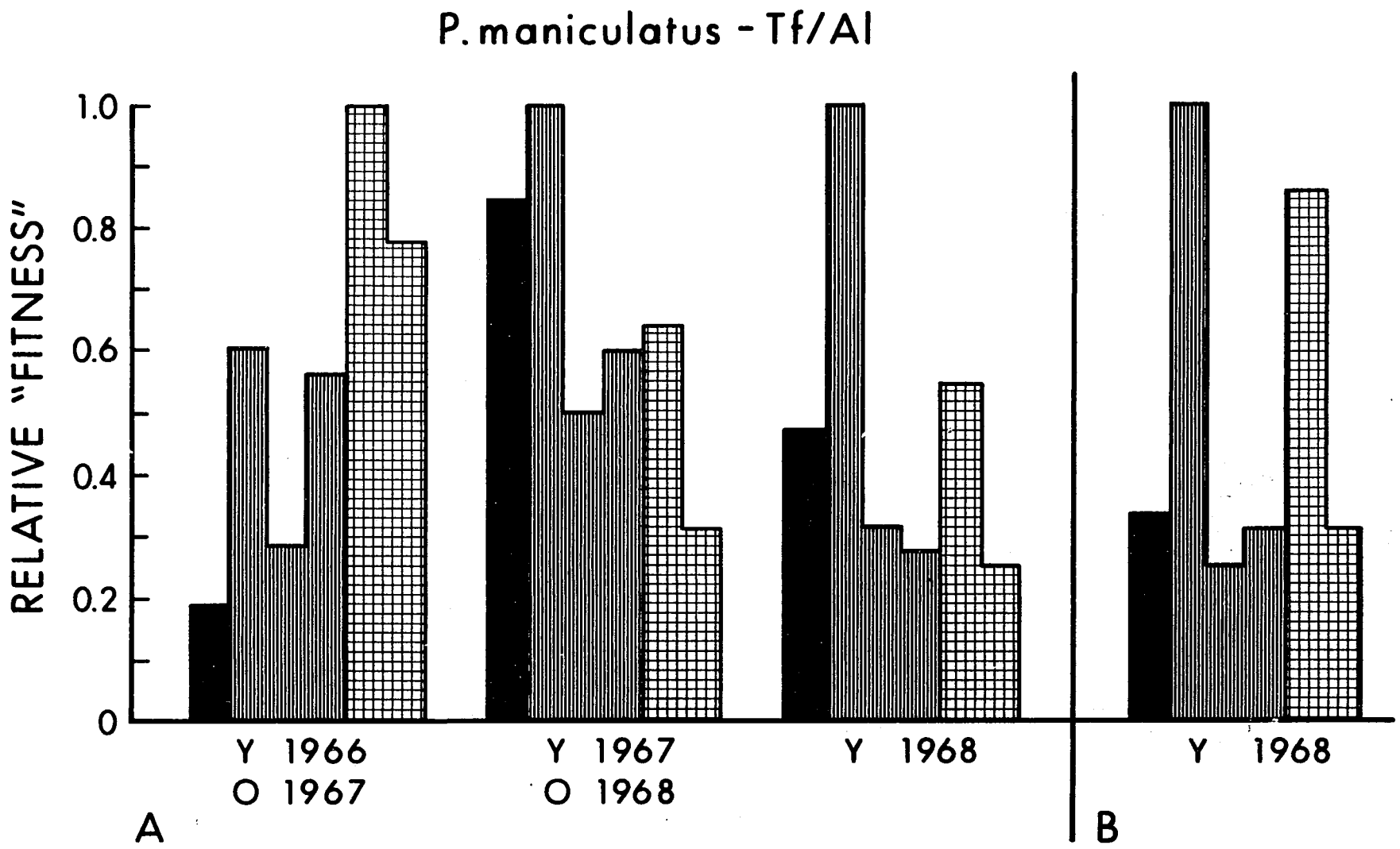

P. maniculatus - Tf/Al
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y 1966
O 1967
Y 1967
O 1968
Y 1968
Y 1968
A
B

Figure 18. Relative "fitness" of the transferrin phenotypes in each sex and age category - C. gapperi from Great Slave Lake. Tf J: stipled. Tf JM: blocked. Tf M: striped. O: overwintered animals. Y: young of the year.

