

Diel activity and demography in an enclosed population of the vole *Clethrionomys glareolus* (Schreb.)

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Diel feeding activity in an enclosed cyclic population of the bank vole *Clethrionomys glareolus* was studied during an increase and peak year in 1983–85. An automatic camera at a feeding station was used. The population was also live trapped monthly to follow its demography. The individual voles visited the feeding station most often during spring and autumn, which was obviously due to nutritive reasons. On the population level a polyphasic and irregular activity rhythm was the main pattern observed. However, when all observations during both years were pooled a rather uniform activity pattern could be recognized over the whole 24-hour period during summer, a diurnal activity pattern during autumn and winter and a nocturnal pattern during spring. During the breeding season the activity of the juveniles and subadults was much higher than that of the adult individuals. The juveniles often moved in groups of two to four individuals — these groups obviously consisted of siblings. During spring, after the onset of reproduction, the feeding activity patterns of adult individuals seemed to differ from the patterns of juveniles and subadults. The feeding activity rhythm of young individuals may be more flexible than that of old ones and constitute one reason for the rather uniform activity pattern during summer. The results do not exclude the possibility that different social groups may have different diel feeding activity rhythms.

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1. Introduction

Social factors have been shown to influence several physiological and reproductive processes in small rodents e.g. maturity both in *Clethrionomys* males (Kalela 1957, Gustafsson et al. 1983) and in females (Kalela 1957, Bondrup-Nielsen & Ims 1986a, b). Social factors seem to affect cyclic populations of small rodents more than non-cyclic populations (Viitala 1977, Gustafsson et al. 1983, Bondrup-Nielsen & Ims 1986a, Hansson 1986).

Activity patterns of small rodents are adaptations to the diurnal and seasonal changes of the environment. In most studies the environment consists only of physical factors. This is often due to the study design where only one, or at most a few, individuals are studied under laboratory conditions on circadian and short-term rhythms. Such studies on microtines have been done by Durup & Saint-Girons (1958), Saint-Girons (1960, 1961), Peiponen 1962, Erkinaro (1961,

1969, 1973a, 1973b), Pearson (1962), Stebbins (1972, 1974, 1975), Lehmann (1976), Lehmann & Sommersberg (1980), Erdakov (1985) and Stubbe et al. (1986). Activity studies at the population level have been carried out by Miller (1955), Brown (1956), Kikkawa (1964), Erkinaro (1969), Dewa (1975), Greenwood (1978), Wolton (1983), Wojcik & Wolk (1985) and recently by Halle & Lehmann (1987). Studies on activity over several seasons or years in areas with permanent snow cover are almost totally lacking (see, however, Halle & Lehmann 1987).

In terms of resource allocation between individuals social factors together with food availability could affect an individual's activity. They may even be more important than physical environmental conditions. For drawing conclusions about populations determining the activity patterns of solitary individuals is of no use; rather one ought to ask who is active *when* in its biotic environment (cf. Pearson 1962,

Chitty & Shorten 1946, Nygren 1978). The question is also important from the predators' point of view: some individuals or groups in the population could be more exposed to predation because of activity patterns maintained by social hierarchy.

This paper is an attempt to answer the following questions on the basis of monitoring the feeding activity of the bank vole (*Clethrionomys glareolus*) under field conditions between 1983–85: 1) Does there exist the same short term (~4 h) vs. dusk/dawn diurnal activity pattern in the population as described for individual bank voles? 2) How does the changing demography affect the diel activity pattern between seasons? 3) Is it possible to find segregated activity times for different social groups in the population during the breeding season?

2. Material and methods

The enclosure (0.8 ha) used in this study is situated near the Konnevesi Research Station of the University of Jyväskylä in Central Finland. It includes two main habitats: a spruce forest and an abandoned field (see Ylönen & Viitala 1985 and Ylönen et al. 1988 for details).

To examine the social structure and demography of the population, live trapping has been performed since 1982 using 81 Ugglan special traps set at intervals of ten metres. Trapping was done throughout the year. A trapping census consisted of ten checkings during one week of each month. When captured for the first time the voles were marked individually by toe-clipping. The following data on each capture were recorded: date, time, trap location, individual code, sex, weight, sexual stage, scars and behaviour.

