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HIGHER REPRODUCTIVE SUCCESS AMONG KIN GROUPS OF BANK VOLES (*CLETHRIONOMYS GLAREOLUS*)¹

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Abstract. According to the kin selection theory the degree of genetic relatedness affects the nature of intraspecific competition and it might promote cooperative and/or altruistic behavior between individuals. We examined kinship effects on reproductive success of territorial females and survival of juveniles in the bank vole *Clethrionomys glareolus*. Four experimental populations were founded in large enclosures (0.5 ha): two consisted of five related (Related, R) and two of five mutually unrelated females (Unrelated, UR). Each population had five males of heterogeneous origin.

Our earlier results showed that populations of the R grew twice as fast as the UR. Here we show that recruitment and offspring survival is connected to spacing behavior of mothers. Unrelated females who had their home ranges close to each other produced significantly fewer recruits than the related ones. Their home ranges overlapped significantly less and ranges were smaller if they were situated close to each other. Furthermore, the survival of juveniles declined with dispersal distance from the natal territory in populations of the UR. Trappabilities of juveniles were also lower among the young whose home ranges were close to unrelated females, indicating avoidance of mature females.

Our results indicate that competition for space is more intense among unrelated neighbors, decreasing their reproductive success. Infanticide towards unrelated nestlings and/or juveniles is one possible mechanism decreasing survival and causing a lower recruitment of young. On the contrary, sharing of space among related neighbors did not seem to cause notable costs on their reproduction. Mature females allowed related young females to use their territory, but still, the young did not acquire an area for their own reproduction, probably due to a mother–daughter conflict. The basic social structure of *Clethrionomys* populations, i.e., exclusive female territoriality, remained the same regardless of a high degree of relatedness.

Key words: infanticide; juvenile survival; kinship; reproductive success; space competition; territoriality; voles.

INTRODUCTION

Since Hamilton (1963, 1964) first emphasized the importance of kinship to the evolution of sociality, much interest has centered on those social systems where genetic relatedness might determine cooperative and/or altruistic behavior between individuals. Most studies on mammals and other vertebrates have focused on kin recognition and/or discrimination, i.e., the mechanisms that should make it possible for individuals to optimize genetic costs and benefits of social interactions (for reviews, see Hepper 1986, Waldman 1988, Barnard 1990). However, field experiments designed to study effects of kinship on social behavior and reproductive success are still rare (but see, e.g., Kawata 1987a, Ims 1989, Ylönen et al. 1990, Lambin and Krebs 1993).

Characteristics of a social system determine how an individual can utilize possible altruistic or mutually beneficial interactions with relatives. Females of several vole species mature and breed only if they gain an

exclusive home range (Bujalska 1973, Boonstra and Rodd 1983). In many cases exclusiveness and little overlap between home ranges indicate active defense of an area (territoriality). Territoriality is generally suggested to be based on intraspecific competition for resources, the spatial distribution, and abundance of food and mating partners (Ostfeld 1985, Ims 1987a, 1988, Ostfeld 1990). Another benefit for territoriality is the prevention of infanticide (Wolff and Cicirello 1989) as it might be advantageous for a female to kill pups or young of other females that compete with their own offspring for resources, but evidence supporting this hypothesis is still limited (Ostfeld 1990, see however, Bujalska 1991, Wolff 1993).

Relatedness between neighbors should shift the cost-benefit balance of territorial behavior. This might be one reason for the considerable individual variation of spacing behavior and reproductive success in *Clethrionomys* voles (Ims 1987a, b, Ylönen et al. 1988). For example, altruistic and cooperative sharing of space and other resources may appear as reduced size and/or increased overlap of home ranges of neighboring related breeding females. On the contrary, space com-

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petition should be more intense and infanticide more common between unrelated neighbors.

We recently showed that the high degree of relatedness stimulates population growth in the bank vole *Clethrionomys glareolus* (Ylönen et al. 1990). The social system of the bank vole is characterized by strict females territoriality and philopatry, which promotes the formation of kin groups (Bujalska 1985, Ylönen et al. 1988) and enables individuals to recognize closely related females mainly by means of familiarization (Ferkin 1988).