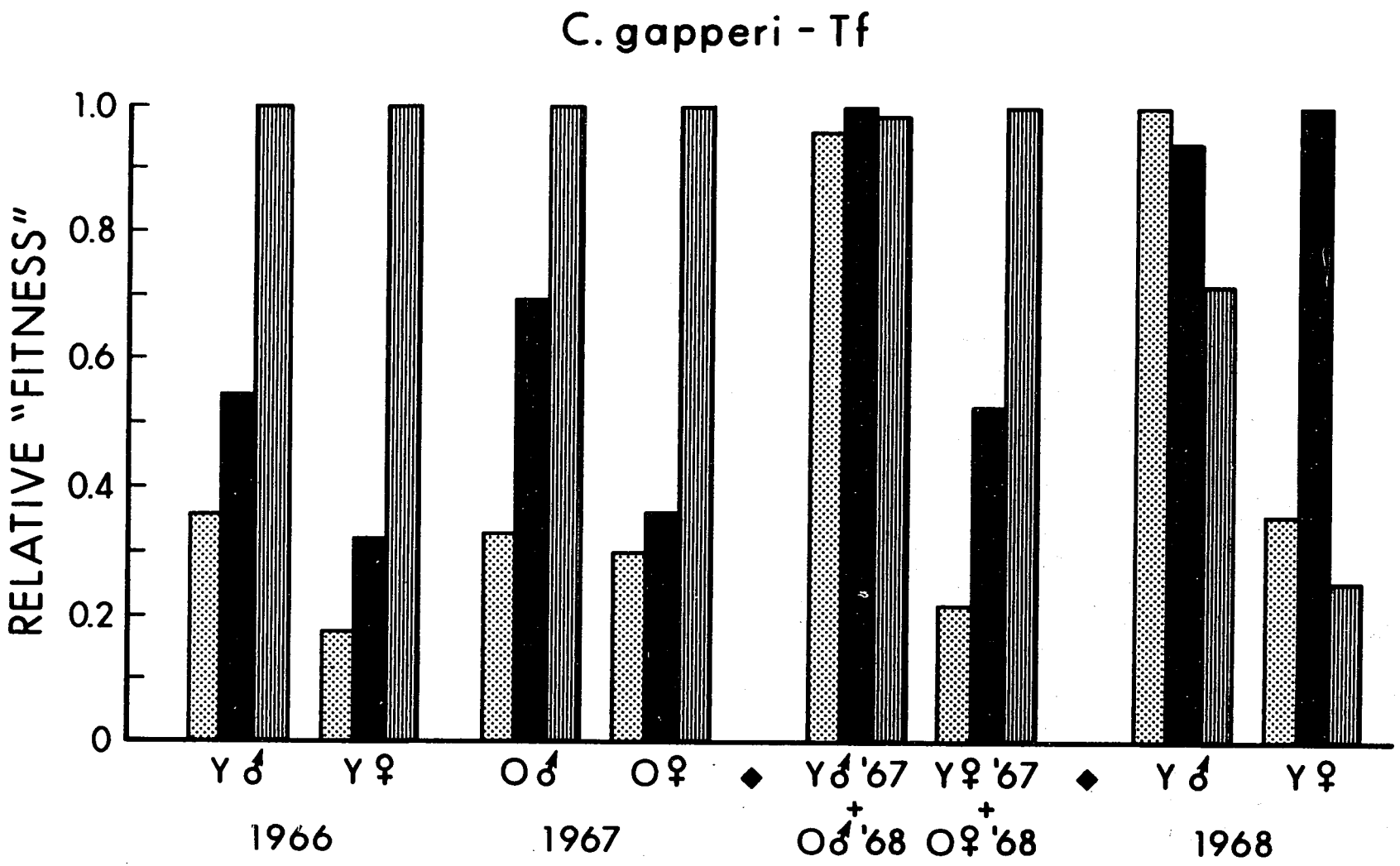

C. gapperi - Tf
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y♂
Y♀
O♂
O♀
Y♂ '67 + O♂ '68
Y♀ '67 + O♀ '68
Y♂
Y♀
1966
1967
1968

Figure 19. Relative "fitness" of the albumin phenotypes in each sex and age category - C. gapperi from Great Slave Lake. Al G: stipled. Al GM: blocked. O: overwintered animals. Y: young of the year.

