

## DO *CLETHRIONOMYS RUTILUS* FEMALES SUPPRESS MATURATION OF JUVENILE FEMALES?

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### SUMMARY

(1) If adult *Clethrionomys* females suppress the sexual maturation of juvenile females, removing adult females should allow juveniles to breed. We removed all adult *Clethrionomys rutilus* females on two areas of white spruce forest in the southern Yukon from June to August 1984 to test this hypothesis.

(2) More juvenile females become sexually mature on the female removal areas. No juvenile females had litters on the control area whereas thirteen juveniles became pregnant and had litters on the female removal areas.

(3) The estimated number of litters on the experimental grids was only 53% that of the controls, so juvenile maturation did not completely compensate for adult female removals. But the number of juveniles caught in live traps on the experimental areas was 88% that of the controls.

(4) Survival of males and juveniles was no different on control and experimental areas. We infer that adult female *Clethrionomys* cause a 30–48% loss of nestlings and post-weanling juveniles before they are caught in live traps.

(5) Although there is social control of juvenile maturation by *C. rutilus* females, this mechanism operates only at high density and cannot explain population fluctuations of *C. rutilus* in the southern Yukon. We have recorded two outbreaks of *C. rutilus* 11 years apart, associated with the decline phase of the snowshoe hare cycle and possibly caused by changes in winter food supplies or winter predation pressure.

### INTRODUCTION

All *Clethrionomys* species are believed to have a social system of female territoriality in which immature females have the choice of delaying maturation or migrating to search for a vacant breeding space (Bujalska 1970, 1973; Koshkina & Korotkov 1975; Stenseth 1985). This inference has been tested experimentally only twice. Bujalska (1973) removed breeding females from an island population of *Clethrionomys glareolus* and observed an increase in the number of second and third litter juveniles reaching sexual maturity. Saitoh (1981) manipulated the age structure of *Clethrionomys rufocanus* females in outdoor enclosures and found a similar inhibition of juveniles by mature females.

In this study we manipulated the density of adult females of *Clethrionomys rutilus* on two areas by removing all adult females after they had weaned their first litter. We monitored the subsequent density changes and sexual maturation of juveniles on control and experimental grids, and we report these results in this paper.

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*Maturation of Clethrionomys*  
METHODS AND EXPERIMENTS

Our study area is in the Shakwak Trench, a broad valley that transects the south-western Yukon from the Coastal Mountains in the south-east to the edge of the Yukon Plateau in the north-east. Kluane Lake dominates the northern part of this valley and our study area ( $61^{\circ}\text{N}$ ,  $138^{\circ}\text{W}$ ) is approximately 5 km south of that lake. Five live-trapping areas were established in a white spruce, *Picea glauca*, forest along the Alaska Highway (MilePost 1050–1052) ranging in elevation from 870 to 950 m (Fig. 1). Each grid (2.3 ha) consisted of a  $10 \times 10$  network of stations 15 m apart with one Longworth trap pre-baited at each station. Trapping began on two study areas (C1 and FR1) in August 1983 and on the other three in May 1984.

The C1 area has been described previously (grid J of Gilbert & Krebs 1981) and a second grid, FR1, was set up in similar habitat 335 m away. Both areas consisted of a mature white spruce forest with an understorey of willows (*Salix glauca*, *S. scouleriana* and *S. planifolia*), and some *Shepherdia canadensis* with a ground cover of moss and some *Arctostaphylos uva-ursi* and *A. rubra*. The next three areas (C2, FR2 and TR) were established in a different habitat 3 km south. These grids were situated on a slight slope with a north-facing aspect and poorly drained soil. Consequently, the spruce trees were smaller, the ground layer of moss was thicker, and the understorey included several ericaceous species of shrub as well as *Empetrum nigrum*. Both the FR2 and TR grids had small patches of grass. The Kluane region lies in the rain shadow of the St Elias mountains and the study area lies along a gradient of annual precipitation so that the C1 and FR1 grids receive less precipitation than the other grids.