Feeding activity was determined using equipment modified from Osterberg (1962) and Törmälä et al. (1980). The equipment consisted of a feeding station with only one entrance hole. Above the entrance there was a watch showing the weekday and, additionally, the week number. On both sides of the entrance hole there was an electromagnetic switch releasing a super-8 movie camera and a flash unit which were placed about 1.5 metres away from the hole.

The equipment was first placed in the forest area where it operated from July 1983 to July 1984. The location was, however, rather poorly visited by the voles during winter because of the aggregation of the population on the abandoned field site and in the brush wood areas (Ylönen & Viitala 1985). In July 1984 the feeding station was moved to the abandoned field, in a small forest pocket which the voles also frequently visited during the winter. Here it operated until April 1985 except for an interruption of eight weeks in October–December 1984 as the flash unit was out of order. On the grounds of long-term trapping data in forest and old field habitats it seems evident that the habitat has either very little effect on the activity of voles, or none at all (Ylönen, unpubl.).

The films were analysed using the following criteria: a vole entering the feeding station hole and coming out was counted as

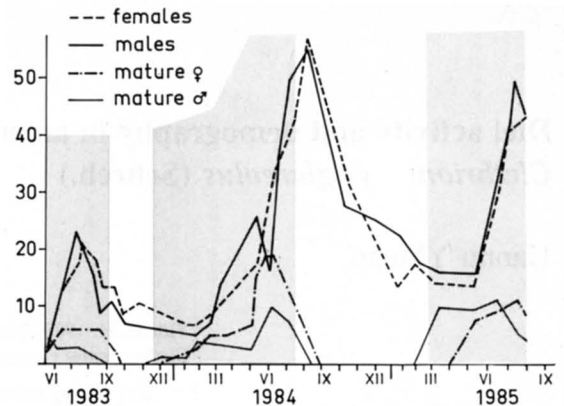


Fig. 1. Density fluctuations in the enclosure population of *Clethrionomys glareolus* during the study period 1983–85. The total number of females and males and the number of mature individuals during each month is given. The breeding seasons are shaded.

a single observation. In some cases the voles did not release the switch twice. Nevertheless, either entering or leaving the hole was regarded as a single observation. Sometimes a vole stayed under the switch and released it several times: this may have happened for social reasons i.e. the feeding place was already occupied. In these cases pictures of a vole in the same position over a period of one or two minutes were regarded as one observation.

The diel activity patterns were evaluated on the basis of counts per one hour of the day during a two-week period. To smoothen the random variation in the two-week activity patterns a moving average for each hour was used, where the value of each hour was determined as an average of the values of that hour, the preceding and the following hour. For seasonal activity the sum of the values of each three hours starting from midnight was used.

For two two-week periods the visits at the feeding station were counted separately for "large individuals" and "small individuals" to obtain a picture of the adult vs. subadult and juvenile activity. These periods applied to both the forest habitat in the spring of 1984 after high winter breeding activity, and the 1984 summer. Animals in the super-8 picture as large as the voles forming the winter population just before the onset of breeding in January were considered, and thus counted as, "large individuals".

The material of this paper consists of 8541 observations divided almost equally (4160/4381) between the two years.

3. Results

Population fluctuations and the main social cohorts of the population during the study period are shown in Fig. 1. In the summer of 1983 the population

