

The effect of extra food and cover on declining populations of *Microtus townsendii*

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Microtus townsendii populations were supplied with extra food and extra cover during a spring decline in numbers in 1979. Compared with the control population, late-winter addition of food resulted in lower rates of decline of males and females. On the area with extra cover, the rate of decline was significantly lower in males, and females actually increased in number. Breeding was earlier in the population with extra cover, and four times as many females became pregnant during the spring. This resulted in twice as many young voles entering the population in early summer. Survival was higher in both experimental populations during the spring. Females with extra food and males with extra cover had the smallest home ranges for their sex group.

The experiments were repeated in summer 1979, except that cover was reduced on one grid. Demography during the summer experiments was similar in all populations. This period coincided with a botfly (*Cuterebra*) larva infection which reduced survival of voles in all populations.

The addition of cover reduced bird predation. If this was the only effect of added cover, the demography of the covered population suggests that predation may be important in the spring decline of *M. townsendii*. Further, we suggest that the severity of the spring decline, particularly in female voles, may determine when the population "cycles."

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Des populations de *Microtus townsendii* ont reçu des soins particuliers (plus de nourriture, plus de couverture) durant un déclin de leur abondance au printemps de 1979. L'addition de nourriture à la fin de l'hiver réduit les taux de diminution des mâles et des femelles. Dans la région à couverture additionnelle, le taux de diminution des mâles a baissé sensiblement et le nombre de femelles a même augmenté. Chez la population à couverture additionnelle, la reproduction s'est faite plus tôt et quatre fois plus de femelles sont devenues enceintes au printemps, ce qui doubla le nombre de petits campagnols qui sont entrés dans la population au début de l'été. La survie s'est avérée plus élevée chez les deux populations expérimentales au printemps. De toutes les femelles, ce sont celles qui ont reçu de la nourriture en plus, et de tous les mâles, ceux qui ont reçu une couverture additionnelle, qui avaient les plus petites aires vitales.

Les expériences ont été répétées durant l'été 1979, mais la couverture a été réduite dans l'une des aires expérimentales. La démographie s'est avérée la même chez toutes les populations en été. Cette période coïncidait avec une infestation d'œstres (*Cuterebra*) qui a réduit la survie des campagnols chez toutes les populations.

L'addition de couverture réduit la prédation due aux oiseaux. S'il s'agit là du seul effet de la couverture additionnelle, la démographie de la population protégée permet de croire que la prédation est un facteur important du déclin des populations de *M. townsendii* au printemps. Il semble en outre que la gravité du déclin de printemps, particulièrement chez les campagnols femelles, puisse déterminer à quel moment se produisent les cycles de densité des populations.

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Introduction

Populations of many microtine rodents decline in number in spring (Sadleir 1965; Watts 1970; Krebs and Boonstra 1978). It has been suggested that these declines result from socially induced mortality and dispersal. Although spacing behaviour is thought to be the proximate mechanism, its relationship to extrinsic and intrinsic variables is unknown. At least three

approaches can be taken to investigate these relationships experimentally.

(1) We can manipulate the social behaviour of individuals, e.g. change aggressive behaviour by hormonal implants, and predict demographic changes that should result (Krebs *et al.* 1977).

(2) We can manipulate extrinsic factors that may be objects of competition, e.g. provide extra food and predict changes in spacing behaviour and dispersal (Fordham 1971; Flowerdew 1972; Taitt 1981).

(3) We could manipulate the agents of mortality, e.g. add cover in an attempt to reduce bird predation and hence prey mortality.

We used all three approaches during the 1979 spring decline in populations of *Microtus townsendii* on West-

