

Z. Säugetierkunde 54 (1989) 223–228
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ISSN 0044-3468

A method to estimate the survival differences among overwintered *Microtines*: Cyclic *Clethrionomys rufocanus* (Sund.) at Kilpisjärvi, Finnish Lapland

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Receipt of Ms. 15. 10. 1987

Abstract

A method is given to calculate the Standardized Root Length (SRL) of molars. It can be used to examine the changes in age structure of overwintered *Clethrionomys* without grouping the animals in separate cohorts. The age structure of overwintered animals indicated by mean SRL reacted on many different environmental factors. The oldest animals survived best in conditions with increasing mortality and in interspecific competitive situations. Thus the mean SRL seems to be a sensitive indicator of increased mortality. The examination revealed one decline starting earlier in oligotrophic and oligo-mesotrophic heath woods, when the populations in eutrophic meadow woods were still unaffected, thus indicating possible causes of the decline. Resource competition between sexes during decline was indicated.

Introduction

The growth and morphology of the molar teeth have been used as bases for age determination in different *Clethrionomys* species (KOSHKINA 1955; TUPIKOVA et al. 1968; VIITALA 1971, 1977; LOWE 1971; VIRO 1974; PERRIN 1978; WIGER 1979). Reference animals of known age are needed to estimate the real growth rate of the molars in different circumstances (VIITALA 1971, 1977; LOWE 1971; PERRIN 1978). Reference materials have not been available in all studies, however (e.g. KOSHKINA 1955; WIGER 1979). This has resulted in some confusing interpretations.

There are no genital markers that can be used to estimate the possible survival differences in their second summer between animals reproducing in their season of birth and those remaining immature (VIITALA 1977).

The aim of the present paper is to describe a method to estimate the changes in age structure and compare different populations of overwintered animals without sorting the animals in cohorts and to examine some social aspects of demographic changes in a cyclic population.

Material and methods

The material of the present study consists of 701 overwintered specimens of *Clethrionomys rufocanus* snap trapped among 2234 individuals of that species (c.f. VIITALA 1977) collected during 55000 trap nights. The trappings were done 1964–1970 by the expedition headed by the late Prof. OLAVI KALELA in arctic-alpine environment of Kilpisjärvi area both above and below the timber line (for a description of the area s. e.g. KALELA 1957 or VIITALA 1977). As a reference material I have used 267 animals of known age reared in the Department of Zoology, University of Helsinki (VIITALA 1977). Information on age structure changes was also obtained by extensive live trapping study in 1967–1970 (VIITALA 1977) and 1972–1974 (VIITALA 1980, 1984 and unpubl.). The snap trapped material was collected mostly by baited commercial mouse traps in optimal *C. rufocanus* habitats. Some was also obtained by bigger unbaited commercial rat traps as a by-product of lemming trappings in paludified or alpine habitats during the years 1968–1970. According to KALELA et al. (1971) such habitats are suboptimal to *C. rufocanus* which is a typical forest species. Densities obtained in lemming habitats were always

lower than those in optimal habitats (VIITALA 1977). Materials from these two types of trappings have been treated separately.

The age indicator used in the present study was the total root length of M^2 (Fig. 1) (HENTTONEN and VIITALA 1982). Because of the extensive variation of the neck length of the tooth the separate root length did not correlate well with age (VIITALA 1971, 1977). The standardized root length (SRL) was calculated on the basis of measured total root length, to represent the situation on 15th June using formula:

$$l_0 = l_1 + (t_0 - t_1)g$$

where l_0 is the root length on 15th June (SRL) and l_1 that at the date of capture, t_0 is the date 15th June and t_1 is the date of capture and g is the growth rate during breeding season i.e. 0.26 mm/month (VIITALA 1977). Thus the differences in mean SRL observed in different times of the breeding season or in different habitats are due to different age structure. The growth value 0.26 mm/month for breeding season was obtained both from 256 animals reared in the laboratory (VIITALA 1977) and in the wild during a time when live trapping revealed no changes in age structure. The tooth growth during overwintering was much slower (VIITALA 1977).