Live-trapping was done for 2 days every second week. We used the same techniques described previously (Gilbert & Krebs 1981). We note one departure from this regime on TR where, after 30 May, we were removing all *C. rutilus*. Due to a temporary shortage of Longworth traps we substituted either Museum Special snap-traps (four trapping periods)

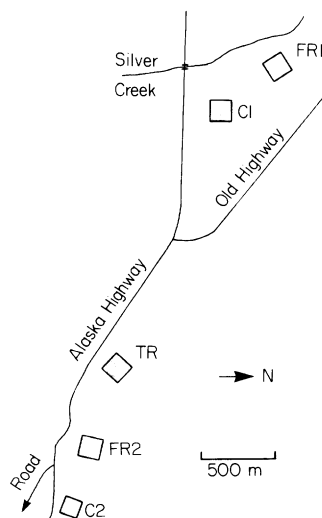


FIG. 1. Map of study area showing location of five live-trapping grids. All grids were of equal size (2.3 ha).

or Sherman traps (one trapping period); however, neither replacement was as successful as Longworth traps ( $\chi^2$  test,  $P < 0.001$ ). We did not pre-bait the replacement traps and their capture rate was low, but there was always a surplus of empty Longworth traps (minimum of thirty-eight) available on the second day of trapping and we think that few animals avoided capture.

We collected information on the timing of parturition and litter size of *C. rutilus* in three ways. We used records from females giving birth in live-traps and also monitored females taken from our removal grids. The latter were either held in the laboratory until parturition or were killed and their litter sizes determined by autopsy.

We were unable to find a suitable site for a sixth grid and thus our experimental design is not fully replicated. We separated the study grids into two groups based on their similarity in initial spring density and habitat. Within each group we assigned the following treatments at random: unmanipulated (control grids C1 and C2) and removal of adult female *C. rutilus* after weaning of the first litter (female removal grids FR1 and FR2). We did a continuous removal of all *C. rutilus* on the fifth grid (total removal TR).

We used weight as an index of age and defined adult *C. rutilus* as animals 21 g or more. Only a few young of the year, born early in the season, bred on control grids to we did not differentiate between subadults and juveniles. In most comparisons we have tried to classify animals as either overwintered adults or young of the year juveniles.

## RESULTS

### *Density*

Rodent densities in the Kluane region were exceptionally high in 1984. In late September 1983, density (minimum number known alive) of *C. rutilus* on C1 was forty animals and final autumn density was probably higher (Fig. 2). Spring density in 1984 of males and females was similar on C1 (26 and 18.7, respectively) and FR1 (27.6 and 17.3). Density

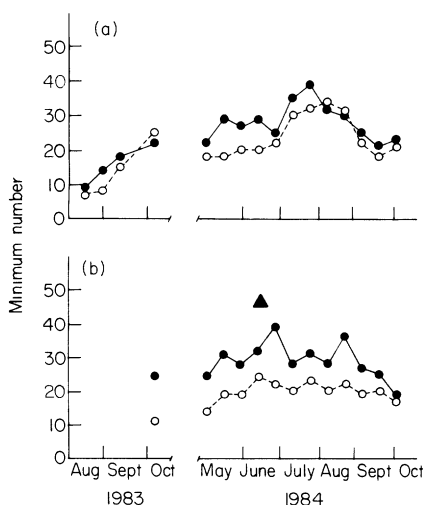


FIG. 2. Population size of *Clethrionomys rutilus* males (—●) and females (—○) on (a) control grid C1 and (b) adult female removal grid FR1. (▲), Female removal started.

was approximately 30% lower on the other grids (Fig. 3). There was a slight excess of males on all grids (overall spring sex ratio of males to females, 57:43), and this ratio was especially unbalanced on FR2 (61:39). Young of the year began to enter traps after the first week of June and all grids subsequently showed an increase in density. Our selective removal of adult females began in the first week of June on FR1 and FR2 and all resident females had been removed by the last week of June. Overall, we removed seventeen females on FR1 and 13 on FR2. Density of the control populations peaked in late July with over seventy animals per grid. Both C1 and FR1 had similar September densities in 1984 and numbers were approximately equal to initial spring densities. Although both C2 and FR2 grids had similar autumn densities these values were much higher than the initial breeding density in spring (68% and 59% increase, respectively). On the TR grid we began to remove all trappable residents at the end of May (Fig. 4). Over the entire season we removed a mean of 17.5 males and 15.7 females per trapping session.

