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Ecology of red-backed voles (*Clethrionomys gapperi*) in a gradient of gamma radiation

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The demography of red-backed voles was monitored in boreal forest in southeastern Manitoba, Canada from 1967 to 1982. Catches on spring index lines and summer removal grids revealed only modest fluctuations in density with no evidence of a typical microtine population cycle. Beginning in 1973, four summer removal grids were exposed to an approximately exponentially decreasing field of gamma radiation from an artificial ^{137}Cs source. Three grids located a few km from the irradiated area served as controls. Voles living in the irradiated area with very high dose rates were more likely to be immature and were smaller than voles living in areas exposed to lower dose rates. No other radiation-specific trends were detected. Major demographic differences occurred from year to year rather than between the irradiated and control area. Features characteristic of *Clethrionomys* species, such as inhibition of sexual maturity in young of the year at high density, were characteristic of all populations.

Chronic exposure to radiation was insufficient to produce a depression in vole numbers. Radiation-induced death or sterility over an area of about 2–5 ha was presumably balanced by recruitment from surrounding areas exposed to lower levels of radiation. The inability of both the snap-trapping program and the radiation manipulation to affect demography suggests that *Clethrionomys* populations are insensitive to additional, random mortality. These results argue against the role of an established social structure in the regulation of population density.

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1. Introduction

Although the red-backed vole (*Clethrionomys gapperi*) is found throughout most of North America, its ecology has been studied extensively only at 61°N latitude in the subarctic boreal forest of the Northwest Territories (NWT) in Canada (Fuller, 1985). Studies in other areas have been of limited scope and duration (Miller & Getz 1977, Merritt & Merritt 1978, Martell 1983). The ecology of its northern counterpart (*C. rutilus*) also has not been studied extensively (Martell & Fuller 1979, West 1982) outside of the marginal NWT population monitored by Fuller and coworkers (Fuller 1985).

Here, we report on the demography of a *C. gapperi* population monitored from 1967 to 1982 at 50°N latitude in southeastern Manitoba, Canada. Vole numbers were monitored in both control and irradiated areas as part of a comprehensive study of the effects of gamma radiation on a boreal forest ecosystem (Guthrie & Dugle 1983); for those unfamiliar with concepts in radiation biology, we have provided a few basic details pertinent to this study in the Appendix. Here we present the collected demographic data in terms of their relevance to our current understanding of *Clethrionomys* population dynamics.

2. Methods

2.1. Summer grid trapping

Small mammals were trapped in control and irradiated areas of boreal forest in vicinity of the Whiteshell Nuclear

Research Establishment near Pinawa, Manitoba, Canada (50°11'N, 96°1'W). Summer populations were sampled on 1.1 ha grids (8×8 stations, 15 m spacing) that were trapped with two Museum Special snap-traps per station for 30 days during June, July or August from 1968 to 1982. These grids were consistent from 1974 on. Full details of methods will be given in Schwartz (1985).

A detailed habitat description is given in Iverson & Turner (1973). A brief synopsis follows:

1) WPG — Woods Grid, a control grid trapped in July 1968 and 1969, and August 1970-1982. It was located in a moist ash (*Fraxinus nigra*) forest with additional deciduous elements.

2) RPG — River Grid, a control grid trapped in June 1970-1973, and August 1974-1982. It consisted of 9×7 rather than the standard stations and was located next to the Winnipeg River in young mixed deciduous forest dominated by aspen (*Populus tremuloides*) and birch (*Betula papyrifera*). A few patches of ash as well as some oak (*Quercus macrocarpa*) were present.

3) CPG — Creek Grid, a control grid trapped in August 1970-1982. It was located in mature mixed deciduous forest dominated by aspen and was divided by a seasonal creek.

4) PPG — Puddle Grid, a control grid trapped in June from 1971 to 1973. This grid was covered by standing water in spring and was covered by scattered bushes of mountain maple (*Acer spicatum*) in dry areas and the occasional ash tree.

5) FIG — Field Irradiator Gamma, a mixed forest (Dugle 1969, 1972) that has been irradiated since March 1973 by a 370 TBq ^{137}Cs gamma-emitting source suspended 20 m above ground level (Guthrie & Dugle 1983).

Four grids were trapped within the FIG area: FIG NWII, FIG N, FIG SW and FIG SE (Fig. 1). FIG NWII was in mixed aspen-birch forest similar to the control grids, but with more coniferous cover. The other FIG grids were in mixed coniferous forest with the canopy dominated by balsam fir (*Abies balsamea*, FIG N), jack pine (*Pinus banksiana*, FIG SW), or black spruce (*Picea mariana*, FIG SE). The FIG SE grid was a sphagnum bog that graded into a mixed spruce and tamarack (*Larix laricina*) bog to the east (Fig. 1). The demarcations in Fig. 1 indicate moderately clear habitat boundaries that occur over a 5-10 m transitional zone. The map was produced from a compilation of data from botanical quadrats (Dugle & Thibault 1974), small mammal habitat studies (Iverson & Turner 1973), and an aerial photo.

All FIG grids were trapped in July from 1970 to 1982 except for FIG SE (June, 1970-1972) and FIG SW (August, 1970). For most years, data from FIG grids trapped in July could be contrasted with three control grids trapped in August.

2.2. Radiation fields within FIG

The radiation field within FIG diminishes approximately as a function of the square of the distance from the irradiator; background levels are reached at a distance of slightly more than 0.5 km (see Guthrie & Dugle 1983: fig. 4). Starting in autumn 1972, the dose rates 2 cm above ground level were measured with plastic vials containing two aluminum foil-wrapped Harshaw TLD-100 LiF dosimeters placed at the 256 mammal trapping stations for four one-year periods. Dose rates were similar to those monitored by other workers, and varied from 0.05 to 50.0 mGy/h depending on the distance from the irradiator. Irradiation was generally continuous with an average of 20% down-time due to visits to the study area (Guthrie & Dugle 1983).

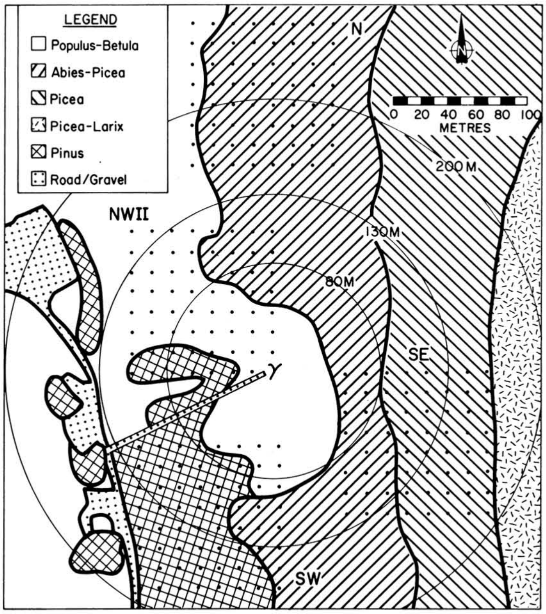

Fig. 1. Gross habitat types and locations of the small mammal trapping grids within the Field Irradiator Gamma area near Pinawa, Manitoba.