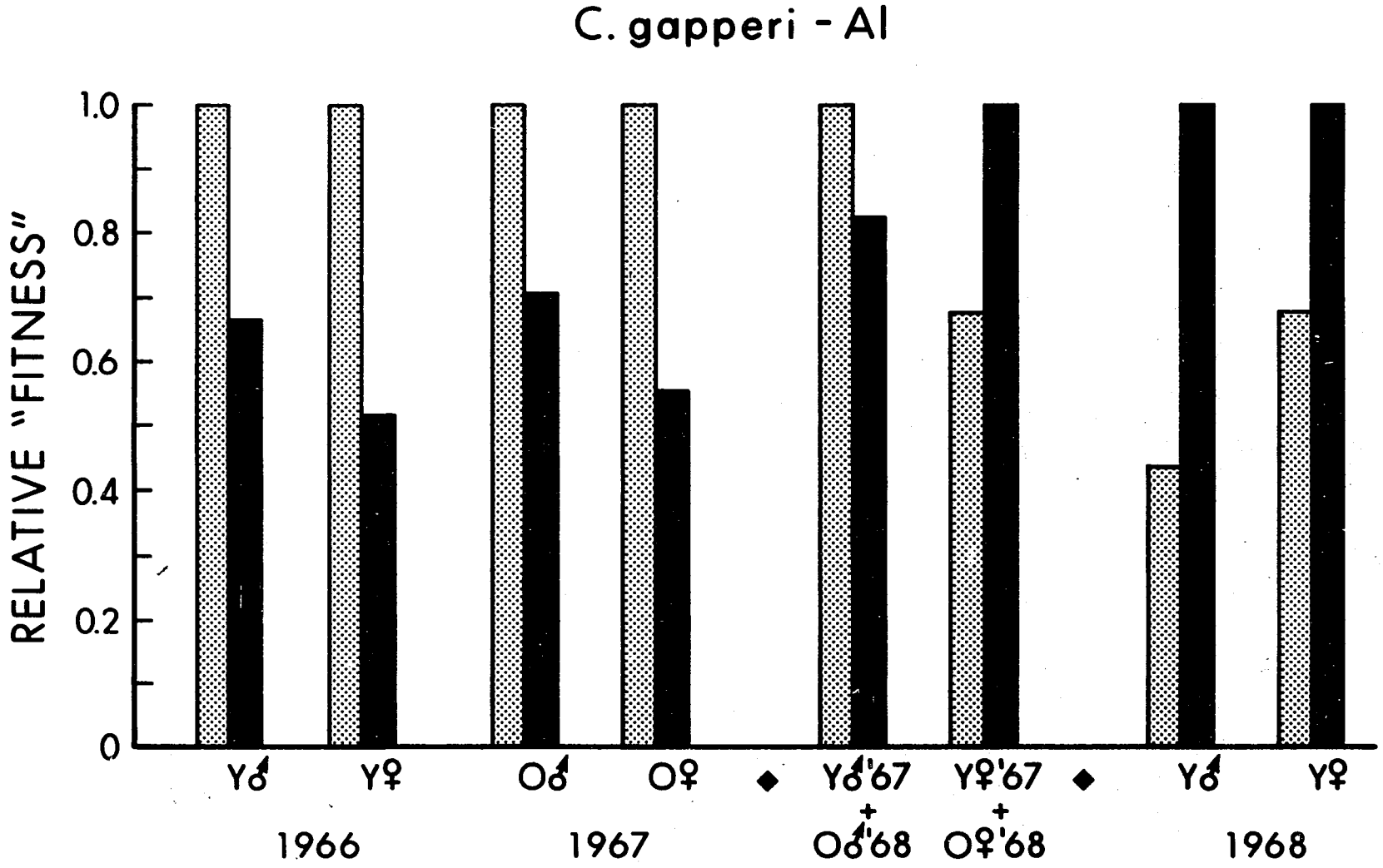

C. gapperi - Al
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y♂
Y♀
O♂
O♀
Y♂'67 + O♂'68
Y♀'67 + O♀'68
Y♂
Y♀
1966
1967
1968

Figure 20. Relative "fitness" of the transferrin and albumin phenotypes in successive generations - C. gapperi from Great Slave Lake. Sexes and age categories pooled within each generation. Tf J and Al G: stipled. Tf JM and Al GM: blocked. Tf M: striped. O: overwintered animals. Y: young of the year.