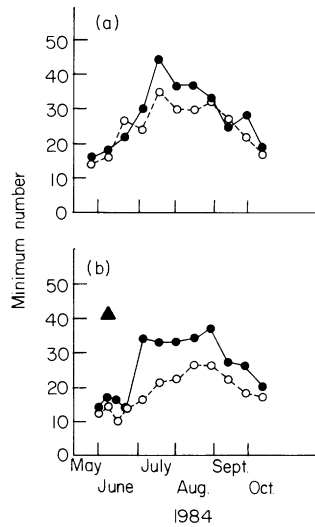


FIG. 3. Population size of *Clethrionomys rutilus* males (—●) and females (—○) on (a) control grid C2 and (b) adult female removal grid FR2. (▲), Female removal started.

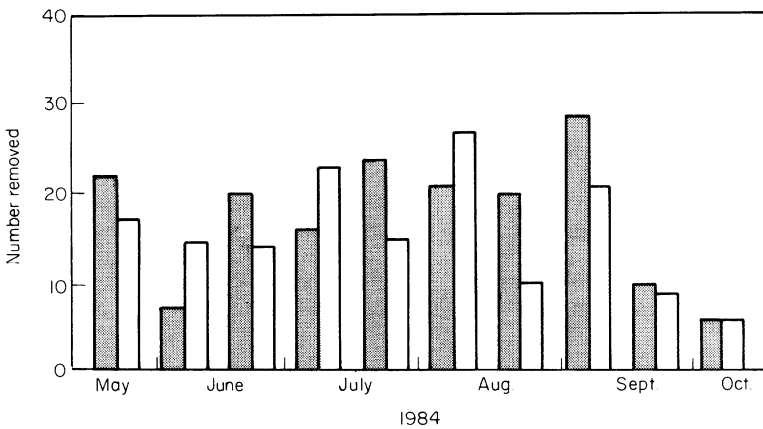


FIG. 4. Numbers of red-backed voles removed at 2-week intervals from the grid TR for males (■) and females (□).

These data allow three conclusions. The absolute density on control grids in 1984 was exceptionally high when compared with results from previous years (Fig. 5). We cleared large numbers of immigrants from the total removal area (33.2 per trapping session) in 1984 compared with the previous total removal experiments where we removed relatively few (1.7–6.0 per 2 weeks, Gilbert & Krebs 1984). Secondly, each control grid and its associated experimental grid had similar spring densities, although the two sets of replicates differed by 30%. Thirdly, the long-term effect of our heavy cropping of all adult females was minor. September numbers were similar on both control and adult female removal grids. We now turn to determine how this was achieved.

### *Immigration*

On the total removal area we defined immigrants as untagged animals that moved onto the grid after the initial resident population had been cleared. Most immigrants were juveniles (89%,  $n = 292$ ). However, two aspects of adult immigration seem noteworthy. Adult females were more likely to immigrate to the area that had been cleared of all animals than to areas where only adult females had been removed (Table 1). We recorded only two instances of adult females moving onto either female removal grid after 25 June, whereas we removed eleven adult females from the total removal grid during that period.