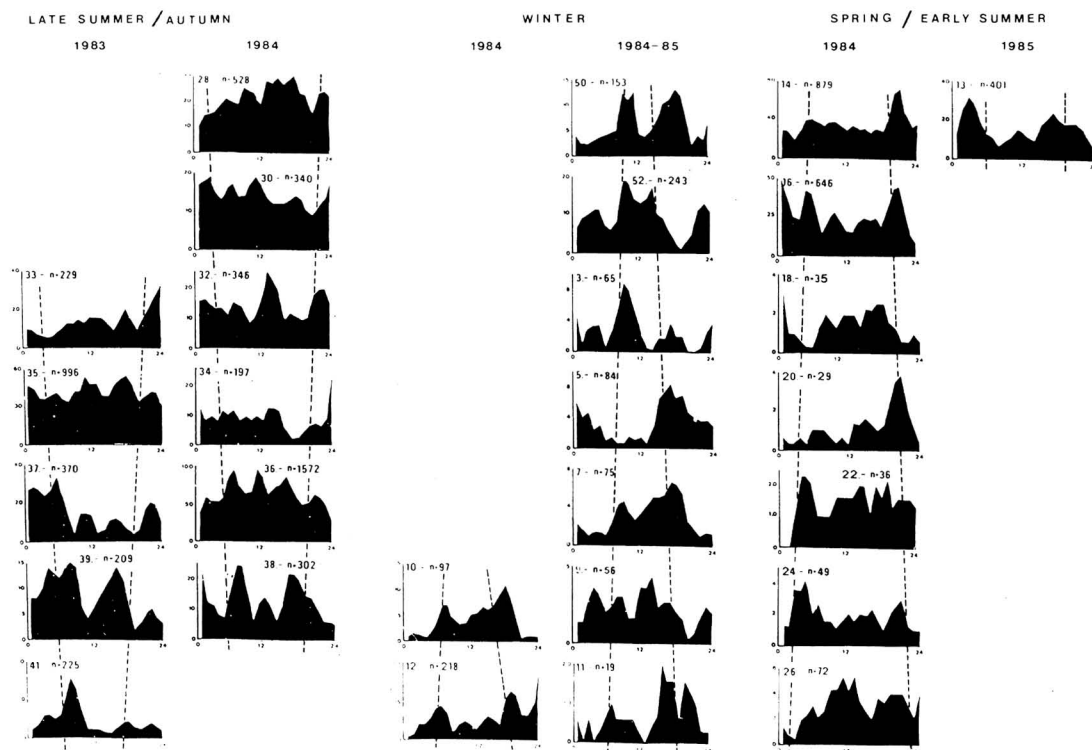


Fig. 2. The moving average of the number of visits at the feeding station during each hour of the day for each pair of weeks during the study period. The value of each hour has been calculated as an average of the values of that particular hour together with the values of the two adjacent hours. Comparative graphs for different years are shown beside each other. For missing graphs see the text. The dotted lines indicate times of sunrise and sunset.

reached densities equal to the previous summer and breeding continued until September. The wintering population was formed at the end of September/beginning of October. During the winter 1983/84 a heavy winter reproduction took place in the enclosure population, resulting in a strong increase in density. This increase continued until the beginning of August and the final population density was almost three times higher than in 1983 (Ylönen & Viitala 1985, Ylönen et al. 1988). During the winter of 1984/85 the density remained high after the autumn decline and reproduction started again as early as February.

The moving average of the numbers of visits at the feeding station for each pair of weeks beginning in the middle of August 1983 is given in Fig. 2. The time of dusk and dawn and the number of visits during the period are also shown in each graph.

In Fig. 3 seasons of both years are compared. Differences in the activity patterns of the seasons of both years were highly significant (Overall G -test of

observed frequencies $G = 1347$, $df = 49$, $P < 0.0001$). In every season except summer the differences in the activity patterns were highly significant (G -test of observed frequencies: autumn $G = 130$, winter $G = 47$, spring $G = 45$ in every case $df = 7$, $P < 0.001$). The two summers differed only at the level $P < 0.05$ ($G = 15$). In spring, at the onset of breeding, the population seemed to have a rather clear nocturnal feeding activity pattern. In summer the distribution of the visits at the feeding station was almost uniform; towards autumn there was more activity during the dusk hours. During the winter months, especially in 1985, we had a diurnal feeding activity pattern with a peak during the afternoon hours.

The relation between the activity during the light hours and dark hours was also counted for each pair of weeks for the whole study period (Fig. 4). The vole population seemed to be significantly more active during the light hours from autumn to the onset of breeding (weeks 39–40/83 $\chi^2 = 4.27$, $P < 0.05$, weeks