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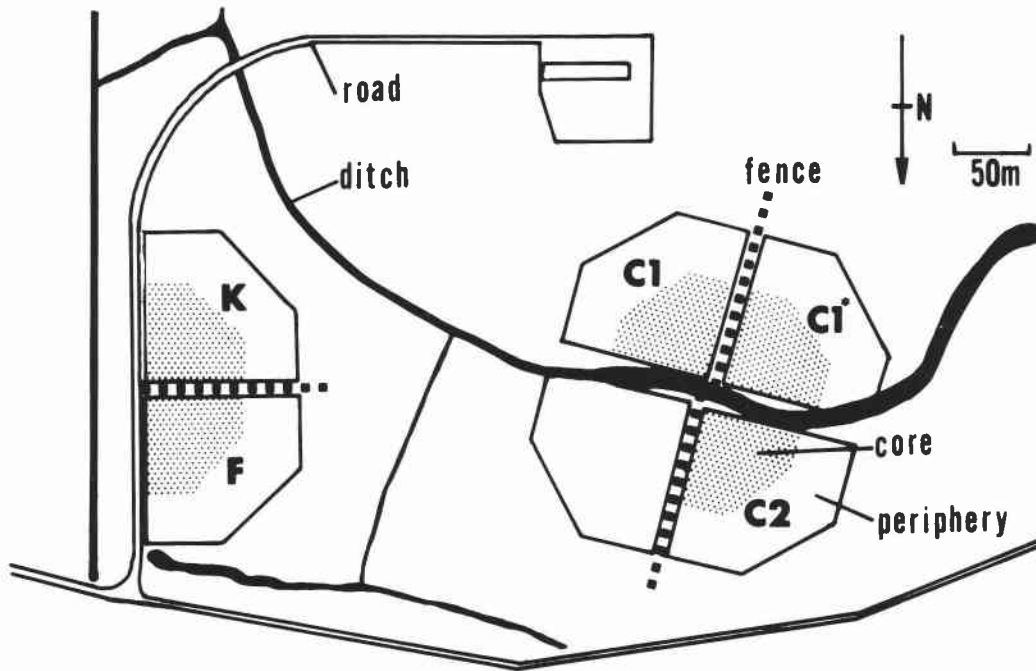


FIG. 1. The location of the grid populations.

ham Island. Populations of this vole have declined every spring but one over 5 years on this study area (LeDuc and Krebs 1975; Krebs 1979). The behavioural manipulations are reported in Gipps *et al.* (1981). In this paper we present the results of attempts to manipulate extrinsic factors by providing extra food and cover.

Methods

Five trapping grids were established in grassland on Westham Island in the Fraser River Delta south of Vancouver, B.C. The grids were bounded on one side by a 6 mm ($\frac{1}{4}$ in.) wire-mesh fence and another side by either a road (grids K and F) or a water-filled ditch (grids C1, C1*, and C2) (Fig. 1). Only 1.4% of all voles captured moved between K and F and <1% crossed the ditch or fences of the other four grids. Movement to and from grid C1* was further restricted by the adjacent horse pasture which was heavily grazed all winter and spring 1978–1979; the grid was essentially a small “island” of vole habitat. Also, the outer two rows on one side of grid F were flooded during the winter.

One or two Longworth live-traps were placed at each of 71 points 7.6 m (25 ft) apart on each grid. Grids had an inner “core” of 30 trap points bounded by three rows totalling 41 “peripheral” trap points. Pitfall traps (Boonstra and Krebs 1978) were used at all except the outer row of trap points in May 1979. Voles were trapped every 2 weeks for 2 nights and the intervening day from November 1978 to September 1979. All traps were locked open for prebaiting between trapping periods. Each new vole was given a numbered ear tag and its location, weight, and breeding condition were recorded then and in all subsequent trapping periods. Males had either abdominal or scrotal testes, females had open or closed

vaginas and small, medium, or large nipples. All pregnancies and trap litters were noted. Voles weighing <30 g were classed as juveniles, subadults weighed 30 to 42 g, and all voles >42 g were adults.

The experimental treatment of each grid is shown in Fig. 2. A mixture of laboratory chow and whole oats was placed in food cans at each trapping station on the core of grid F in both experimental periods. But, during experiment 1 (February 12 to April 20, 1979), waterfowl from the nearby refuge frequently robbed the food cans and grazed on the grid. As a result, this vole population received less extra food than we had intended, and the grass cover was reduced somewhat compared with the controls. We spread straw to a depth of 15 cm (6 in.) on the core of grid K during experiment 1. We never observed a bird predator on this grid through the period late January to the end of March when they were seen on the other grids. By the end of experiment 1, grass had grown through the straw on grid K and the area looked the same as the controls by this time. Cover was reduced in experiment 2 (July 17 to August 24, 1979) when squares of grid K were mowed to within 5 cm (2 in.) of the soil over an area equivalent to half the