The trapping stations within FIG were divided into areas of very high dose rates (mean of 15.3 mGy/h, 0-80 m from the irradiator), high dose rates (1.9 mGy/h, 80-130 m), medium dose rates (0.4 mGy/h, 130-200 m) and low dose rates (0.09 mGy/h, > 200 m, Fig. 1). These categories were chosen to balance the vole captures across habitat types so that each dose category would be represented by a spectrum of habitats. The very high dose area underwent severe changes in canopy cover during the first few years of irradiation (Dugle & Mayoh 1974, Amiro & Dugle 1985). Most trees out to about 50 m died within a few years. At present, gross effects are not obvious past about 80 m, although some conifers appear to be dying out to about 100 m.

As an interpretive guideline, we can reasonably assume that voles living within the very high dose rate area (2.0 ha) accumulated a gamma-ray dose equal to a laboratory LD$_{50,30}$ X-ray dose (Buech 1971) in about 5.7 weeks. Voles in the high dose rate area (3.3 ha) accumulated the same dose in 46.2 weeks. Although based on ground-level dosimeters, these estimates are probably not substantially different from actual values obtained with dosimeters carried by voles (Mihok, unpubl. data).

2.3. Spring index lines

Spring numbers were estimated by trapping permanently-marked, 20-station lines for three days shortly after snow-melt with three Museum Special snap-traps per station. Trapping covered a six-week period around the month of May, thereby sampling the overwintered population. Lines were trapped from 1967 to 1982; consistency in the dates, sequence, and lines trapped occurred from 1975 on, with partial consistency from 1972 on. These studies are more fully summarized in Mihok et al. (1985), with a complete tabulation of methods, numbers, etc. in Schwartz (1985).

2.4. Acute radiation sensitivity

Recently-captured local *Clethrionomys* were exposed to acute dose rates of X-rays in October, 1976 by methods identical to those used for meadow voles (*Microtus pennsylvanicus*; Iverson & Turner 1976a). Seven groups of 36 *Clethrionomys* each (18 male, 18 female) were exposed to acute total doses of 7.8, 8.8, 9.5, 10.0, 10.5, 11.3 and 12.3 Gy. From probit analysis (Finney 1971) of the proportions surviving for 30 days in the laboratory, the $LD_{50,30}$ for *Clethrionomys* was 11.8 Gy (95% fiducial limits of 11.3-12.2 Gy).

2.5. Autopsy procedures

Most animals were weighed fresh, and then frozen for later autopsy. After thawing, body lengths were taken and reproductive organs were examined for macroscopic signs of sexual maturity (females: perforate vagina, pregnancy, placental scars; males: testis length larger than or equal to 8 mm, large, coiled epididymis). Testis length was measured in males, and macroscopically visible embryos or recent placental scars were counted in females. To examine trends in age structure and sexual maturity we chose 18 g as a cut-off weight for the classification of voles as juveniles or definite young of the year (juvenile vole, see Perrin, 1979). Here we are using the term "juvenile" to indicate youth as opposed to sexual immaturity. This conservative classification probably excluded all overwintered voles at the expense of excluding some young of the year (Perrin 1978). As autopsies were done on previously frozen material, faint placental scars or very small embryos may have been missed, leading to some bias toward classification of females as immature.

2.6. Demographic statistics

We calculated descriptive statistics for the FIG area as a whole and for each of the controls for each year. These statistics were compared by ANOVA or G-tests, with a priori planned multiple comparisons for heterogeneity among controls, or between FIG and the pooled controls (Sokal & Rohlf 1981:239, 745). Unless noted otherwise, we considered differences significant only for $p < 0.01$, so that our interpretation of radiation effects would be relatively conservative. The eleven variables chosen for statistical tests were: male weight and length, female weight and length, male testis length, proportion of population male or juvenile, proportion of males that was mature, proportion of females that was mature or lactating, proportion of juveniles that was mature. Litter sizes as estimated by embryo or recent placental scar counts were tested only for the whole data set as sample sizes were small. We also calculated fluctuation indices, *s*, for our populations (see Henttonen et al. 1985), defined as the standard deviation of the logarithm (with base 10) of each year's catch (grids) or density index (lines, catch per trap-night).

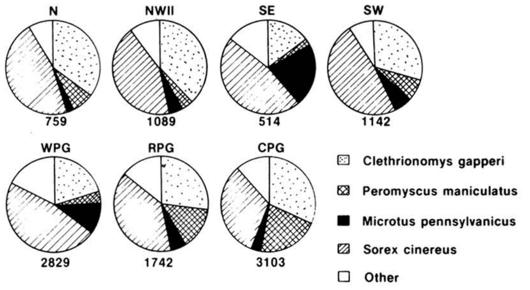

Fig. 2. Species composition of seven removal grids trapped from 1968 to 1982 in deciduous (WPG, RPG, CPG, FIG NWII) or coniferous (FIG N, SE, SW) forests near Pinawa, Manitoba. The total number of animals captured in each area is given at the base of each pie diagram.

3. Results

3.1. Species composition

A total of 11 178 small mammals was captured on the summer removal grids, with the masked shrew (*Sorex cinereus*) numerically dominant (Fig. 2). *Clethrionomys* was the most abundant rodent in all areas except the spruce bog in FIG SE, where the meadow vole (*M. pennsylvanicus*) was most abundant. Modest numbers (9%) of southern bog lemmings (*Synaptomys cooperi*) were also captured in FIG SE. In other areas, the deer mouse (*Peromyscus maniculatus*) was the second most common rodent. Meadow jumping mice (*Zapus hudsonius*) accounted for 2-6% of the captures on FIG SW and the three control grids. Three species of shrews (*S. arcticus, Microsorex hoyii, Blarina brevicauda*) accounted for most of the "other" category in Fig. 2.

Overall, the FIG grids were most comparable to WPG and RPG. CPG had the largest *Peromyscus* population as well as the largest *Zapus* population, and hence was the most divergent grid after FIG SE. CPG accounted for 997 *Clethrionomys* out of a total of 2110 for the three main control grids. The catch on PPG was only 241 small mammals, most of which were *Peromyscus*, and hence data from

Table 1. Distribution of captures (%) of *Clethrionomys gapperi* within FIG among habitat types. $G = 100.83$, $P < 0.001$ for goodness of fit of aspen-birch, pine, and fir captures to random distribution based on number of stations sampled. Numbers in parentheses are for 3 habitats (spruce excluded).

Habitat	Captures		Stations	
Aspen-birch	37.3	(38.6)	21.9	(26.3)
Pine	26.6	(27.5)	21.4	(25.8)
Fir	32.8	(33.9)	39.8	(47.9)
Spruce	3.3		16.9	
Total *N*	1074		256	

this grid were not included in the control data set. Within FIG, *Clethrionomys* preferred mixed aspen-birch forest over fir and pine forest (Tab. 1). Very few *Clethrionomys* were caught in the spruce bog.