In this study we analyzed the mechanisms behind the different population growth between the related and unrelated populations (Ylönen et al. 1990). We studied (1) whether size and distribution of territories of female bank voles differ between related and unrelated groups, (2) whether the spatial organization of related and unrelated females is connected to their breeding success, and (3) whether breeding females affect space use and trappability of juveniles, indicating avoidance of territorial females.

METHODS

The experiment was carried out at Konnevesi Research Station, central Finland (62°37' N, 26°20' E) during the summer of 1988. Experimental populations were established on four 0.5-ha enclosures in a homogeneous abandoned field (for details, see Ylönen et al. 1990).

Another experiment with bank voles was conducted in the enclosures during the winter preceding our experiment. Four populations were monitored by live trapping in order to study the effects of resource distribution on space use of bank voles from October to May (Ylönen and Viitala 1991), and two of these populations were randomly selected for the present experiment. From both of these populations five mature females were used in the kin populations of the experiment (called Related or R hereafter in the text). One founder population consisted of a mother and her three daughters (R1) and another, a mother and her four daughters (R2). The mothers were overwintered, and the daughters were born between the middle of April and late May. We accidentally added one unrelated female to the population of R1. However, we excluded this female and her offspring and one of their close neighbors when analyzing space use and reproductive success of individual females in the different populations (see *Results*). This was reasonable as the non-kin relationship seemed to decrease the number (mean \pm 1 SE) of recruits per birth of these three females (\bar{X} = 1.78 \pm 0.22, N = 3) compared to the other females in the same population (\bar{X} = 4.48 \pm 0.27, N = 4) (Mann Whitney U test, one-tailed, U = 0, P = 0.028). These two founder females with a non-kin relationship were also the only mature females in R1 that died before the end of the experiment.

The other two groups (called Unrelated or UR here-

after in the text) were formed mostly from the individuals remaining in the enclosure populations of the previous experiment (four females per enclosure) and from voles trapped at different locations in the Konnevesi area (one female per enclosure). The compositions (the number, ages, and masses) of these two non-kin female groups were similar to the populations of the R.

The founder populations had five males each, where some males were related in populations of the R but not in the UR (for details, see Ylönen et al. 1990). We found no differences in behavior, survival, or reproductive status of males among the experimental populations. Also, males did not seem to affect survival or spacing behavior of juveniles (T. Mappes et al., *unpublished data*), and we have therefore restricted the scope of the present paper to the behavior of founder females and their offspring.

The experiment was carried out from 18 June until 28 September (103 d). The four experimental populations were randomly assigned to the four enclosures, with the exception that each kin population had to be transferred from its original enclosure. The animals were released simultaneously at the same coordinate point in the middle of each enclosure. For monitoring the populations we used 50 Ugglan Special multiple-capture live traps in each enclosure with 10 m between the trap stations. Four trapping periods were carried out during the study (early July, late July–early August, late August and late September) (for details, see Ylönen et al. 1990). At their first capture new individuals were marked by toe-clipping. Trap location, sex, mass, and reproductive status for each capture of each individual were recorded.

Number of births was estimated by mass loss of pregnant females (Kawata 1987b). Reproductive success of each female was determined by number of juveniles recruited into her territory per number of births during the experiment. The juveniles were trapped within their natal home range when they were 2.5–3 wk old before dispersing (T. Mappes et al., *unpublished data*). Home range center, home range size, home range overlap and trappability were estimated for individual voles separately for each trapping period. In statistical analyses we used the mean values of these separate estimations. Home range center was calculated as the mean point of each individual's capture coordinates. Nearest neighbor distance was calculated from distances between the centers of home ranges of the neighbors. Home range size was estimated as the number of different trap sites (one site = 100 m²) an individual visited. This method is quite robust, but sufficient for comparisons of space use between our treatments. Also, trappability of an individual greatly affects the home range estimate. This bias was considered in the space use analyses and we did not compare the home range sizes of the individual groups between which trappability differed significantly. Home range overlap was measured as the num-