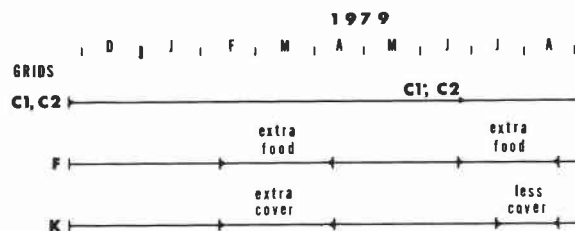


FIG. 2. The experimental design.

core area. Grid C1 was the control up to July 17, then grid C1* was the control for experiment 2. Male voles on grid C2 had "dummy" subcutaneous implants of silastic tubing, but the implants did not affect the demography of this population (Gipps *et al.* 1981), so the grid is used as a second control for the present experiments.

Results

The results are described for the "core" areas of each grid. Minimum trappability ranged from 52% on grid F to 64% on grid C1 during experiment 1. Therefore, minimum number alive (MNA) has an error of approximately 12% as an estimate of population size through this period (Hilborn *et al.* 1976). Trappability was lower during the summer when experiment 2 was conducted; the lowest value was 43% on control 1*, thus the error in MNA was 15% during this period. Between the experiments (April 20 to July 12), trappability was the same as during the first experiment.

Population size

The number of male voles declined on all grids throughout the spring experimental period (Fig. 3a). The rate of decline in males was less on the experimental grids, and by Duncan's multiple range test ($p < 0.05$), significantly so on grid K with extra cover (Table 1). Female numbers remained stable over the 1st month of experiment 1, but then declined rapidly on all grids except that with extra cover, where the number of females increased (Fig. 3b). The ranking of the rate of decline was the same in both sexes: control > food > cover.

Male and female numbers increased on all grids during the period between experiments. The number of male voles on grid K peaked at twice control densities, as did females (Fig. 3).

The second experiment spanned the middle of the breeding season. The number of voles in all populations declined. The reduction of cover (K) and the addition of dry food pellets (F) did not change the rate of decline of these populations compared with controls (Table 1).

Immigration and births

The total number of new voles caught on control C1 and the two experimental grids (F and K) was similar during the spring experiment (Table 2). The second control (C2) had few immigrants which was probably related to the location of the grid beside a horse pasture. More new adult voles (>42 g) were caught on all grids between the experiments, whereas adult immigration was generally low everywhere during the second experiment.

It is not possible to separate young (<43 g) new voles into those born on and off the grids. However, we do know how many females were lactating and pregnant. No females were lactating on control grid 2 during the