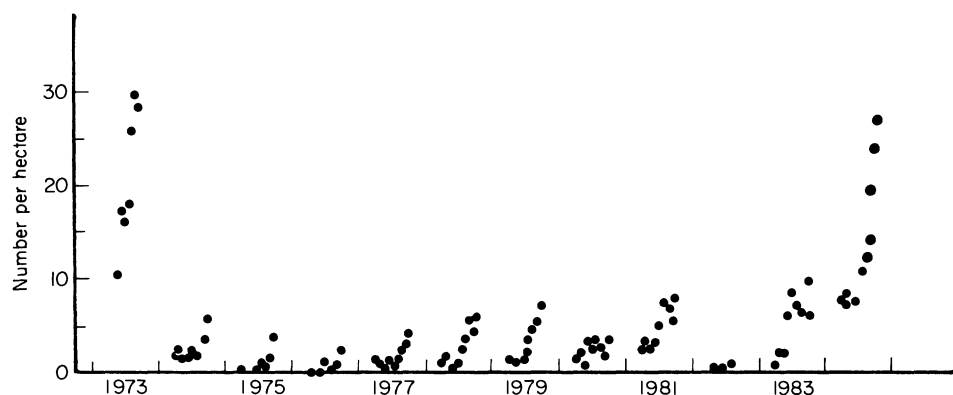


FIG. 5. Long-term fluctuations in density of red-backed voles *Clethrionomys rutilus*, pooled data, Kluane Lake, Yukon, 1973–84. Data drawn from control populations: 1973–75, C. J. Krebs (unpublished); 1976–79, Gilbert & Krebs (1981); 1980–81, Gilbert & Krebs (1984); 1982–83 C. J. Krebs (unpublished); and 1984, this study.

TABLE 1. Numbers of adult (overwintered) *Clethrionomys* immigrants in 1984

	Grid*				
	C1	FR1	C2	FR2	TR
<b>Males</b>					
15 June–14 July	1	0	0	3	16
15 July–October	0	0	3	1	2
Total	1	0	3	4	18
<b>Females</b>					
15 June–14 July	0	1	1	1	5
15 July–October	1	0	0	0	6
Total	1	1	1	1	11

\* C, control; FR, female removal; TR, total removal.

Immigration of adult males was important in only one period from mid-June to mid-July when sixteen animals moved onto the total removal area. There was no pattern to the small amount of immigration to our other grids. To conclude: adult immigration seemed numerically unimportant on control grids and on areas where only adult females were removed. Significant immigration of adult males and females was observed only on the total removal area.

### Reproduction

Population increase may be caused by either immigration or births and in this section we concentrate on births with particular emphasis on juvenile reproduction. The breeding season was already underway when live-trapping began in May. By this time all males had scrotal testes and all females perforate vaginae. Except for one adult female that failed to become pregnant, all adults were in breeding condition and breeding intensity of adults approached 100% during the main breeding season. Most overwintered female *C. rutilus* had their first litter of the season between 14 May and 6 June, to judge from our autopsy results and records of females giving birth in live-traps or the laboratory. Young of the year were first caught in live-traps between 7 and 14 June. The male breeding season finished at the end of August. Most adult males had scrotal testes in mid-August (83%,  $n = 24$ ), but the testes of all males had regressed by September. All adult females on the two control grids were lactating or pregnant until mid-August and the proportion of females breeding declined until September.

We have measured the reproductive success of the female population by calculating an index of juvenile production which equals the number of juveniles tagged divided by the estimated number of litters weaned on a grid. The number of litters produced can be estimated from live-trapping records but the figure for the number of juveniles tagged represents both animals born on the grid and an unknown number of juvenile immigrants. Both control grids had lower estimates of juvenile production than the female removal grid (Table 2) and we offer two explanations. Juveniles on the female removal grids may have survived better to a trappable age. It is also possible that more juveniles immigrated to the adult female grids, so inflating the estimate of *in situ* juvenile production.

Some juvenile female *C. rutilus* come into breeding condition (perforate vagina) in the summer of their birth, but rarely have we recorded one of them having a litter in a control population. This seems incongruous because the external sign of a perforate vagina is usually a reliable indicator of puberty (Bujalska 1970). Live-trapping of individual adults show a predictable time sequence of a perforate vagina followed by pregnancy and eventually lactation after parturition. We cannot explain why young of the year in a control population fail to become pregnant but a few possible explanations are: (i) the external sign of a perforate vagina may not always indicate oestrus, (ii) juveniles may come into oestrus but fail to conceive, and (iii) juveniles may conceive, but the pregnancy may be lost by resorption.