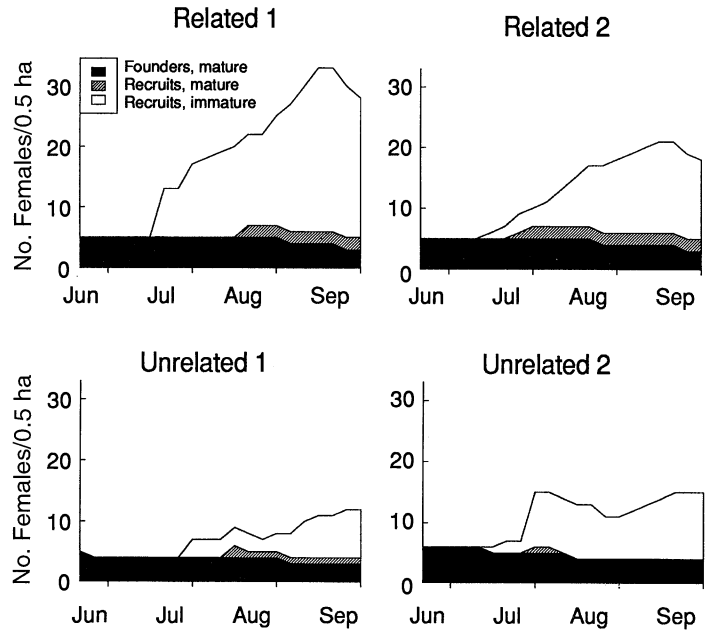


FIG. 1. Numbers and survival of female cohorts during the experiment.

ber of trap sites (one site = 100 m²) in each female's home range visited by other reproductive females, too. Trappability of voles is a percentage expressing the times when individuals were caught in relation to the number of possibilities to enter the traps during the trapping period.

Nonparametric statistics were used to test the effects of treatment and replicate on the variables of space use and trappability (see Tables 1 and 2, Fig. 3). First, values of the variables were ranked and then sum squares and mean squares were estimated as in parametric two-way ANOVA. The test value $H (= SS_{SOURCE}/MS_{TOTAL})$ follows asymptotically the chi-square distribution with df_{SOURCE} . Details of analyses are described by Zar (1984).

RESULTS

Density of breeding females

The initial density of breeding females in each enclosure was 10 individuals/ha (Fig. 1) which approximately corresponds to spring densities in a peak year of cyclically fluctuating populations in Central Finland

(Ylönen et al. 1988). Two founder females died in each population during the experiment. The overall density of breeding females was lower among the Unrelated (UR) due to the earlier death of founder females and poorer survival of younger mature females (Fig. 1). All the four female recruits, which matured among the Related (R), survived until the end of the experiment in contrast to a single one of three among the UR (Fig. 1). Populations of R grew significantly faster (13.8 individuals/mo, $SE = 0.075$) than Non-relatives (5.7 individuals/mo $SE = 0.030$) ($t = 3.35$, $df = 20$, $P < 0.01$) (Ylönen et al. 1990). At the end of the experiment the population density of R was on average 116 voles/ha, which was twice as high as that of UR, which averaged 55 voles/ha.

Reproductive success and space use of breeding females

The related females produced significantly more offspring per birth than the unrelated ones (Table 1). Among the UR the number of recruits per birth was positively correlated with the distances between the

TABLE 1. Reproductive success, space use, and trappability of reproducing females in the treatments.

Variable	Related ($N = 11$)	Unrelated ($N = 11$)	df	H^*	P
No. recruits/birth†	3.0 (2.3, 4.3)‡	1.7 (0.0, 3.0)	1	4.11	0.043
Nearest neighbor distances (m)	21.8 (13.5, 23.5)	20.6 (13.3, 20.6)	1	0.07	0.791
Size of home ranges (m ²)	600 (533, 700)	700 (600, 767)	1	1.41	0.235
Trappability (%)	74.8 (61.6, 80.7)	72.8 (64.3, 75.9)	1	0.91	0.340

* H is the test value for the effect of treatment on ranked values of variables (see details of variance analyses in the *Methods*). In all models the effect of replicate is insignificant ($P > 0.05$).

† In the model nearest neighbor distance was used as a covariate.

‡ Median (quartiles at 25% and 75% points).