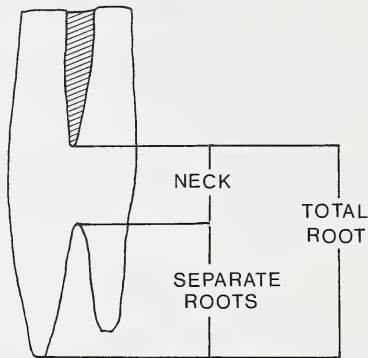


Fig. 1. The way to measure the root length of the second upper molar (according to HENTTONEN and VIITALA 1982) used in calculating the SRL. Because of the extensive variation in the neck length the separate root length did not correlate well with age

C. rufocanus may be the most suitable species for using SRL in a study on age structure since it has bigger teeth and more rapid growth of molar roots than the other *Clethrionomys* species and the root growth starts a month later at the age of two months (VIITALA 1977 and unpubl.). Hence it is easier to measure the age indicator. However, this kind of examination would be possible in other *Clethrionomys* species, too. It could probably be based also on other age indicators than molar root.

Results and discussion

Mean ages in different phases of cycle

In increasing and peak years 1968 and 1969 significant differences did not exist in mean SRLs between late and early summer (before and after July 15). In decline years 1967 and for females in 1964 the mean length was increasing through the summer (Kendalls rank correlation coefficient = 2.735, $P < 0.01$ and 3.884, $P < .001$, respectively). Also in 1967 the mean SRL was higher in late than in early summer (Table 1) (separate variance estimate $t = 2.89$, d.f. = 11.65, $P = .014$; SPSS/PC+, t-test groups; all t-tests have been made by the same procedure).

In 1964 the SRLs of females were significantly higher in late than in early summer ($t = 2.72$, d.f. = 137.33, $P = .007$) but smaller for males ($t = 2.27$, d.f. = 28.4, $P = .031$). Males had significantly higher SRLs than females in early summer ($t = 3.34$, d.f. 26.76, $P = .002$) but not in late summer ($t = .54$, d.f. = 126.09, $P = .591$). This kind of difference between sexes did not exist in other years. This could be understood on the basis of differential

regulation of the sexes (VIITALA 1977). There exists much less space for males that have large home ranges when high ranking mature males are ousting all the younger competitors (c.f. KALELA 1971). In high density situations dispersal may be almost the same as mortality (TAMARIN 1977). The young females are not ousted but they just do not attain maturity in their season of birth (KALELA 1957; VIITALA 1977). Because of the high density attained in late summer 1963 the males may have been sorted by rank already at that occasion with only postbreeding males of equal rank being left. During the decline in the following summer other factors may have become important. I suggest that during a decline, rank is the first factor improving survival. If all animals are equally ranking then young animals may be favoured (c.f. VIITALA 1977). In optimal situation there did not exist other differences in survival of different age groups except those in males during high density.

During severe summer decline in 1970 the SRL was increasing from May to July (means 1.505, 1.652 and 1.811, respectively). Because of the rapid decline (VIITALA 1977) only 8 animals were captured in mouse traps after the end of June. The difference between June and July samples was not significant ($t = 1.55$, d.f. = 8.91, $P = .157$) but the May value was significantly smaller than those of June and July ($t = 2.24$, d.f. = 19, $P = .037$ and $t = 2.74$, d.f. = 11.5, $P = .018$, respectively) (Table 1). The better survival of the oldest animals during that summer was demonstrated by live trapping data, too (VIITALA 1977).

The different development of age structure in males and females during the early decline in summer 1964 was associated by habitat preferences, too. The males were captured significantly more often on barren ground than were females (chi square = 7.606, d.f. = 1, $p = .005$). Data for such examination were available for peak summer 1969, too. The distribution of the sexes was the same (chi square = .0004, d.f. = 1, $p = .979$) in the case. The difference between years 1964 and 1969 was also in interspecific competition which was more severe in the latter year (VIITALA 1977). Also 1964 was a decline year but 1969 a peak year. The *Clethrionomys* males seem to be subordinate to females (МИНОК 1976; VIITALA 1977). Thus, the females may have been ousting males from eutrophic habitats to barren ground during the decline 1964.