TABLE 2. Estimates of female *Clethrionomys* production for 1984

	Grid			
	C1	FR1	C2	FR2
Number of juveniles	125	119	146	117
Estimated number of litters	44	22	34	19
Juvenile production per litter	2.84	5.41	4.29	6.16

The experimental removal of adult females had a significant effect on the breeding activity of females born in June and July (Table 3). More female juveniles were in breeding condition on the adult female removal grid than on the control and at least thirteen juveniles became pregnant on these removal grids while there were no pregnancies on the controls. Relatively few individual females were involved in breeding activity on any single grid. There was no decrease in the age at sexual maturity of males on the experimental grid and the absolute number of juvenile males that developed scrotal testes was very small (<10 males, all grids pooled).

The main conclusion from this section is that young of the year females of *C. rutilus* were capable of successful reproduction when adult females were removed. The ratio of the number of young recruited per litter was also increased on these experimental grids, and this implies that adult females inhibit juveniles either through poorer juvenile survival or more emigration.

### Survival

We now consider the impact of the adult female removal experiment on the survival or loss rate of the tagged population. Was the survival of adult males and juveniles altered by removing adult females? For ease of comparison we have standardized our survival rates to 14-day periods (Krebs 1966). Adult males showed similar trends in survival on both control and experimental grids (Table 4). There was no evidence that males emigrated from the female removal grid after all adult females had been removed. Juvenile males and females had very similar trends in survival on both control grids. Differences in juvenile survival rates between the control and experimental grids were slight and there was no statistical difference in mean survival between the grids for the 2-month period from mid-June to mid-August (Table 4).

If juvenile survival rates did not differ on all grids (Table 4) and the number of juveniles produced per litter was higher on the female removal grids (Table 2), this must mean that the survival of nestlings and small post-weanling juveniles was higher on the two female

TABLE 3. Percentage of female juvenile (young of the year) *Clethrionomys* entering breeding\* condition in 1984

	Grid				
	C1	FR1	C2	FR2	TR
June	12 (8)†	31 (13)	53 (15)	82 (11)	87 (23)
July	7 (29)	32 (28)	20 (30)	46 (24)	3 (33)
August	0 (30)	7 (27)	0 (27)	24 (33)	3 (36)
Number pregnant	0	4	0	9	0

\* Breeding is defined as females with perforate vagina, or lactating, or obviously pregnant.

† Sample size in parentheses.

TABLE 4. Probability of survival per 2 weeks ( $\pm 1$  S.E.) estimated from the Jolly-Seber model for adult males and juveniles for the summer of 1984

	Grid			
	C1	FR1	C2	FR2
Adult males	0.86 $\pm$ 0.04	0.80 $\pm$ 0.04	0.83 $\pm$ 0.05	0.78 $\pm$ 0.04
Juvenile males	0.72 $\pm$ 0.04	0.76 $\pm$ 0.04	0.72 $\pm$ 0.03	0.76 $\pm$ 0.03
Juvenile females	0.70 $\pm$ 0.04	0.74 $\pm$ 0.04	0.73 $\pm$ 0.04	0.76 $\pm$ 0.04

TABLE 5. Overwinter survival from September 1983 to April 1984 of tagged *Clethrionomys* standardized to 8-month periods

	Grid	
	C1	FR1
Males	0.65 (24)*	0.68 (24)
Females	0.64 (26)	0.70 (11)
Total	0.64 (50)	0.69 (35)

\* Sample size in brackets.

removal areas. From Table 2 we calculated a 48% higher loss rate of these small juveniles on the C1 grid relative to the FR1 grid, and a 30% higher loss rate of small juveniles on C2 relative to the FR2 grid. We infer that this increased loss resulted from the presence of adult breeding females on the control areas after mid-June.

We estimated overwinter survival (1983–84) of tagged animals on two grids (C1 and FR1) and these estimates were standardized to an 8-month period (Table 5). Overwinter survival was very high for this particular winter and there were no statistically significant differences between sexes or grids.

#### *Female spatial distribution*

Do breeding *C. rutilus* females avoid contact with other breeding females by utilizing exclusive areas? Our analysis here was limited by the incomplete nature of live-trapping data as well as by the fact that we had few data for each female. Many females were caught along the perimeter of the grid and more than half of all adult females on control grids were caught ten times or less during the breeding season. Only seven adult females on C1 and four on C2 had less than 50% of their captures on the core of the grid. The activity ranges of these females overlapped little. A second analysis included all adult females caught during the breeding season on our two control grids. If adult females are intolerant of contact with each other then we should rarely catch two females at the same trap station during a single trapping session. On C1 we recorded this on fifteen (5.5%) occasions out of a total of 275 captures and on C2 nine (4.8%) times out of 189 captures. We conclude tentatively that breeding adult females avoid contact with each other by maintaining separate areas of activity.