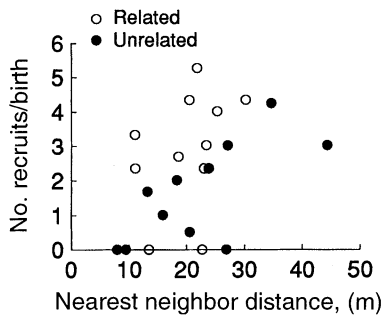


FIG. 2. Significant positive correlation between number of recruits per birth and nearest neighbor distances among the female Unrelated (Spearman rank correlation, $r_s = 0.73$, $N = 11$, $P = 0.011$). Among the Related this relationship was not found ($r_s = 0.32$, $N = 11$, $P = 0.339$). Replicates are pooled together as the variables did not differ between them (Mann-Whitney U test, two-tailed, $P > 0.05$).

nearest breeding females ("nearest neighbor distance") (Fig. 2). Among the R this relationship was not found. Reproductive success correlates with home range size neither among the UR ($r_s = 0.23$, $N = 11$, $P = 0.500$), nor among the R ($r_s = -0.35$, $N = 11$, $P = 0.285$). Trappability of breeding females which might bias the calculation of home range size, did not differ between the treatments (Table 1).

Home ranges of the R overlapped significantly more than the ranges of the UR (Fig. 3). Nearest neighbor distances and home range sizes of breeding females did not differ between the treatments (Table 1). However, home range size of female UR increased with nearest neighbor distances ($r_s = 0.62$, $N = 11$, $P = 0.042$). Data from two replicates are pooled as home range sizes and nearest neighbor distances did not differ between them (Mann-Whitney U test, two-tailed, for home range size: $U = 15$, $P = 0.927$, for distance: $U = 11$, $P = 0.523$). Among the R home range sizes and nearest neighbor distances were not correlated ($r_s = 0.02$, $N = 11$, $P = 0.946$). Also the body mass of female UR (just after birth) has a tendency to correlate with their nearest neighbor distances ($r_s = 0.53$, $N = 11$, P

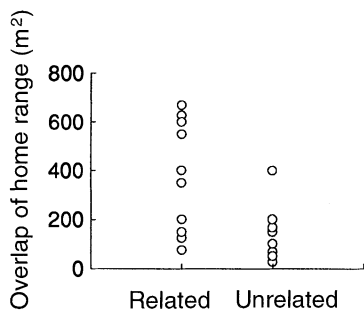


FIG. 3. Mean overlap of female's home range with another breeding female in the treatments. The overlapped area was greater among the Related than among the Unrelated ($H = 4.86$, $df = 1$, $P = 0.027$). The effect of replicate was not significant ($H = 2.88$, $df = 2$, $P = 0.237$).

$= 0.091$), contrary to R ($r_s = -0.005$, $N = 11$, $P = 0.989$).

Survival and maturation of juveniles

The survival of juvenile UR declined with dispersal distance from the natal territory. The home ranges of juveniles that disappeared during their first trapping period were at a greater distance from the territory of the mothers (The distance [mean \pm 1 SE] between home range centers: $\bar{X} = 24.6 \pm 3.6$ m, $N = 6$) than those of juveniles that survived ($\bar{X} = 15.4 \pm 1.5$ m, $N = 42$) (t test, $t = -2.18$, $df = 46$, $P = 0.034$). Among the R this relationship did not occur (the distance for disappeared juveniles: $\bar{X} = 12.2 \pm 1.4$ m, $N = 14$, and for survivors: $\bar{X} = 11.1 \pm 0.6$ m, $N = 76$, $t = -0.70$, $df = 88$, $P = 0.489$).

Four young females matured and showed clear signs of pregnancy among the R and three females among the UR (Fig. 1). Relatedness did not seem to affect maturation of young females, especially as one mature young female in the R1 was the daughter of the only non-related founder female in that population. Territories of young females did not necessarily border on the territory of their own mother, either among the UR (one of four) or among the R (two of three). Number of mature young males (four to five in each population) did not differ between the treatments.

Space use and trappability of juveniles

We calculated space use and trappability of juveniles during their first trapping period when they were 3–5 wk old. Masses of juveniles did not deviate between experimental populations (Kruskal-Wallis nonparametric one-way ANOVA, $H = 2.94$, $P = 0.401$), indicating that age of juveniles might not differ significantly. Between female and male juveniles there were no differences in nearest distances to a breeding female, home range sizes, trappabilities, or masses. Sex and replicate did not have joint effects on these factors (two-way ANOVA, $P > 0.3$ in all cases).