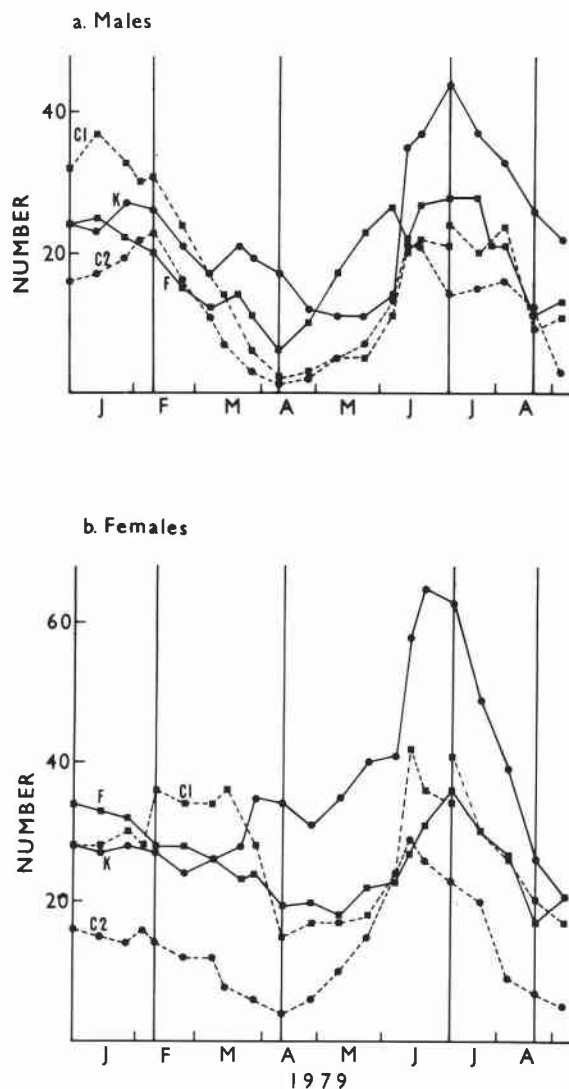


FIG. 3. The minimum number of males (a) and females (b) alive. Vertical lines delimit the experimental periods. ...■... grid C1 (control); ...●... grid C2 (control); —■—, grid F (food); —●—, grid K (cover).

first experiment. Lactating females were first caught on control 1 and the food grid in April, but, with extra cover, females were lactating a month earlier on grid K. In fact, the number of pregnant females was much higher on the covered grid compared with all other grids during experiment 1, and during May and June (Table 3). Apart from grid C2, the number of pregnancies was equal on all grids during experiment 2. The higher reproductive rate (earlier breeding and more females breeding) on the covered grid probably resulted in twice as many young recruits being caught on this grid compared with all other grids between experiments (Table 2).

TABLE 1. The average instantaneous rate of population change per week during experiments 1 and 2. Duncan's multiple range test showed significant differences as indicated

	Control C1 ^a	Control C2	Food (F)	Cover (K)
Experiment 1 (February 12 to April 20)				
Males	-0.29	-0.35	-0.17	-0.06
Females	-0.08	-0.17	-0.04	+0.04
Both sexes	-0.19	-0.26	-0.10	-0.01
Experiment 2 (July 17 to August 24)				
Males	-0.16	-0.03	-0.16	-0.09
Females	-0.12	-0.20	-0.13	-0.15

NOTE: Values underlined are not significantly different.

^aIn experiment 2, this is control C1* grid.

TABLE 2. New voles captured on each grid during and between each experiment. "Emigrants" are voles that are trapped once only

	Control C1 ^a	Control C2	Food (F)	Cover (K)
Experiment 1				
Adults	22	6	17	33
Subadults and juveniles	15	2	9	12
% "emigrants"	35	75	50	29
Between experiments				
Adults	45	26	52	62
Subadults and juveniles	34	34	42	78
% "emigrants"	32	21	26	36
Experiment 2				
Adults	30	12	14	14
Subadults and juveniles	10	6	19	26
% "emigrants"	62	90	71	62

^aIn experiment 2, this is control C1* grid.

TABLE 3. Total number of pregnancies on each grid in and between the experiments

	Control (C1) ^a	Control (C2)	Food (F)	Cover (K)
Experiment 1	4	0	6	18
Between experiments	18	8	10	32
Experiment 2	10	3	10	10

^aIn experiment 2, this is control C1* grid.*Emigration and death*

It is not possible to differentiate between these two components of demography when a vole ceases being trapped. However, we suggest that voles that are captured once only are more likely to have emigrated or dispersed rather than died. The percentage of new voles in this category ("emigrants") was lowest in both sexes

on the grid with extra cover (K) over the spring experiment (Table 2). "Emigration" from all grids was lower and similar in the between experimental period, then high on all grids during the second experiment.

All voles captured in at least two trapping periods could be considered as "residents." When such voles cease being trapped they may still have emigrated

TABLE 4. Average 2-week survival of voles alive for at least 2 weeks

	Control C1 ^a		Control C2		Food (F)		Cover (K)	
	♂	♀	♂	♀	♂	♀	♂	♀
Experiment 1	0.54	0.75	0.58	0.73	0.65	0.83	0.73 ^b	0.93 ^c
Between experiments	0.86	0.92	0.91	0.95	0.79	0.81	0.81	0.89
Experiment 2	0.62	0.63	0.70	0.50	0.49	0.61	0.59	0.60
With botfly larvae	0.07	0.29	0.40	0.14	0.10	0.35	0.36	0.43

^aIn experiment 2, this is control C1* grid.

^bCompared with controls, chi-square (Yate's correction) $p < 0.025$.

^cCompared with controls, chi-square (Yate's correction) $p < 0.005$.