## DISCUSSION

Our results from reducing adult female densities of *Clethrionomys rutilus* on experimental areas in the southern Yukon are consistent with the observations of Koshkina & Korotkov (1975), and the experiments of Saitoh (1981) and Bujalska (1973). Mature *Clethrionomys* females do seem to suppress the sexual maturation of young females. Bujalska (1973) claims that territorial behaviour of mature females during the breeding season results in a constant density of breeding females. This complete compensation was not found in our study (Table 3). Less than 70% of the adult females that we removed were replaced by juveniles although there was an excess of juveniles present. Our data on the spatial distribution of animals on our live-trapping grids suggest that breeding females have non-overlapping home ranges. Hence we cannot understand why some empty territories on the female removal grids remained vacant. Although there was significant movement of adult females to a total removal area, we did not find adult females moving in to replace females that had been selectively removed earlier on the two female removal areas.



We never recorded obviously pregnant juvenile females on the total removal area, and in July very few females there had perforate vaginae (Table 4). This inconsistency may be explained by our trapping technique. Since we removed all animals at bi-weekly intervals, we suspect that some of these juvenile females may have been in the early stages of pregnancy. If we had maintained these females in the laboratory after their removal we would have been able to detect eventual pregnancies.

Several workers have described the population dynamics of subarctic populations of *Clethrionomys* in North America. Both Mihok (1979) and West (1982) suggested that the failure of *Clethrionomys* to show social control of juvenile reproduction was due to low population density. We also found low density of *Clethrionomys* in most years in the southern Yukon (Fig. 5), and the breeding density in any given year is controlled more by overwinter survival than by reproductive output. Increasing *C. rutilus* populations do not stop increasing because of reproductive suppression, but rather because of heavy overwinter mortality. At high densities, such as in 1984, reproductive output was reduced because juveniles of either sex rarely matured in control populations. At these densities our present experiments did show social control of juvenile reproduction.

Koshkina & Korotkov (1975) found that the start of the breeding season of *C. rutilus* was delayed in years of high spring density. We did not find such a delay in 1984. Adult voles began breeding in the spring at the same time as in years of low numbers.

Our long-term data on *Clethrionomys* numbers suggest an 11-year interval between high populations (Fig. 5). Grant (1976) similarly found a 10-year interval between high numbers of *Clethrionomys gapperi* in Québec, Canada. We suggest that these outbreaks of *Clethrionomys* are linked to the 10-year cycle of snowshoe hares in the Canadian boreal forest and tend to occur 2 years after the peak of the hare cycle. Two mechanisms are possible. Food plant production might be increased after hares decline and this might allow better survival of voles. Alternatively, predation on voles might be reduced after the hares decline and their associated predators also crash (Hansson & Henttonen 1985). Since the key to *Clethrionomys* outbreaks is high overwinter survival (Table 5), we must be dealing either with winter predation or winter food supplies. The white spruce (*P. glauca*) cone crop was extremely large in 1983 at Kluane and could be part of the mechanism that generates outbreaks in vole numbers.

Stenseth (1985) has shown that female territoriality tends to stabilize the population dynamics of *Clethrionomys*. We suggest that in our study area *C. rutilus* populations are not often affected by female suppression of juvenile maturation. The dominant pattern of population outbreaks at long intervals is produced by other destabilizing factors such as large changes in food supply or predation.

#### ACKNOWLEDGMENTS

We thank Jean Carey, Mark Simpson, Alice Kenney and Kelly Nordin for their help with field work. The Arctic Institute of North America provided support at their Kluane Lake Research Station. This work was funded by the Natural Sciences and Engineering Research Council of Canada. We thank Adam Watson for a critical review of this paper.

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(Received 9 July 1985)