Home range centers of juvenile UR were farther from the center of the nearest unrelated breeding female ("nearest distance to breeding female") than were home range centers of juvenile R (Table 2.) Trappability of juveniles did not differ between the treatments during their first trapping period (Table 2), but was significantly lower among the UR when calculated for the entire time that the individual was present in the population (Ylönen et al. 1990).

Among the juvenile UR trappability declined with shorter distance to the nearest breeding female, which was not the case among the juvenile R (Fig. 4). Moreover, the mass of juveniles was positively correlated with their trappability among the UR ($r = 0.498$, $N = 24$, $P = 0.013$), but not among the R ($r_s = -0.036$, $N = 62$, $P = 0.782$).

TABLE 2. Characteristics of juveniles in the experimental populations. Variables were estimated during the first trapping period when juveniles were captured. Variables did not differ between sexes (see *Methods*).

Variable	Related	<i>N</i>	Unrelated	<i>N</i>	df	<i>H</i> *	<i>P</i>
Nearest distance to breeding female (not mother) (m)	21.1 (17.2, 27.5)†	93	29.4 (18.5, 37.4)	57	1	12.2	0.000
Distance to mother (m)	11.4 (8.0, 14.8)	95	18.2 (8.1, 23.7)	55	1	14.1	0.000
Size of home ranges (m ²)	300 (300, 600)	64	400 (300, 500)	23	1	0.07	0.791
Trappability (%)	42.1 (28.6, 52.9)	64	44.2 (28.8, 64.3)	24	1	0.57	0.450

* *H* is the test value for the effect of treatment on ranked values of variables. See details of variance analyses in the *Methods*. In the models the effect of replicate on all variables is insignificant ($P > 0.05$).

† Median (quartiles at 25% and 75% points).

DISCUSSION

Spacing behavior and reproductive success

Our results indicate that the reproductive success of female bank voles, *Clethrionomys glareolus*, is connected with their space use if neighboring breeding females are non-kin. The home range sizes of unrelated neighbors decreased when ranges were near each other. However, the distance to the territory of neighbor was the only factor that affects their breeding success, not the size of home ranges. This may indicate that the reduced breeding success of unrelated females was not directly caused by intraspecific competition for food resources.

Some of the female Non-relatives, especially the lighter ones, occupied their territories close to each other, although that obviously decreased their reproductive success. Thus, there was no overall difference in the distribution and sizes of territories of related and unrelated females. A possible explanation is that dominant females forced lighter unrelated females to live close to each other in the fenced enclosures where space is rather limited and dispersal impossible.

Clethrionomys species, and especially *C. glareolus*, have been regarded as "model" species of female territoriality during the breeding season (Bujalska 1973, 1985, Ostfeld 1985, 1990). Phenotypic plasticity in so-

cial behavior expressed as increasing overlap of female home ranges has been explained mainly as a result of exceptionally good food resources (Ims 1987a, Ylönen et al. 1988). Our results indicate that kinship between territorial females may allow substantial overlap in the home ranges of bank voles. These findings agree with recent studies by Lambin and Krebs (1993) in Townsend's voles (*Microtus townsendii*). Further, we also found that the costs of using overlapping ranges seemed to be insignificant or very small on the reproductive success of related females. If low, such costs could be outweighed by the possible benefits (e.g., higher inclusive fitness) of space sharing among relatives. Lower quality of habitat may, instead, induce more "selfish" behavior between close relatives (Brown and Brown 1993a, b).

Altruistic and/or cooperative space sharing should result in dense groups of breeding females. In the present study there seemed to be space enough for the founder females to breed both in Relative and Non-relative treatments. So, space sharing might only increase the possibilities of maturation of juvenile females. However, in spite of a greater tolerance of kin-neighbors and their offspring, we did not find a higher frequency of maturation among juvenile Relatives. The density of breeding females seemed to be saturated at 10–12 voles/ha, regardless of kinship. Breeding females allowed related young females to use their home range but, still, they might suppress breeding of young (even their own daughter). This parent-offspring conflict may force young females either to stay and delay breeding (Bujalska 1985), or to disperse from their mothers' home range in order to find a vacant territory to breed in their first summer (Gliwicz 1989). Our experimental design could not take dispersal into account but by using fenced populations without the option of emigration we could estimate the effect of kinship on the survival of young more accurately.