3.2. Density fluctuations

Densities on the FIG grids were generally about half those on the control grids, with NWII > SW > N > SE (Fig. 3). This ranking reflected the habitat preferences of *Clethrionomys* within FIG: aspen-birch better than pine better than fir better than spruce (Tab. 1). For the control grids, densities were usually highest on CPG (Fig. 3).

The FIG grids were mostly trapped in July. Thus, we presumably sampled first litter young of the year and a few overwintered voles. Control grids were trapped a month later, and hence were sampling mostly young of the year (Perrin 1979). Some of the unusual densities observed in 1970 probably resulted from differences in the dates of trapping. FIG SW, WPG and CPG were all trapped rather late (start August 14–15), and hence had unusually high densities. Similarly, FIG SE and RPG were trapped rather early (start 8 June) and hence had unusually low densities. We therefore believe that the low densities observed in FIG in later years reflect the trapping schedule rather than any habitat or radiation effect.

In 1978 and 1979, there was a noticeable decrease in vole densities in FIG (Fig. 3). On the control areas, densities remained stable throughout this period at either high (CPG) or medium (WPG, RPG) levels (Fig. 3). Spring snap-trapping also indicated no significant change in *Clethrionomys* densities (Fig. 4). Densities of potential competitors such as *Peromyscus* (Fig. 4) or *Microtus* (Mihok et al. 1985) were also relatively stable during this apparent decline in FIG. Since the catch on all FIG grids declined, irrespective of radiation level, it is unlikely that this decline was related to irradation. Overall, the density flcutuations across all habitats and seasons were crudely synchronous. This is best shown by a comparison of density indices (catch per trap-night) for 1970 to 1982 from the four grids with the least variation in sampling dates (WPG, CPG, FIG N, FIG NWII). Density indices were highly positively correlated among all these grids (Tab. 2). Summer indices were also

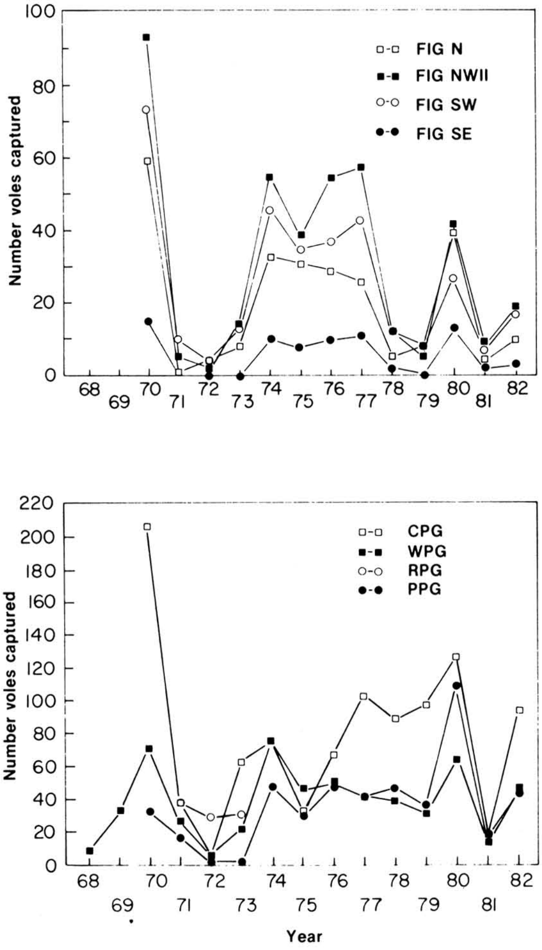

Fig. 3. Number of *Clethrionomys gapperi* captured on 30-day, 1.1-ha summer removal grids in control forests and in FIG.

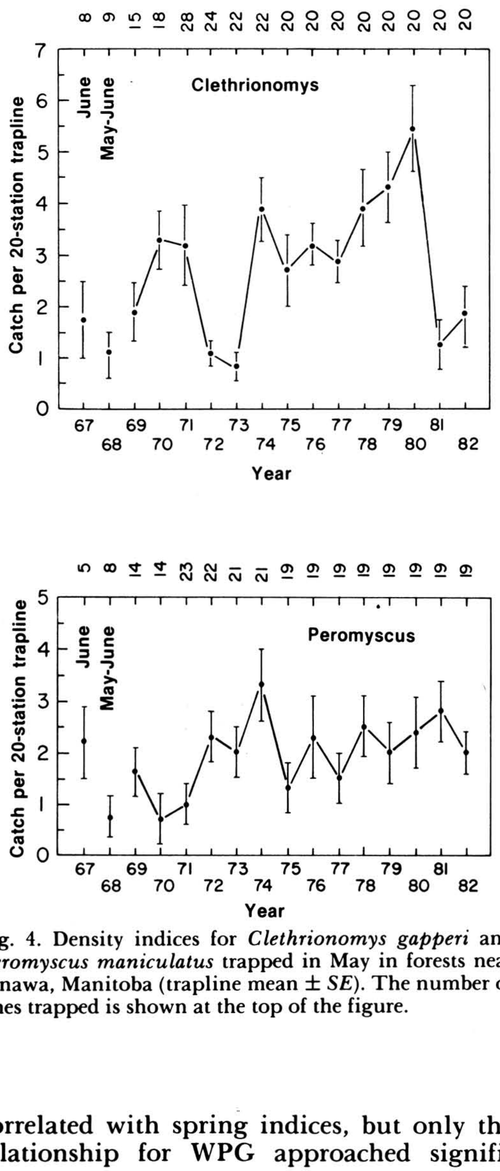

Fig. 4. Density indices for *Clethrionomys gapperi* and *Peromyscus maniculatus* trapped in May in forests near Pinawa, Manitoba (trapline mean ± *SE*). The number of lines trapped is shown at the top of the figure.

Table 2. Correlation coefficients among density indices for spring trapping on index lines, late summer trapping on control grids (WPG and CPG) and early summer trapping on irradiated grids (FIG, 1970-1982). Critical values for 11 *df* are: 0.55 ($P<0.05$), 0.68 ($P<0.01$).

	Spring	WPG	CPG	FIG N
WPG	0.66			
CPG	0.52	0.72		
FIG N	0.45	0.85	0.72	
FIG NWII	0.34	0.82	0.70	0.95

correlated with spring indices, but only the relationship for WPG approached significance.

To compare our density fluctuations with those reported by other workers, we calculated fluctuation indices (*s*) for the spring and summer data from areas with reasonable consistency in sampling dates. Fluctuation indices were: spring lines 1969-1982 (0.245), RPG 1974-1982 (0.212), WPG 1970-1982 (0.309), CPG 1970-1982 (0.402), FIG 1973-1982 (0.353). These low values are characteristic of non-cyclic populations of *Clethrionomys* (Henttonen et al. 1985), and are similar to those reported for subarctic *Clethrionomys* monitored by Fuller and co-workers (Mihok et al. 1985, Fuller 1985).