TABLE 5. Home ranges (square metres) of male and female voles on all grids during the spring decline. Sample size is in parentheses

	Controls (C1, C2)	Food (F)	Cover (K)
Males	326.9(20)	275.5(10)	233.9(20)
Females	180.4(30)	95.7(13) ^a	149.0(15)

^aCompared with controls, significant t-test, $p < 0.05$.

though more of them probably died or were killed *in situ*. The average 2-week survival of "resident" males was low on all grids except K in the spring experiment (Table 4). The number of females, unlike males, was fairly constant on all grids until early March (Fig. 3) and this is reflected in the higher average female survival (Table 4). But, female survival dropped suddenly to 0.66 and 0.36 on the controls in March and remained low over the next 6 weeks and population density declined. Female survival on experimental grids F and K was 0.78 and 1.00 respectively at this time, and it remained higher than on the controls for the next 6 weeks. Meanwhile, female population size declined more slowly on the food grid compared with the control grids, and actually increased on the covered grid over the same 6 weeks.

In the period between the experiments, survival of "residents" of both sexes was good on all grids. By contrast, survival was poor on all grids without exception during the second experiment. This period coincided with the appearance of botfly (*Cuterebra*) larvae in voles. In August, 40 to 60% of the voles on all grids were infected with botfly larvae. Voles with more than one botfly larva rarely survived to the next trapping period (Table 4). Also at this time the grassland around the grids was cut and we do not know what effect this had on the grid populations.

Use of space

Home ranges were calculated for all voles with four or more captures using the method of Koeppl *et al.* (1976). Voles on both experimental grids had smaller home ranges than voles on the controls during the spring

decline (Table 5). The smallest male home ranges were recorded on the grid with extra cover. Females with extra food had significantly smaller home ranges than females on the control grids. Thus, spacing behaviour of the two sexes appeared to respond differently to the manipulation of food and cover.

Discussion

Spring declines in microtine populations are interesting because they are a repeatable phenomenon and hence experimentally tractable. They are easier to define demographically than other stages of population fluctuations, because they begin before the breeding season is underway so there are few recruits. The predominant factors causing changes are death and dispersal. The experiments reported here were attempts to reduce mortality from bird predation and reduce deaths and dispersal caused by food shortage during a spring decline.

The most significant result was produced by the addition of cover to a population in spring. Predators, namely Great blue herons (*Ardea herodias*), Marsh hawks (*Circus cyaneus*), Short-eared owls (*Asio flammeus*), and Barn owls (*Tyto alba*), were frequently observed on all grids, but not on the grid with the straw covering. Male voles in this population declined at a fifth the rate of males in the control population. Females with cover increased in number, whereas females in all other populations declined. The survival of both sexes of "resident" voles with cover was significantly higher than survival on the controls.

Boonstra (1977) suggested that predation was not a driving variable in *M. townsendii* declines. But, as

Beacham (1979) pointed out, it is difficult to estimate predation by doing a descriptive study because one cannot find all the pellets and scats produced by predators. We suggest that Boonstra's conclusion may be in error, and agree with Beacham (1979) that a direct experimental test is the best way of determining the importance of predation. If, as the present results suggest, predation is important at this time of year, this may help to explain why we failed to duplicate the results of a previous feeding experiment on this species (Taitt and Krebs 1981). Waterfowl not only robbed food stations but also reduced the cover somewhat on the food grid.

It is possible that the presence of extra cover attracted voles to grid K during our experiment. However, only 45 new voles were captured on the grid comparing closely with 37 on the control C1. We have another indicator of dispersal because we know how many of the voles that disappeared from the "core" were later caught in the "periphery" of each grid. We caught 12% and 26% of the voles leaving the control "core" in the "periphery" of the control grids. This compares closely with 17% on the straw covered grid, so voles were not attracted to this grid.

Simultaneously with this experiment, we manipulated behaviour of males in two other populations (Gipps *et al.* 1981). The results of these experiments were disappointing because we were unable to stop the spring decline in either population. But in the population where large males were rendered less aggressive by implants of scopolamine, the rate of decline was reduced. If voles on the covered grid survived well because of reduced predation, and if predation is acting as a driving variable on these populations in spring, then we might expect such a result. If the large, "passive" males fought less with small subordinates, small voles may have been chased less and hence may have been less exposed to predation.