Is infanticide more common in non-kin breeding groups?

There is direct evidence of infanticide in a wide range of rodent species (Elwood 1977, vom Saal 1984, Wolff 1985, Wilson et al. 1993), but, so far, not in the bank vole. However, recent experimental studies by

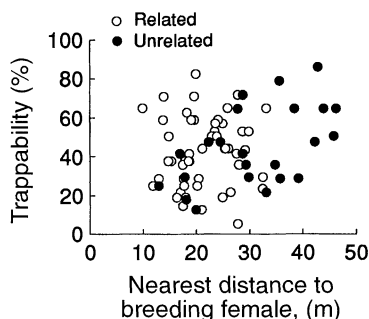


FIG. 4. Among the juvenile Unrelated trappability declined with shorter distance to the nearest breeding female (Partial correlation, controlled for replicate, $r = 0.563$, $N = 23$, $P = 0.005$), which was not the case among juvenile Related (Pearson $r = -0.040$, $N = 54$, $P = 0.773$). Replicates are pooled together as the variables did not differ between them (Mann-Whitney *U* test, two-tailed, $P > 0.05$).

Wolff and Cicirello (1989, 1991) and Cicirello and Wolff (1990) indicate that this phenomenon might be more common than expected in the social system of the bank vole, too. Based on his own long-term data and literature sources Wolff (1993) argues that female territoriality in small mammals, and especially in microtines, should be to protect pups against infanticide rather than to protect food resources. Wolff and Cicirello (1989) found, e.g., that territorial female *Peromyscus leucopus* killed pups that were placed within or at the edges of their territories. They proposed that resource competition between females induces infanticide. Resident males did no commit infanticide but dispersing and unmated males did.

According to the kin selection theory (Hamilton 1963, 1964), the benefits of killing juveniles should decline with increasing relatedness. This argument agrees with findings of Getz et al. (1990) in communal nesting prairie voles (*Microtus ochrogaster*) where females frequently kill pups but not related ones. In the present study female bank voles produced fewer recruits if their territory bordered very closely to the territory of an unrelated neighbor. This indirect observation might support the idea that unrelated juveniles could be killed during the first days of lactation when they should be most vulnerable to infanticide (in *Peromyscus* the first 12 d) (Wolff 1985), but they might also be killed during weaning and/or when leaving their nest an ≈ 2 wk of age. We found that survival of 3–4 wk old juvenile Non-relatives declined when they moved farther away from their mothers' territory. Furthermore, trappability of juveniles declined significantly with shorter distance to the territory of the nearest unrelated female, which indicates avoidance of traps scented by unrelated breeding females. Trap avoidance also depends on the mass of juveniles. In conclusion these results suggest agonistic behavior towards non-kin young, especially towards the smaller ones.

The sex ratio of recruits was not biased in our study. Assuming a balanced sex ratio at birth this indicates equal survival for both sexes. Male and female juveniles did not differ in their avoidance of the old females. It seems that breeding females near to their territory centers responded to unrelated young of both sexes as competitors of their own offspring. On the contrary, competition with related juveniles was tolerated probably because their survival will improve the female's own inclusive fitness.

Female relatedness and population changes

Charnov and Finerty (1980) proposed that changes in the degree of relatedness between breeding populations might be a significant factor that regulates multiannual vole cycles (Krebs and Myers 1974). The hypothesis is based on the idea that in low densities voles mostly breed in kin groups and that in these groups breeding success is high due to altruistic interactions. When density increases, enhanced dispersal leads to a

more heterogeneous population and disrupts these kin groups, which leads to a more intense competition, increasing aggression, lower breeding success, and the crash of populations. Our results and those of Ylönen et al. (1990) indicate that breeding success is higher in kin groups of bank voles and the same was shown for the Townsend's vole (*Microtus townsendii*) by Lambin and Krebs (1993). So, the basic assumption of the Charnov-Finerty hypothesis about the population growth phase appears to be true in field populations. However, we could verify only the positive impact of relatedness on the population growth, but we could not estimate the effect of unrelated immigrants on the social system of kin groups. Thus we have to be very careful to interpret our results at the population level.

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