3.3. Dispersal

The extended trapping periods used on the grids presumably sampled large numbers of dispersing voles, particularly within FIG where four grids were located within a relatively small area. Although there was an initial drop in captures after the first few days of trapping, voles continued to be captured at a modest rate throughout the trapping session (Fig. 5a). The proportion of males increased only slightly during the first few days and then fluctuated from about 0.55 to 0.65 with no clear trends (Fig. 5b). The proportion of males that was mature also fluctuated erratically (Fig. 5c). There was a relative shortage of mature males during the latter half of control grid trapping, presumably because of the normal disappearance of reproductive voles towards the end of the breeding season (Iverson & Turner 1976b). A similar trend was seen in the proportion of females that were mature (Fig. 5d). This proportion decreased during the first two weeks of trapping in both July (FIG) and August (controls), but recovered substantially only in the FIG trapping (Fig. 5d). Since continuous removal prevented voles from attaining maturity after dispersal, these types of changes must have reflected the frequency of mature voles present at different times in the breeding season.

3.4. Characteristics of voles prior to irradiation

The FIG grids differed from the control grids in three main ways: (1) they were ex-

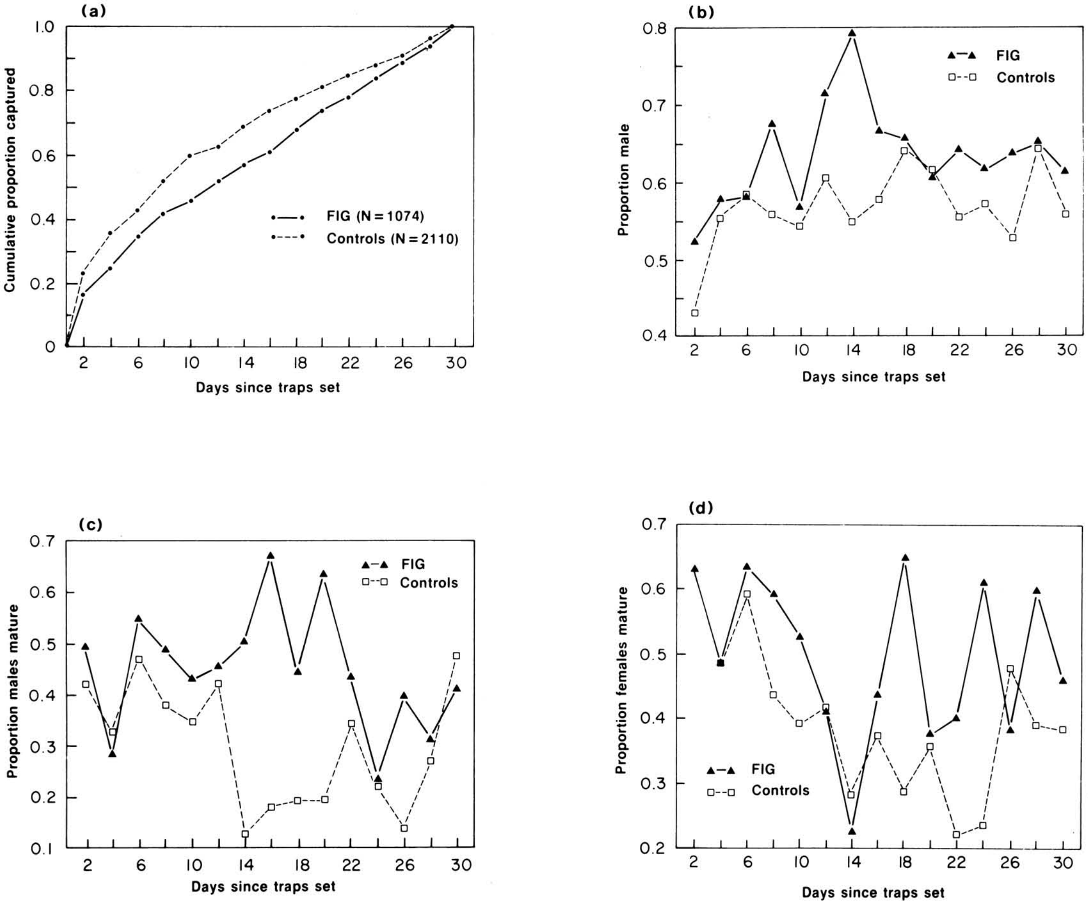

Fig. 5. Demographic statistics for *Clethrionomys gapperi* by 2-day intervals on the FIG and control grids. (a): Accumulated captures, (b): Proportion male, (c): Proportion of males that was mature, (d): Proportion of females that was mature.

posed to gamma radiation, (2) they were located in mainly mixed coniferous rather than mixed deciduous forest, and (3) they were trapped a month earlier in the breeding season. The relative contribution of these factors to differences between the results from the FIG and the control grids could only be investigated adequately using the 1970 data (prior to irradiation).

In 1970 FIG SW was trapped in August at the same time as CPG and WPG. FIG N and FIG NWII were trapped in July. The data were collected later than in subsequent years with trapping starting mid-month rather than at the beginning of the month. It was also a year of very high vole densities in summer (Fig. 3), although spring densities were average (Fig. 4). All statistical comparisons revealed no significant heterogeneity among the grids (habitats) either in July or August. Comparisons of July and August data revealed that in July more juveniles were mature, females weighed less, and testis lengths were longer (Tab. 3). Nonsignificant trends also indicated that voles trapped in July were smaller in weight and length and were more likely to be sexually mature.

3.5. Characteristics of voles during irradiation

Initial tabulations indicated that large fluctuations in demographic statistics occurred among the unmanipulated control grids during the irradiation period. Consequently, we chose to compare all FIG data to that from the three main control grids (CPG, WPG,

Table 3. Comparison of characteristics of *Clethrionomys gapperi* among grids trapped in 1970, prior to irradation.

	August			July		Significance of July - August comparison
Variable	CPG	WPG	FIG SW	FIG NWII	FIG N	
Males (%)	48	55	55	54	55	0.99
Mature juveniles (%)	0	1	0	6	13	<0.01
Mature males (%)	3	8	8	16	19	0.23
Mature females (%)	16	22	6	28	35	0.33
Lactating females (%)	16	22	6	16	27	0.99
Juveniles (%)	88	81	86	83	81	0.99
Female weight (g)	16.7	16.8	15.8	14.5	14.0	<0.01
Female length (mm)	89.5	90.3	88.2	87.0	89.3	0.15
Male weight (g)	16.2	16.4	15.7	15.6	15.5	0.11
Male length (mm)	90.8	89.1	88.7	90.0	86.7	0.57
Testis length (mm)	3.3	3.6	3.3	4.8	4.7	<0.01
Total sample size	203	71	71	93	58	

RPG) on a year-to-year basis from 1973. In most figures that follow, CPG and FIG are highlighted since they were the most divergent grids in terms of population density and species composition. Only points based on a minimum sample of six voles are plotted.