After the beginning of the decline in 1964 the females had significantly higher mean SRL i.e. were older in oligotrophic heath forests than in eutrophic meadow forests (Table 1). Thus, the decline may have began in these barren habitats. The SRL of females in meadow

Table 1. Mean SRLs of molars in *C. rufocanus* in eutrophic and oligotrophic habitats in 1964 and 1969 i. e. years when data are available

Time habitat	1964Jn		1964mJn		1964fJA		1964mJA		1969f		1969m	
	eur.	oligotr.	eur.	oligotr.	eur.	oligotr.	eur.	oligotr.	eur.	oligotr.	eur.	oligotr.
mean	1.6072	1.5776	1.7720	1.7590	1.5608	1.6896	1.5725	1.6325	1.8289	1.5680	1.7100	1.8412
s. dev.	.183	.263	.437	.266	.241	.246	.196	.269	.245	.171	.294	.290
s. err.	.044	.062	.195	.067	.049	.037	.057	.039	.082	.111	.038	.057
N	18	17	5	16	24	45	12	48	9	7	7	26
t/P	.39/.701		.06/.954		2.08/.041*		.87/.391		2.89/0.014*		1.06/.319	

Explanations as in Table 1 except Jn = June, JA = July and August, t/P = Students t-test score/probability, * = significant

Table 2. The mean SRLs of second upper molar of *C. rufocanus* in June samples in different years and ways of trapping

Year	1964fo	1964mo	1965o	1967o	1968L	1969o	1969L	1970o	1970L	totals
mean	1.5288	1.7368	1.5455	1.6823	1.9056	1.6924	1.8377	1.6337	1.8514	1.694
N	34	56	11	13	18	49	30	88	21	340
s. dev.	.354	.246	.203	.355	.273	.335	.278	.299	.270	.312
s. err.	.061	.033	.061	.099	.064	.048	.051	.032	.059	.017

Explanations: o = catches on optimal habitats made with small mouse snap traps; L = samples in suboptimal lemming habitats made with bigger rat traps; N = sample size; s. dev and s. err. = standard deviation and standard error, f = females and m = males. Columns without either sign = both sexes combined

woods in late summer 1964 did not deviate from that in early summer. Thus the decline had not yet begun there! This may be related to the finding of OKSANEN and OKSANEN (1981) that the dwarf shrubs of oligotrophic habitats formed antiherbivory phenols during high browsing pressure but the herbs and grasses dominating eutrophic meadow woods did not. Thus, it is suggested that food may have been the main reason of the beginning of decline in that particular case.

In the severe interspecific interaction during summer 1969 the mean SRL of females was higher in eutrophic than in oligotrophic woods (Table 1). This was caused by the intrusion of *Microtus agrestis* on meadow woods. Only the high ranking old animals could resist them, others were ousted (VIITALA 1977). Field voles are unable to occupy heath forests, however (KALELA et al. 1971). Thus the age structure of *C. rufocanus* remained unchanged there (c.f. VIITALA 1977).