It is possible that other extrinsic factors are acting as driving variables on these vole populations and their effects may also be seasonal. For example, experiments were repeated in summer 1979, but gave no significant results (Gipps *et al.* 1981; present paper). Voles in the area became infected with parasitic botfly larvae, and the survival of infected voles was considerably reduced (Table 4) (also Boonstra *et al.* (1980)). Further, the summer mowing of the area around the grids kills some voles directly and reduces cover considerably for those that remain. (We established a grid in such an area during the winter 1979–1980; the population reached a winter peak of only 48 voles compared with 108 on an uncut area.)

Elton (1939), Frank (1957), Birney *et al.* (1976), and Taitt and Krebs (1981) have considered the possible importance of cover to vole populations. Experimental

reduction of cover by cattle grazing has been observed to result in very low density vole populations (Birney *et al.* 1976). As far as we know, the present experiment is the first attempt at increasing cover. As well as reducing predation, we increased the complexity of surface vegetation by adding straw. If dense cover reduces rate of encounter, and if female reproductive behaviour is sensitive to interaction rate (Saitoh 1981; Taitt 1981), this might explain why females became reproductive earlier and maintained higher densities on the covered grid.

The spring decline and population fluctuations

It is interesting to look at this vole population when a substantial spring decline takes place and when the decline is slight (Fig. 4). The change in numbers from winter 1972–1973 to summer 1974 is typical of the annual fluctuations exhibited by *Peromyscus maniculatus* populations (Sadleir 1965) and the noncyclic island population of *M. breweri* (Tamarin 1977). The repeated features are fall cessation of reproduction, a midwinter peak in numbers, then and a substantial spring decline in both sexes which starts in late winter and extends through the spring. By contrast, the pattern from winter 1974 to spring 1976 is similar to that of a cyclic species (see *M. pennsylvanicus* and *M. ochrogaster*: Krebs *et al.* 1969; Keller and Krebs 1970; Tamarin 1977; *M. townsendii*: Beacham 1980; Krebs 1979). Most of these populations breed into the winter, increase in number throughout the winter, and have little or no spring decline. If they do decline it is because of a decline in males but little or no decline in females. Numbers then peak over an often shortened breeding season, then both sexes decline dramatically.

Taitt and Krebs (1981) suggested how spacing behaviour, the seasonal availability of patches of habitat (food and cover), and predation might interact to maintain

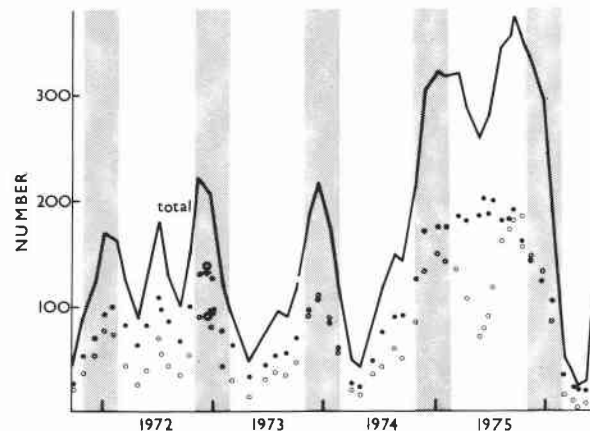


FIG. 4. Population size of *Microtus townsendii* on a control grid (0.8 ha) on Westham Island. Winter months are shaded. —, total; ○, males; ●, females.

annual fluctuations in *M. townsendii*. We suggest that spacing behaviour may "decide" which voles disperse and which are subject to predation, but the extent of temporally suitable habitat and the visibility of voles to predators may be the driving variables. Such factors, by "removing" some voles (as emigrants and (or) prey) from the population, may determine the severity of the spring decline. Further, if there is any generality to the observation that populations with substantial spring declines fluctuate annually while those with little or no decline cycle, then do these driving variables determine the form of population fluctuation exhibited by these small rodents?

We suggest that future attempts to explore the role of behaviour and other factors on rodent declines will be hard to interpret unless the habitat (as food and cover) and predation can be measured and, if possible, controlled. For example, behavioural manipulations or feeding experiments should be done on both "open" and "covered" populations if predators are present and cover is poor.

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