Sex ratios were mostly male-biased with a slightly higher proportion of males in FIG (Fig. 6). There was no heterogeneity among the controls within a given year. None of the comparisons between FIG and the pooled controls was significant. The proportion of juveniles that were mature varied considerably from year to year with FIG voles more likely to be mature (Fig. 7a). Differences were significant in 1975, 1976, 1977 and 1980 and approached significance in 1978 and 1982. Controls were heterogeneous in 1975 (high proportion of mature animals on CPG) and 1979 (high proportion of mature animals on WPG). In males, the proportion of mature voles was occasionally higher in FIG (Fig. 7b), but was significantly higher only in 1977 and 1980. Controls were heterogeneous in 1975 as a result of the low proportion mature on WPG. Heterogeneity among controls in the proportion of females that were mature was pronounced (Fig. 7c). Differences were significant in 1975 and 1982, and approached significance in other years. Significantly more females were mature in FIG during 1977 and 1980, but there was no clear trend across all years. No significant difference was deteced in the proportion of females that were lactating, or in litter size, among controls or between FIG and the controls. Testis lengths in FIG supported the finding of a higher proportion of mature males in FIG. FIG males had significantly larger testes in every year except 1981, and there was no heterogeneity among the controls (Fig. 7d).

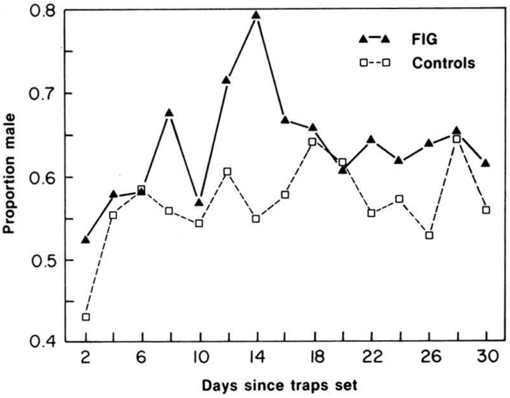

Fig. 6. Proportion of male *Clethrionomys gapperi* on the FIG control grids.

The proportion of the population that was juvenile in FIG never differed from the controls, largely due to significant heterogeneity among the controls in each year. Males were significantly heavier in FIG in 1974, and the controls were heterogeneous in weight in 1975, 1978 and 1982 (Fig. 8a). The size differences in male voles from FIG in 1974 was not apparent for body length (Fig. 8b). Voles were significantly heterogeneous in length among the controls for the same three years. Female weights were moderately variable among the control grids with most heterogeneity tests approaching significance (Fig. 8c). Weights were significantly heterogeneous only in 1976,

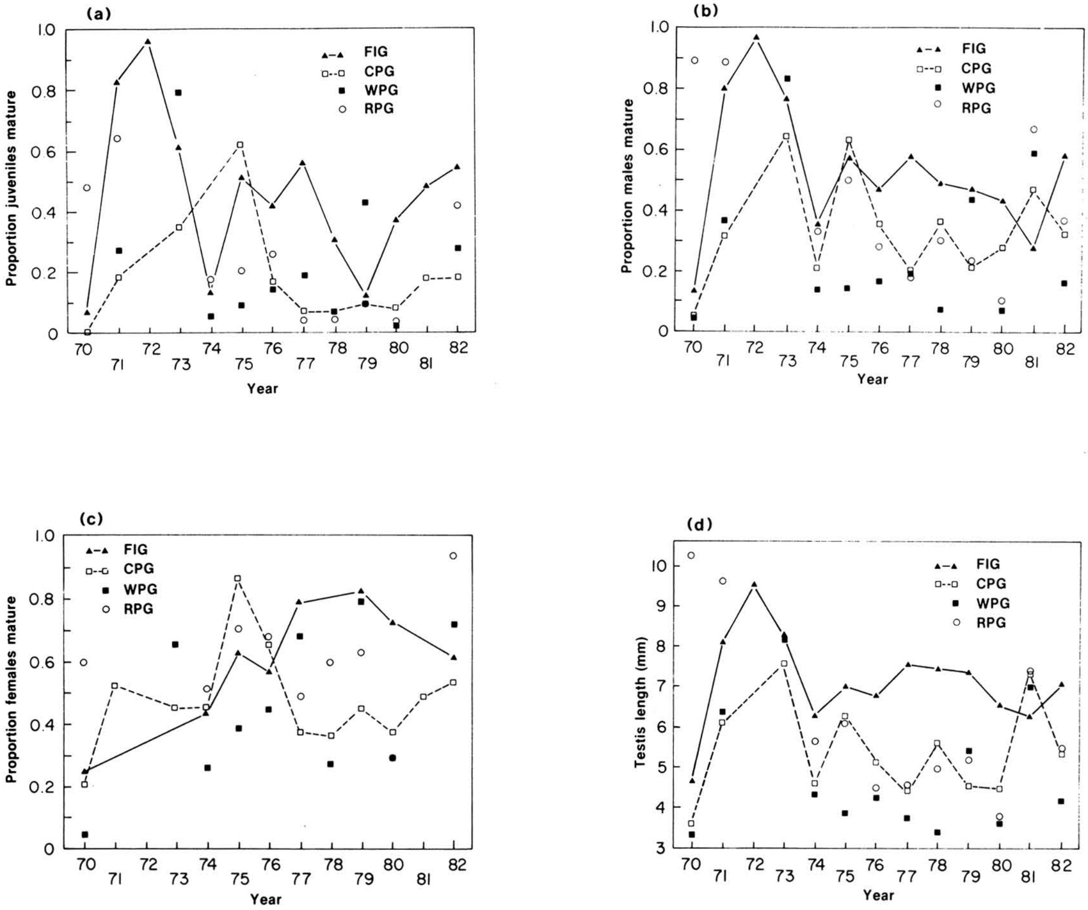

Fig. 7. Sexual maturity status of *Clethrionomys gapperi* on the FIG and control grids (a): Proportion of juveniles (≤ 18 g) that was mature, (b): Proportion of males that was mature, (c): Proportion of females that was mature, (d): Male testis length.

mainly as a result of the large size of voles from CPG. FIG voles were significantly lighter than the controls in 1975. Tests in other years approached significance in some cases as FIG voles were often the lightest ones captured (Fig. 8c). Female body lengths were less variable than weights and were not heterogeneous among the controls (Fig. 8d). FIG females were uniformly shorter than control voles with differences significant in 1974, 1975 and 1976.

In summary, the clearest differences between voles in the irradiated area and the controls occurred in testis length, female body size and sexual maturity. These differences essentially reproduced the types of differences we would expect to see from grids sampled at slightly different times of the year (Tab. 2). The magnitude of these differences was small when compared with the large changes that occurred among control grids within or between years.