Mean ages in optimal vs. suboptimal habitats

There was a statistically highly significant difference between the mean SRLs in samples collected in optimal habitats with baited mouse traps and those collected in suboptimal lemming habitats with unbaited rat traps in 1968–1970 indicating higher mean age in suboptimal habitats ($t = 6.11$, d.f. 129.59, 2-tail $P = 0.000$) (Table 2). The same was true for yearly samples 1969 and 1970 ($t = 2.08$, d.f. 70, $p = .041$ and $t = 3.24$, d.f. 32.86, $P = .003$, respectively). There is some doubt, however, that this difference is at least partly caused by trapping method since in simultaneous trappings in July 1969 in EMT-(*Empetrum-Myrtillus*) heath wood the mean age was higher in animals captured with unbaited rat traps than in those captured with baited mouse traps! ($t = 2.11$, d.f. 34.99, $P = .042$, $N = 16/21$). However, the reason may be that the lemming habitats were moss dominated but the mouse trappings were done in dwarf scrub covered heath woods. This view was supported in June 1968 after a decline when the mean SRL was the same both in lemming and mouse trappings ($t = .17$, d.f. 44.86, $p = .867$) and even in optimal habitats was significantly higher than in other years in optimal habitats ($t = 5.09$, d.f. 28.14, $P = .000$, $N = 251/20$). The small sample obtained after decline in June 1965 did not deviate from other years in optimal habitats, however. This may have been caused by anomalies in tooth growth or by accident due to small sample size.

Conclusions

ZEJDA (1961) first observed the better survival of oldest *C. glareolus* during winter decline. The M²-method without

calculating the mean SRL may not allow careful examination of survival of overwintered cohorts. Thus in all previous studies the overwintered animals are grouped in one cohort.

I conclude that high age may be an advantage in stressful environment and phases of cycle. I believe the most likely reason is social the high ranking animals being able to guarantee sufficient resources even in a deteriorating environment. There seem to be differences in the social status among old breeding animals, even among territorial females. The differences among mature males have previously been discussed e.g. by VIITALA (1977), GUSTAFSSON et al. (1980), and HOFFMEYER (1982, 1983).

Social dominance may be an important demographic factor in any circumstances causing increased mortality. It has been shown that most reproducing animals do not die during winter, but several of them continue to reproduce in their second summer in the subarctic Kilpisjärvi region. In most years this age group is of little importance but after the decline it seems to be the fraction that leads the population to a new increasing phase (VIITALA 1977).

In *Clethrionomys* the changes in mean SRL can be used as a sensitive indicator of changes in mortality. It is much less laborious than the other method available i.e. extensive live trapping. Increasing mortality takes more the youngest overwintered animals thus favoring animals that have been reproducing already in their first summer. Their fates can not be estimated on the basis of any genital markers which disappear at last in the beginning of a new breeding season (VIITALA 1977).

I believe, that other age indicators than molar roots, also can be standardized in same way to study changes in age structure by time without to group the animals in separate cohorts.

Acknowledgements

I am greatly indebted to the late Prof. OLAVI KALELA for providing me most of the material of the present study. His stimulating enthusiasm and deep realism have greatly affected my thoughts. Prof. MICHAEL S. GAINES has kindly read the first draft of the manuscript and made valuable suggestions on it. The errors are my own, however. This study has been supported by grants by The Finnish Academy of Sciences, the State Board of Science and the Eemil Aaltonen foundation.

Zusammenfassung

Eine Methode zur Bestimmung von Unterschieden im Überleben von Graurötelmäusen (Clethrionomys rufocanus) in Kilpisjärvi, Finnisch Lappland

Die auf den 15. Juni bezogene, standardisierte Wurzellänge (SRL) am M² von Graurötelmäusen (*Clethrionomys rufocanus*) kann als Maß für das mittlere Alter Indikator für die Mortalität sein. Mit dieser Methode konnte die Überlebensrate im 2. Sommer zu verschiedenen Zeiten des Dichtezyklus, in unterschiedlichen Habitaten und zwischen den Geschlechtern verglichen werden. Dabei zeigte sich, daß während eines Populationsrückganges das mittlere Alter zunimmt, und daß dieses in oligotrophen Wäldern früher eintritt als in eutrophen. Männchen und Weibchen verhielten sich während des Populationsrückganges unterschiedlich.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1989

Band/Volume: [54](#)

Autor(en)/Author(s): Viitala Jussi A.

Artikel/Article: [A method to estimate the survival differences among overwintered Microtines : Cyclic Clethrionomys rufocanus \(Sund.\) at Kilpisjärvi, Finnish Lapland 223-228](#)