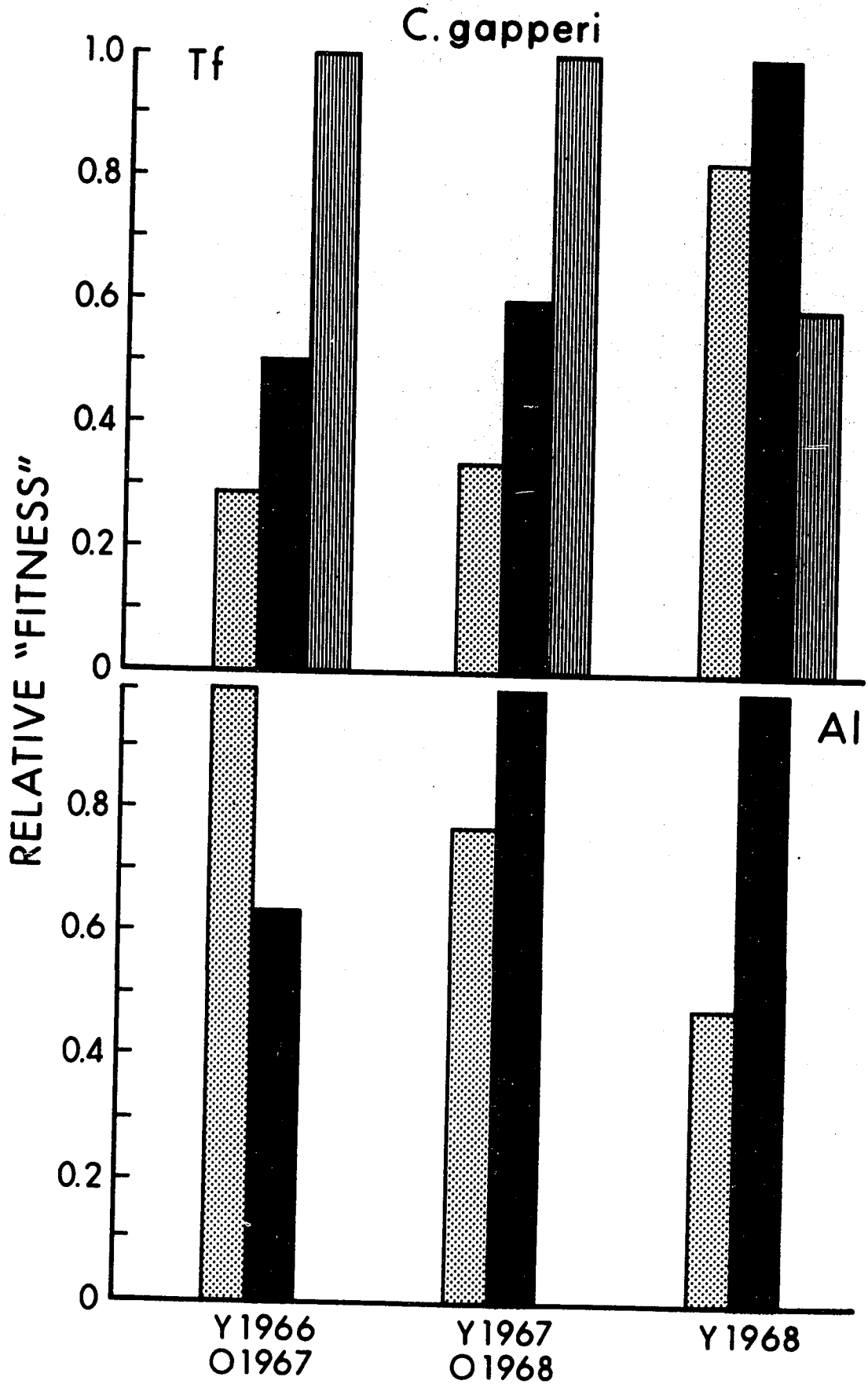
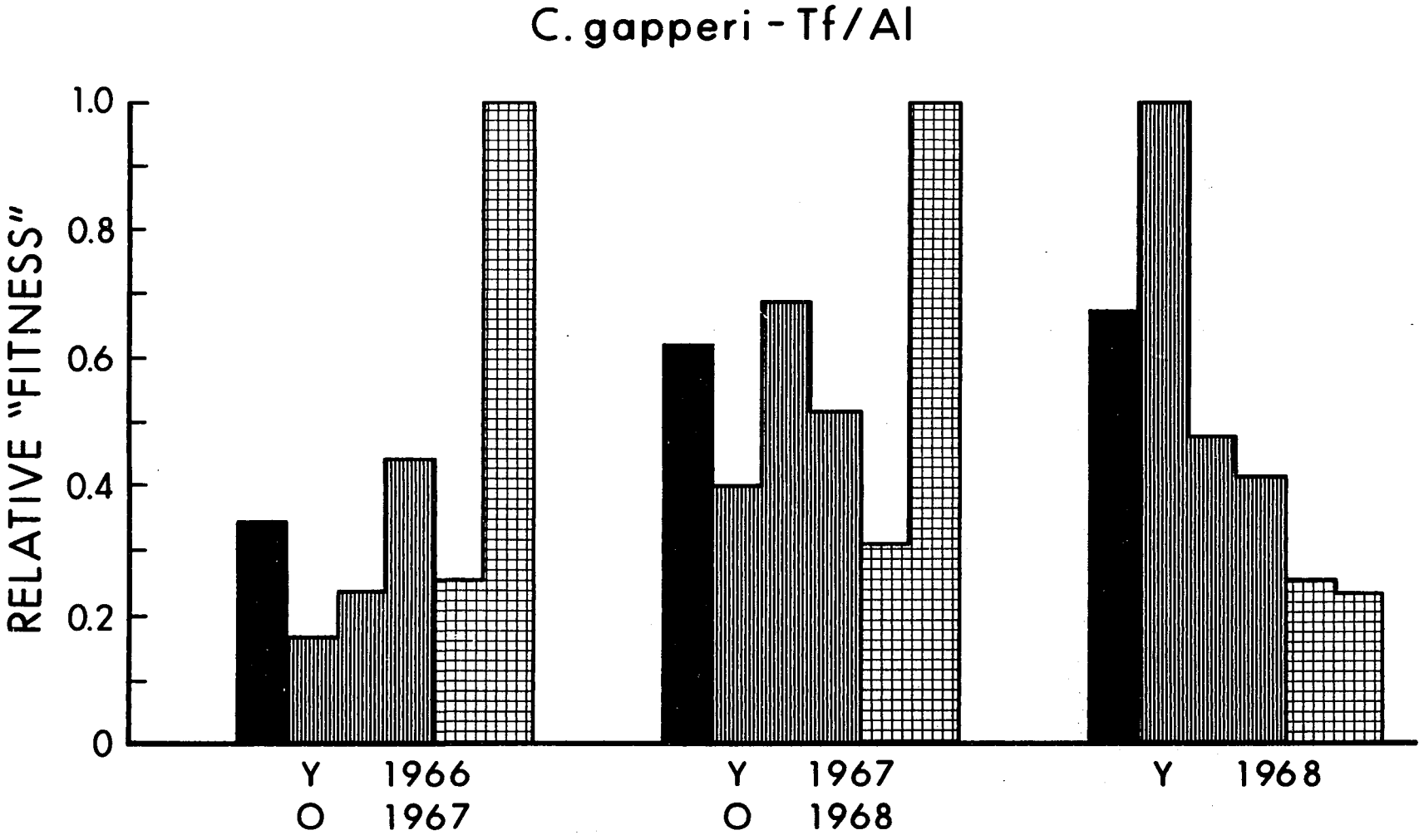

C. gapperi
Tf
Al
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y 1966
O 1967
Y 1967
O 1968
Y 1968

Figure 21. Relative "fitness" of the transferrin/albumin phenotypes in successive generations - C. gapperi from Great Slave Lake. Sexes and age categories pooled within each generation. Tf JM/Al GM: blocked. Tf J/Al GM, Tf M/Al GM and Tf JM/Al G: striped. Tf J/Al G and Tf M/Al G: checked. O: overwintered animals. Y: young of the year.


C. gapperi - Tf/Al
RELATIVE "FITNESS"
1.0
0.8
0.6
0.4
0.2
0
Y 1966
O 1967
Y 1967
O 1968
Y 1968