In an attempt to account for the considerable unexplained heterogeneity among the controls, we calculated correlation coefficients between demographic statistics and the average catch on the FIG grids and on each of the control grids. Four variables shared significant positive correlations with each other, as well as significant negative correlations with density: proportion of males, proportion of juveniles that were mature, proportion of males that were mature, proportion of females that were mature. Since all correlations were of similar magnitude and direction, we present

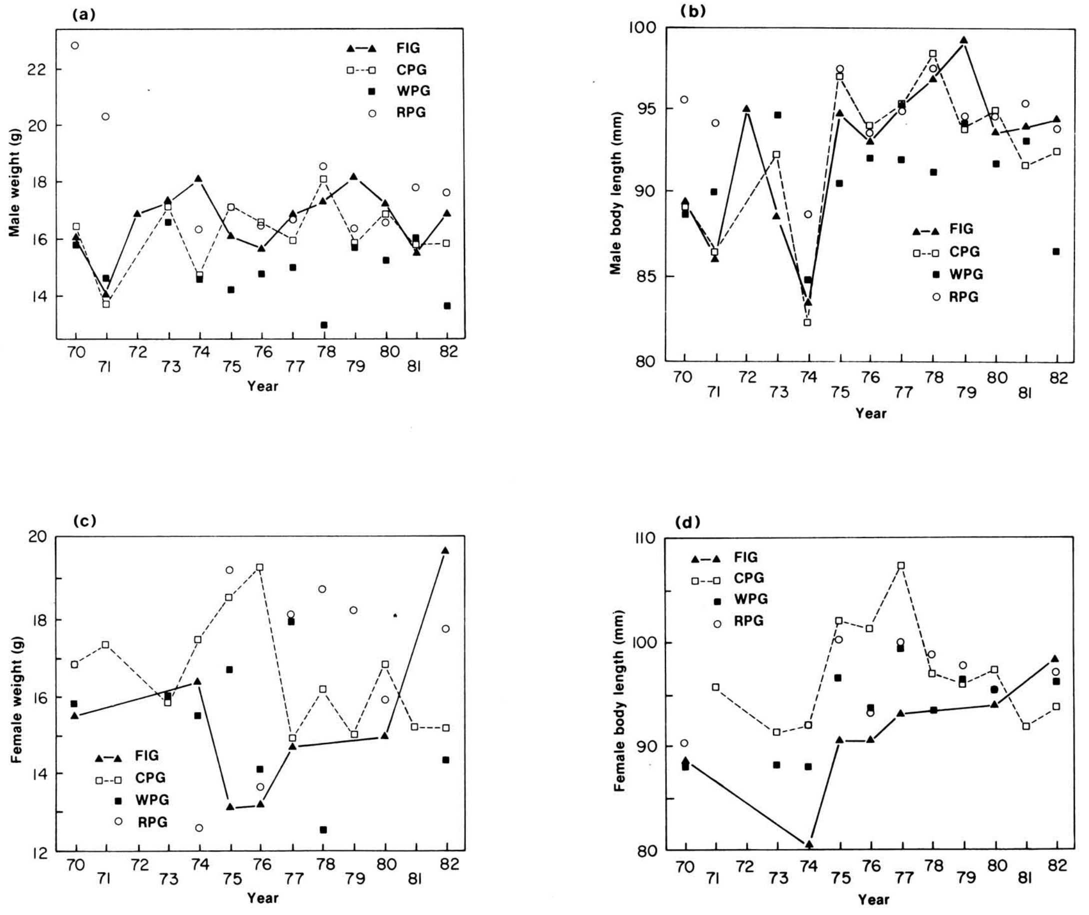

Fig. 8. Body size of *Clethrionomys gapperi* on the FIG and control grids. (a): Male weight, (b): Male body length, (c): Female weight, (d): Female body length.

only the relationship between density and the proportion of juveniles that were mature (Fig. 9).

3.6. Patterns within the radiation gradient

If irradiation had an effect that was independent of site effects, we would expect to see heterogeneity among voles from different dose-rate areas during irradiation that was not present prior to irradiation. Consequently, we analyzed the characteristics of voles captured before (1970–1972) or during (1973–1982) irradiation within each of the four dose-rate areas. In all pre-irradiation comparisons the characteristics of voles from the four dose-rate

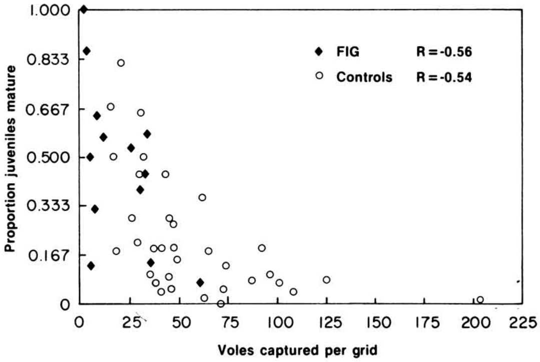

Fig. 9. Relationship between proportion of juveniles that was mature and number of *Clethrionomys gapperi* captured per grid plotted for each control grid and for the average of the four grids from FIG.

Table 4. Comparison of voles caught (mean ± *SE*) in four dose-rate areas within FIG before irradiation (1970-1972) and during irradiation (1973-1982). Sample size within parentheses. *G*-test for heterogeneity or oneway ANOVA among dose-rates.

Variable	Irradiation period	Signif.	Dose Rate			
			Very high	High	Medium	Low
Males (%)	Before	0.19	43 (40)	62 (94)	51 (78)	58 (52)
	During	0.36	66 (85)	63 (304)	61 (199)	70 (138)
Mature juveniles (%)	Before	0.92	14 (29)	16 (76)	13 (70)	18 (40)
	During	0.07	30 (67)	47 (219)	46 (138)	39 (89)
Mature males (%)	Before	0.77	29 (17)	31 (58)	22 (40)	23 (30)
	During	<0.001	29 (56)	53 (192)	62 (122)	57 (97)
Mature females (%)	Before	0.03	39 (23)	33 (36)	13 (38)	45 (22)
	During	0.45	55 (29)	69 (112)	60 (77)	63 (41)
Lactating females (%)	Before	0.09	26 (23)	22 (30)	8 (38)	32 (22)
	During	0.65	21 (29)	13 (112)	19 (77)	17 (41)
Juveniles (%)	Before	0.08	73 (40)	81 (94)	90 (78)	77 (52)
	During	0.12	79 (85)	72 (304)	69 (199)	64 (138)
Female weight (g)	Before	0.19	14.53±0.99 (20)	16.46±1.00 (35)	15.88±0.53 (37)	13.76±0.87 (14)
	During	0.78	15.07±1.12 (27)	14.44±0.53 (90)	15.32±0.69 (66)	14.92±1.01 (30)
Female length (mm)	Before	0.69	87.57±2.24 (23)	88.18±1.89 (34)	88.73±1.14 (37)	91.00±2.64 (20)
	During	0.53	86.62±2.51 (29)	89.63±1.21 (104)	90.03±1.49 (68)	91.08±2.11 (40)
Male weight (g)	Before	0.78	16.67±0.68 (16)	15.88±0.50 (56)	15.61±0.46 (39)	15.76±0.77 (28)
	During	0.11	15.66±0.49 (50)	16.76±0.29 (185)	17.31±0.41 (119)	17.13±0.47 (94)
Male length (mm)	Before	0.48	88.56±1.55 (16)	89.78±1.08 (55)	90.95±0.91 (37)	87.68±1.23 (28)
	During	0.21	89.82±1.15 (50)	92.63±0.66 (184)	91.97±0.90 (116)	92.98±0.96 (91)
Testis length (mm)	Before	0.55	5.71±0.64 (17)	5.36±0.34 (58)	4.80±0.45 (39)	4.90±0.44 (29)
	During	0.01	5.92±0.36 (47)	6.89±0.19 (171)	7.28±0.27 (115)	7.36±0.29 (88)
Embryo count	Before		6.00±0.58 (3)	7.00 (1)		5.50±0.34 (6)
	During		7.00±1.00 (2)	5.81±0.29 (16)	6.33±0.42 (6)	6.33±0.47 (9)
Placental scar count	Before		5.67±0.67 (3)	6.89±0.87 (9)	6.25±0.75 (4)	5.00 (1)
	During		4.00±0.00 (2)	4.33±0.67 (3)	4.67±0.33 (3)	7.00 (1)

areas were statistically homogeneous (Tab. 4). Once irradiation began, voles captured in the very high dose rate area appeared to differ from those caught elsewhere. There was a significant change in the proportion of males that were mature and in testis length, with supporting trends in most other variables (Tab. 4, Fig. 10). Male voles living within the very high dose rate area were smaller, were mostly immature, and had shorter testis lengths. Nonsignificant trends of a similar nature occurred in females. Trends in other variables also paralleled the expected order of a radiation effect with mean values decreasing or increasing depending on the distance from the irradiator.