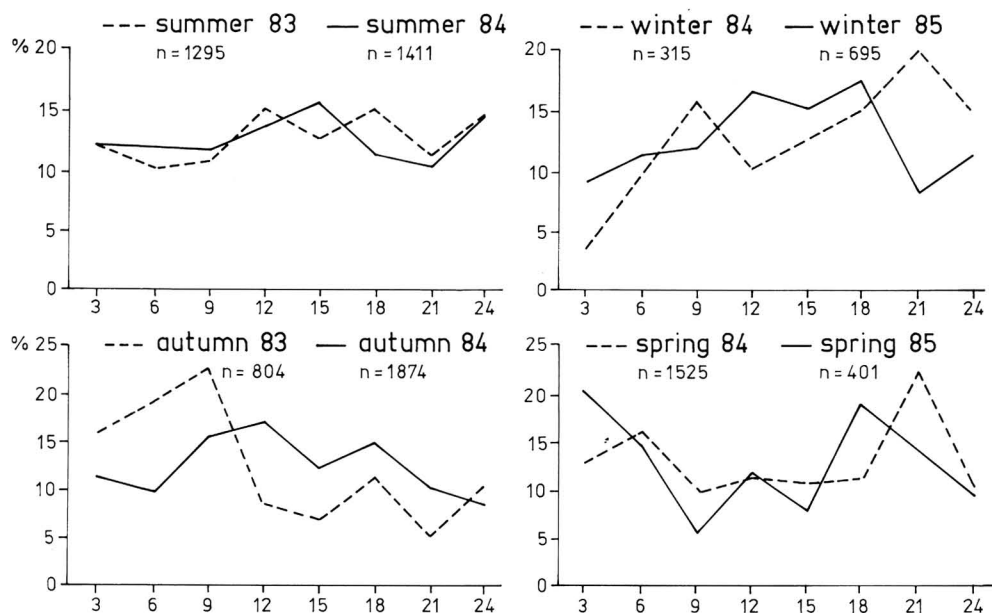


Fig. 3. The relative feeding activity of the bank vole population for each season of both years counted for each three hours of the day. Total numbers of observations per each season are given above the graph.

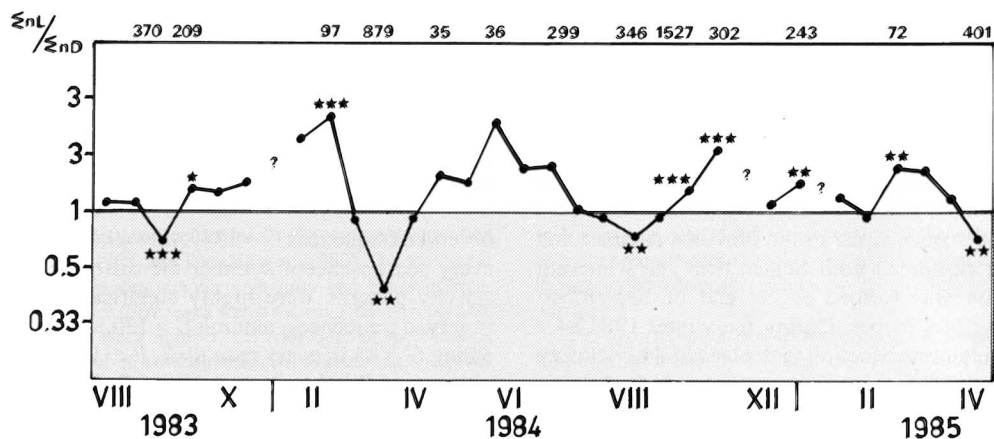


Fig. 4. The relation between the activity during the light hours and the activity during the dark hours for the whole study period. For statistical analysis the Willcoxon rank correlation test and χ^2 -test were used. For more details see text the text. The numbers of observations for each two weeks' period are shown above the graph. Note the discontinuity in the X axis due to failures in the activity determination apparatus. For breeding season see Fig 1.

10.–11./84 $\chi^2 = 22.00$, $P < 0.001$, weeks 36.–37./84 $\chi^2 = 40.89$, $P < 0.001$, weeks 7.–8./85 $\chi^2 = 6.90$, $P < 0.01$. The visible diurnal activity during the summer of 1984 was not significant but the number of visits at the feeding station was low during that time. The

preference of nocturnal activity in spring and in autumn was also significant at least at the level $P < 0.01$ (weeks 37.–38./83 $\chi^2 = 15.71$, 14.–15./84 $\chi^2 = 9.06$, 32.–33./84 $\chi^2 = 8.41$, 13.–14./85 $\chi^2 = 10.38$, n -values in the Fig. 4).