As a final test for radiation effects, we examined the distribution of captures within the radiation gradient. If voles detected the radiation field, died as a consequence of it, or simply dispersed after starting to feel sick, we would have expected a redistribution of the captures within habitat types after irradiation began. This effect should have been relatively easy to detect if it existed, but was further complicated by the alteration of habitat with time (Dugle & Mayoh 1974, Amiro & Dugle 1985). Hence, we compared the capture distribution within habitats for three periods: before irradiation (1970-1972), early irradiation (1973-1975, canopy cover changes), and late irradiation (1976-1982, minor canopy changes and possible understory changes). We detected no change in the capture distribution in aspen-birch or pine habitats, even though considerable habitat changes occurred within the FIG NWII grid. Nevertheless, we detected a significant change in the fir forest ($G=17.5$, $df=6$, $P<0.01$). Contrary to our expectation of a decrease in captures close to the irradiator in the early period, we found a decrease in captures in the medium dose-rate area in the late period, with a concomitant increase in the high dose-rate area (Fig. 11). At present, we have no explanation, botanical or otherwise, for this effect.

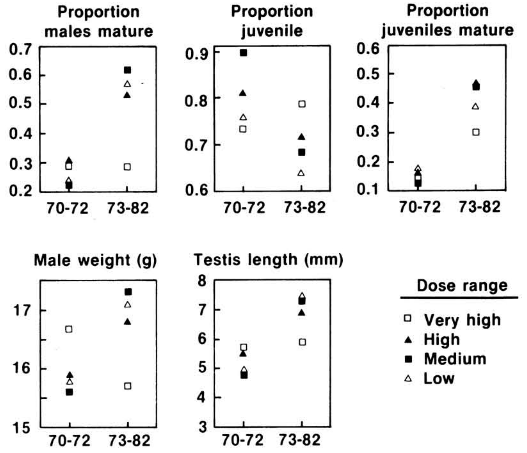

Fig. 10. Selected characteristics of *Clethrionomys gapperi* captured in FIG before (1970–1972) irradiation and during (1973–1982) irradiation.

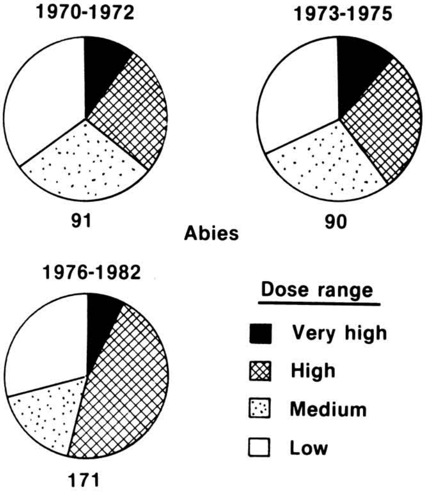

Fig. 11. Distribution of *Clethrionomys gapperi* in the fir forest among the dose-rate areas shown in Fig. 2.

4. Discussion

4.1. Radiation biology

Acute $LD_{50,30}$ studies of *Clethrionomys* have shown that it is one of the more radioresistant genera of microtine rodents (*C. rutilus*: 9.6 Gy, Il'enko et al. 1974; *C. glareolus*: 9.6 Gy, Il'enko et al. 1977: *C. gapperi*: 12.0 Gy, Buech 1971). Our laboratory experiment confirmed this observation with the finding of an $LD_{50,30}$ of 11.8 Gy for Manitoba *C. gapperi*. The different values obtained by North American and Soviet workers may reflect species differences, methodological differences (Kitchings 1978), or the seasonal generations of voles sampled (Iverson & Turner 1976a). This apparent radioresistance has been supported by comparisons of the response of bone marrow and corneal epithelium of *C. glareolus* and the house mouse *Mus musculus* to X-rays (Samokhvalova et al. 1978, Popova et al. 1978). Similar techniques have been used to show that arctic populations of *C. glareolus* are more radioresistant than temperate populations (Domareva et al. 1977; Popova et al. 1980). Populations of *C. rutilus* inhabiting areas of slightly elevated natural background radiation have also been the subject of hematological and chromosomal studies (Borodkin & Testov 1980; Borodkin 1981).

Studies of wild rodent species in forest (Buech 1977), and desert (French et al. 1974), have shown that these mammals can maintain viable populations at moderately high levels of chronic exposure. French et al. (1974) concluded that dose rates of about 0.4 mGy/h decreased early survival in long-lived pocket mice (*Perognathus formosus*). Fertility effects were not monitored rigorously, but appeared to be minimal. Altogether, the multiplication rate per generation was reduced by about 50% in French and coworkers' irradiated population.

Extrapolation of French and coworkers' results to our study is possible given the similar $LD_{50,30}$ values for *C. gapperi* (11.8–12.0 Gy) and *P. formosus* (13.0 Gy, Gambino & Lindberg 1964). Hence, we can assume that life-shortening effects were pronounced within the 2 ha very high dose-rate area close to the irradiator (Fig. 1). These effects probably killed most of the overwintering population, and reduced substantially the reproductive output of summer residents. Within the 3.3-ha high dose-rate area, the overwintered population may also have accumulated enough radiation damage for survival to be depressed. How much survival was depressed is unknown. Fertility was probably affected only to a small extent, principally in voles resident on the area throughout the winter. Despite these presumed radiation effects, we found that voles were of normal body size and reproductive status throughout the FIG area. Effects that may have been the result of irradiation were noted only at very high dose rates where voles accumulated chronic doses comparable to acute $LD_{50,30}$ doses in 1-2 months. Mortality and fertility effects present in a 5.3-ha area over ten years were therefore insufficient to produce a depression in numbers. Radiation effects were presumably compensated for by considerable immigration from surrounding areas receiving relatively low doses of radiation. No cumulative effects were noted over the 10-year period, presumably due to the extensive turnover in voles each year, and the removal of a large number of residents each summer.

4.2. Dispersal

The results of this demographic program have confirmed some features of *Clethrionomys* biology while simultaneously raising some puzzling questions. The persistance of vole captures throughout the 30-day trapping period is particularly interesting. In FIG, an area much larger than that used by most workers was saturated with a large number of traps for an extended period of removal trapping. In combination with the presumed 5.3-ha area of radiation effect, this program should have depressed population density. Contrary to expectation, little effect was detected during the course of each individual trapping session, or during the entire course of the ten years of trapping. These results strongly argue against the ability of conventional methods to create anything more than a temporary vacuum in vole numbers. Apparently, there are large numbers of immigrant voles present during the breeding season that are drawn into these artificial vacuums. Similar results were obtained for *M. pennsylvanicus* captured on a live-trapping grid trapped for five years with selective removals at two-week intervals (Mihok et al. 1985). Other workers have observed this phenomenon for many species of rodents (Calhoun 1963, Pucek et al. 1971, Kozakiewicz 1976, Zejda et al. 1977), but have not appreciated the scale of these movements. We suspect that efficient removal of a vole population is beyond the capabilities of field biologists in an open system when breeding is occurring. Removal may be possible with intensive pitfall trapping (Kozakiewicz 1976, Doyle 1979), but would be effective only in the nonbreeding season.

If we accept the existence of large numbers of dispersing voles during the breeding season, we must account for this phenomenon in hypotheses of population regulation. We must also account for the ability of populations subjected to intensive removal studies to behave in a fashion similar to those not subjected to such manipulations. In the case of FIG, we have an example of a population that was subjected to considerable additional, random mortality, but still behaved like control populations sampled by similar or less intensive removal techniques. Within FIG, the overwintering population was presumably killed each year through radiation-induced mortality over an area of a few hectares. In addition, the summer population was killed each year by snap-trapping over a much larger area. Consequently, the existing social structure was grossly perturbed twice each year, and yet there was no overall difference in population dynamics over a 10-year period. Clearly, behavioral hypotheses (Mihok 1981, Wiger 1982) that require a series of interactions between animals within a stable social structure are unable to account for these population fluctuations. At least for *C. gapperi* in Manitoba, we cannot assume that demography is controlled or regulated by local events, as there is a large degree of local population dilution by immigrant voles.

Although our data tend to refute behavioral regulation of population density, they clearly do not support any alternative. Our population fluctuations were modest by microtine standards, hence we never observed the striking peaks or crashes found in other microtines. Our populations were kept at low to moderate densities despite a presumed gradient in factors such as food, competitors, or predators associated with a diversity of forest types. Given the hypothesized role of such factors in *Clethrionomys* biology (Hansson 1979a, b), it is perplexing that we saw so little variation in vole numbers across habitats and years. Again, this leads to the conclusion that vole demography is regulated on a relatively large scale in our area.

4.3. Demography

From a comparison of fluctuation indices with those from other cyclic microtines (Henttonen et al. 1985), this Manitoba population of

C. gapperi appears to be non-cyclic based on either spring or summer density indices. Our spring fluctuation indices are strikingly similar to those obtained from a 9-yr census of vole densities conducted in Wisconsin, U.S.A. with methods similar to our spring index lines (*s* about 0.37, fig. 1, Patric 1962). Grant (1976) also found only erratic fluctuations in *C. gapperi* sampled at low densities in maple and beech forest in Quebec. Given the similar lack of cycles in a population sampled at low density in the Northwest Territories (Fuller 1985), we can probably assume that *C. gapperi,* as a species, is not cyclic. This is particularly unusual given the geographical gradient in cyclicity found it its ecological counterpart, *C. glareolus,* in Scandinavia. Hansson (1979b) and Erlinge et al. (1983) have suggested that noncyclicity of rodents in southern Sweden is related to predation and food, with important requirements being the availablity of alternative prey, the availability of prey throughout the year, and a heterogeneous environment. These three factors all vary substantially between the Manitoba and NWT study sites, and yet both populations have a nearly identical pattern of noncyclic density fluctuations. At present we can think of no factor unique to areas as divergent as Manitoba, the NWT, and Wisconsin, that would explain the lack of a cyclicity gradient in North America. Similarly, we find it difficult to explain the lack of clear cycles in *C. gapperi*'s arctic counterpart in North America, *C. rutilus* (Henttonen et al. 1985).

At present, the most reasonable conclusion is that single factors such as habitat gradients, food habits, weather, and predators, are unlikely to account for the lack of cyclicity in North American *Clethrionomys.* These factors must necessarily vary considerably between arctic and temperate study areas, and yet neither species shows cyclic behaviour in North America. If we assume that an interaction of various factors is necessary, then our hypotheses become untestable and will continue to be debated for many years to come. Hence we are inclined to support a simpler alternative, such as the existence of cycles in vole food plants (Laine & Henttonen 1983). These cycles may be specific to certain areas of the world for reasons of plant ecology rather than animal ecology, and hence explain the present enigma. A good strategy might be to concentrate efforts on the mechanism responsible for the release of vole breeding potential in increase years. *Clethrionomys* reproductive output appears to be suppressed by a mechanism of female territoriality common to many species (Bujalska 1985). In our Manitoba population, we saw evidence of this type of suppression at relatively low densities (Fig. 9). Cyclic populations may be released from reproductive inhibition at all but the highest of densities, and hence produce the dramatic peaks and crashes we recognize as cycles. Whether this change in both reproduction and survival is caused by behaviour or nutrition is not established, and should therefore be the subject of concentrated investigation.

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Appendix

The FIG area was irradiated with an elevated ^{137}Cs source that was lowered into a lead castle to allow safe access to the study area. The source was raised by compressed air and was held electromagnetically in the irradiating position 20 m above ground level. In March 1973 the source had an activity of 3.7×10^{14} Bq. Due to the 30-year half-life of ^{137}Cs, this activity decreased about 20 % by the end of the small mammal study. The ^{137}Cs source emitted 0.66 MeV gamma rays that were capable of producing both immediate and latent damage to biologial tissues. The energy absorbed by biological tissues is measured in Gray (1 joule of energy absorbed per kg of matter). Although this unit measures the energy absorbed, it does not necessarily reflect the damage inflicted on an organism. The net effect of radiation also depends on a quality factor that incorporates modifying factors such as the type and energy level of the radiation used (neutron, gamma, beta, etc.).

Biological systems have natural repair mechanisms that accomodate radiation damage if it is not overwhelming. For the same total dose, biological effects can therefore be very different for chronic versus acute exposures. Voles of the genus *Clethrionomys* are among the more resistant mammal species with doses greater than 10 Gy required to kill 50 % of animals within 30 days of acute exposure. The $LD_{50,30}$ for other mammals is mostly between 5 and 10 Gy. Acute radiation doses above about 1 Gy result in hematopoietic, gastrointestinal, and cerebrovascular syndromes of damage at successively higher doses. At lower doses, effects occur mostly at the cellular or biochemical levels and are therefore not obvious. Most of the voles living in the FIG area were exposed to these types of low dose effects due to the steep decline in dose rates close to the irradiator. Natural background dose rates are typically about 0.1 μGy/h. FIG voles were therefore exposed to a minimum of about 500× background. Further information about radiation biology can be found in Pizarello & Witcofski (1975) as well as in a recent publication on radioecology (Schultz & Whicker 1982).

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