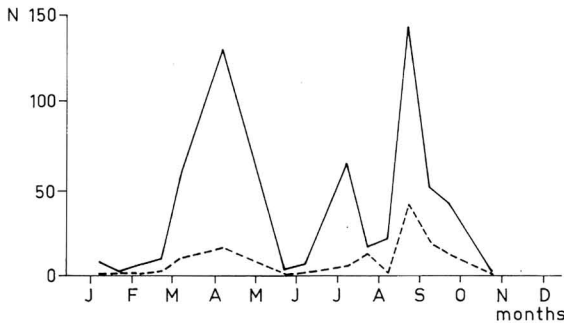


Fig. 5. The number of visits to the feeding station per the number of individuals in the whole population (dotted line) vs. the number of individuals in an area of 0.25 hectares around the feeding station (solid line) during each live trapping period. The data from both years are pooled and shown for the calendar year. Whether the decrease in August is due to actual biological causes or to a technical failure in the apparatus is unknown.

No positive correlation was found between the total number of visits to the feeding station during each pair of weeks and the population density in the enclosure. In Fig. 5 the number of observations per individuals present both in the whole enclosure and in an area of 0.25 hectares around the feeding station is shown for each pair of weeks. The latter relation was counted in order to obtain a picture of the activity of the individuals that obviously made the majority of visits to the feeding station. The graph shows that the mean activity is very high during spring and autumn and low during summer and winter. The high usage of the feeding station overlaps with the times of the spring and autumn phase shifts between diurnal and nocturnal activity (Fig. 4).

The results of the activity determination of large individuals (adults) and small individuals (juveniles and subadults) are shown in Fig. 6. In spring, after the winter breeding, the number of visits of juveniles and subadults to the feeding station was already 85% of the total (according to the trapping data juveniles and subadults made up 32% of the whole population at the beginning of March and 53% at the end of April). This was mainly due to the behavioural fact that

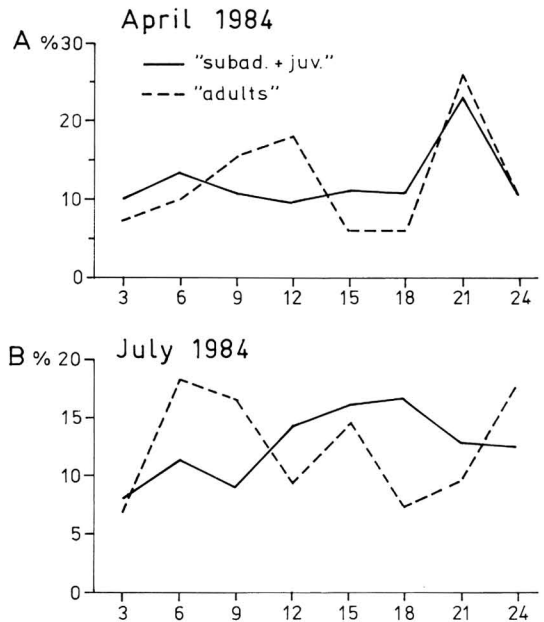


Fig. 6. The relative feeding activity of large individuals ("adults") and small individuals ("juveniles and subadults") in April 1984 after the winter breeding, and in July 1984 at the time the high summer population density.

juveniles move in small groups, siblings obviously often keeping together, as evidenced also by live-trapping data (Ylönen unpubl.).

In spring the activity pattern of the adults seems to be more distinctly bimodal than that of the juveniles ($G = 17.7$, $df = 7$, $P < 0.025$). During summer the large individuals seem to maintain the same kind of pattern as in spring (difference "adults spring/ adults summer", $G = 15.1$, $P < 0.05$) as the small individuals change their feeding activity drastically ("juveniles and subadults spring/summer" $G = 37.7$, $P < 0.001$).

The distribution of the longterm diel feeding activity during the study period July 1983 – April 1985 is shown in Table 1. It seems to reflect the relative evenness of the activity patterns of the voles throughout the whole study period.

Table 1. Diel distribution of the total number of visits in the feeding station during the whole study period between July 1983 and April 1985.

Time of day	0–3	3–6	6–9	9–12	12–15	15–18	18–21	21–24	Mean
No. of visits	1019	1065	1088	1163	1028	1161	1072	945	1067 (SD 72.9)
in %	11.9	12.5	12.7	13.6	12.0	13.6	12.6	11.1	

4. Discussion

The present study shows (Fig. 2) that the activity pattern of a population can be fairly flexible during one season. Possible stable short-term endogenous rhythms of individuals do not necessarily cause the same pattern to appear on the population level.

In *Clethrionomys* there do not seem to exist such radical phase-shifts between seasons as in *Microtus* (Erkinaro 1961, 1969). However, when the light/dark activity relation of several seasons is compared the phase-shift is found both in spring and in autumn (Fig. 4). These are also the times of year when the individual voles visited the feeding station most often (Fig. 5). It can be assumed that these times are also the most critical periods for the survival of the population because of shortage of food together with the onset of breeding in the late winter/spring and the declining of the vegetation by the forming of the wintering population and possible aggregations in the autumn (see Ylönen & Viitala 1985). The efforts of individual voles to survive both critical phases could also cause far higher feeding activity than during summer and winter. The change of the main activity time for these short periods could also decrease the predation pressure during the time of the declining vegetation and the lack of snow.

Otherwise the changing demography in the population can be seen in the rather uniform activity distribution during the high population phases in summer (Fig. 3). This uniform distribution of visits to the feeding station could also be caused due to social reasons, if the visiting times are shared between individuals or social groups (Pearson 1962, Nygren 1978). During this time the number of juveniles and subadults with common group movements (Ylönen, unpubl.) is also highest in the population. Group movements or even group dispersal of juveniles and subadults has also been observed in *C. rufocanus* Viitala (pers. comm.) but for adult bank voles, even with communal nesting, separate feeding activity and distinct feeding movements seem to be more common (Karlsson & Ås 1987).

During seasons when the population consists mainly of immature animals or individuals familiar to each other (Ylönen & Viitala 1985) more distinct activity peaks, e.g. during dawn and dusk hours, may develop based on the endogenous rhythmicity of the animals. This has also been shown in several laboratory studies (Durup & Saint-Girons 1958, Saint-Girons 1960, 1961). In terms of feeding activity dis-

tribution the bank vole seems to be able to react flexibly to physical and social environmental conditions.

There were significant differences between the study years when the seasons or even shorter periods were compared with each other (see Halle & Lehmann 1987). This is proof of the flexibility inherent in the short-term behaviour of the population. However, the increase of the visits to the feeding station and the phase shifts during autumn and spring indicate the influence of great seasonal environmental changes, e.g. snow and vegetation cover, and the availability of food on the formation of activity patterns (see Miller 1955). I suppose that the influence of weather on the activity patterns of the population could only be of secondary importance because great differences were also observed between the winter weeks in spite of relatively steady "weather conditions" under the snow (c.f. Getz 1968, Lehmann & Sommersberg 1980).

The comparison of the diel activity patterns of adult and subadult/juvenile individuals during the breeding season did not show any conclusive differences between the groups. The change in the activity pattern of juveniles was significant between spring and summer as the adult individuals seemed to maintain the same kind of pattern during both seasons.

Finally I conclude that the endogenous rhythm, together with timing by the environmental Zeitgebers (e.g. light) can produce "classical" diel activity patterns described for *Clethrionomys* in several studies (e.g. Brown 1956, Durup & Saint-Girons 1960). In the field at population level the activity seems to be determined by many factors: light, temperature, snow cover, predation pressure and social relationships between individuals and groups. If the overwintering takes place in aggregations (Ylönen & Viitala 1985), according to Karlsson & Ås (1987) the social component in the foraging activity and movements of the individuals outside the nest are still apparent (see, however, Dewa 1975). During the breeding season the population is formed of different cohorts with some degree of avoidance and antagonism between them (Johst 1967, Ylönen unpubl.). This could lead to sharing of the time niche between members of the population exploiting the same resources and cause a rather uniform activity pattern.

The rather uniform activity pattern during the breeding season — and not only the preferred wooded habitat — could explain the rather small amount of *Clethrionomys* remains in owl pellets (e.g. Korpimäki

1984). In *Microtus* we have strict diurnal/nocturnal activity patterns followed by similar activity by birds of prey (Erkinaro 1973, Daan & Slopesma 1978, Rijnsdorp et al. 1981). As far as the polyphasic or uniform activity patterns of *Clethrionomys* are concerned, we can expect them to have only slight influence on the activity of predators.

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