Friends and strangers: a test of the Charnov-Finerty Hypothesis

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Summary. We tested the hypothesis that populations composed of unrelated animals should perform worse than those composed of related animals by setting up two moderately dense field populations in adjacent enclosures: one was composed of related females and one of unrelated females; both had unrelated males. The survival and reproductive success of a number of litters located by spooling were determined. Final population size, pregnancy success, number of young recruited per pregnancy, and survival were similar in both populations. Thus, differences in relatedness produced no differences in demography. We conclude that the Charnov-Finerty Hypothesis is unlikely to be an explanation for microtine population fluctuations.

Key words: Charnov-Finerty Hypothesis – Population cycles – Voles – Dispersal – Kin selection

An animal may increase its fitness by behaving preferentially towards relatives (Hamilton 1964). To do this, it must be able to recognize related individuals and this ability is found in a variety of mammals (for a review see Blaustein et al. 1987), including microtines (Gavish et al. 1984; Boyd and Blaustein 1985; Caley and Boutin 1987). Microtine fluctuations remain an enigma for population ecologists, but behavior appears to play a major role (Krebs 1985).

Charnov and Finerty (1980) hypothesized that differential behavior through kin selection was the causal mechanism for these fluctuations. They proposed that in populations at low density, individuals are surrounded primarily by related neighbors to which they behave amicably; at high density, individuals are surrounded primarily by unrelated individuals to which they behave aggressively. They suggested that high dispersal rates in increasing populations cause the relatedness between neighbors to decline as the population grows from low to high density. This attractive hypothesis has been cited regularly as one of the possible causes of microtine fluctuations (e.g. Stenseth 1983; Lidsicker 1985; Taitt and Krebs 1985; Gaines and Johnson 1987; Tamarin and Sheridan 1987), but no empirical tests have yet been published. Theoretical studies indicate support for it (Warkowska-Dratnal and Stenseth 1985). A major difficulty in performing such a test is knowing the relatedness of animals in field populations. To circumvent this

problem, we tested this hypothesis by setting up two enclosed populations at the extreme of what is likely to be found in natural situations – one population in which all the breeding females were related and one in which all were unrelated. We predicted that the population of related animals (which we designate as the Friends population) should perform significantly better than the population of unrelated animals (the Strangers population). We focused only on the female component of the population because previous work has indicated that breeding females in *Microtus pennsylvanicus* are the territorial sex (Madison 1980; Webster and Brooks 1981) and are predominately responsible for population growth (Krebs 1971; Krebs and Myers 1974), regulation of breeding density (Boonstra and Rodd 1983), and juvenile survival (Boonstra 1984; Rodd and Boonstra 1988).

Methods

The experiment was carried out at the Station for Atmospheric Experiments just north of Toronto, Canada (see Boonstra and Boag 1987 for a description of the site). Two 0.145 ha enclosures were set up in 1982 with hardware cloth (0.64 cm mesh size) extending 0.5 m above and below ground level. In addition, to prevent weasels and raccoons from getting into the enclosures, we extended the height of the enclosure walls facing open grassland by 1 m with plastic mesh (Vexar L33 – Dupont). These enclosures were kept clear of voles in 1985 prior to this study. During the 1986 growing season, a 0.3 m strip was mown regularly on both the inside and outside perimeters of the enclosure. This reduced cover, helped to minimize burrowing near the fence, and allowed a clear view for detection of any escape holes.

One side of each enclosure was shared, one side was shared with adjacent enclosures used for other experiments, and two sides faced open grassland. The open grassland contained three trapping grids nearby. We detected no animals escaping from the enclosure to any other trapped population. However, two males from the other adjacent enclosures did enter the Friends grid near the end of the study, apparently by climbing over the fence and negotiating an inverted V flange on top of the hardware cloth, as we could find no tunnel burrows between the two enclosures.

Each enclosure had 25 trapping stations arranged in a 5 × 5 pattern, with a station interval of 7.6 m. Each trapping

station had two Longworth live-traps which were covered by shelter to protect the traps from heat and rain. All new voles were ear-tagged and on each capture the following were recorded: tag number, toe-clip number if present, location, sex, sexual condition (males – testes abdominal or scrotal; females – vagina perforate or imperforate, nipples lactating or not, and obviously pregnant or not), and number of wounds. Each trapping session consisted of three checks. To prevent lactating females from being away from their nestlings too long, we set traps at 5:00 A.M., checked them at 10:00 A.M., and again at 3:00 P.M., when they were locked closed. They were reopened at 5:00 A.M. the next morning for a final check at 10:00 A.M. During the hottest part of the summer, we trapped only in the morning. We usually trapped every other week, though on three occasions did trap every week.

To assess juvenile survival and look for evidence of infanticide, we tried to find as many active nests as possible by spooling lactating females (see Boonstra and Craine 1986 for the technique). Because of the length of time it took to find nests, we only spooled about half of the lactating females. Nestlings were aged (see Hamilton 1941 for criteria) and given individual toe-clip numbers, weighed, sexed, and examined for wounds and parasitism by the grey flesh fly (*Wohlfahrtia vigil*) (Craine and Boonstra 1986).

Source of animals

On 20 June 1986, 14 related females and three unrelated males were introduced to the Friends grid. The related females consisted of three sisters and their daughters. All the daughters were fathered by one male and thus they were related both through their mothers and through their father. They were produced in the lab during the late winter and early spring of 1986. The three sisters gave birth in separate cages. Littermates of the same sex remained together after the mother was removed for another breeding attempt. Both mothers producing two litters remained with the last litter produced until they were introduced into the field enclosure. Therefore no attempt was made to increase familiarity among sisters and cousins by having all of them in one cage prior to the introduction. Female 5765 contributed seven daughters from two different litters (one with two daughters and one with five), female 5768 contributed one daughter, and female 5770 contributed three daughters from two litters. The males were caught at widely separated points on the field site shortly before the experiment started. We biased the operational sex ratio in favor of females because other studies have shown that males are polygynous (Madison 1980; Webster and Brooks 1981) and because breeding females appear to be most tightly linked to demographic change (see Introduction).

Fifteen unrelated females and four unrelated males were introduced into the Strangers grid at the same time. Six of the females were overwintered animals which came from widely separated points on the field site, six were overwintered animals which came from the airport site which was about 15 km from the field site (see Boonstra and Rodd 1983 for a description of the airport site), and three were born in the lab to different parents. All females from the field were brought to the lab, kept in separate cages for about one month to ensure that they were not pregnant, and then released into the enclosure.

Results

Trappability

Trappability was estimated using the Jolly method (Krebs and Boonstra 1984). On the Friends grid, trappability was 56% for males and 75% for females; on the Strangers grid, it was 61% for males and 78% for females. Thus the animals in the two populations showed similar trappabilities and the demographic estimates we obtained should be reasonably robust.

Population changes

The initial population densities on the enclosures (17 animals = 117/ha on the Friends grid; 19 animals = 131/ha on the Strangers grid) were intermediate to those found on adjacent grassland. Boonstra and Boag (1987) report densities varying between 38/ha during a low phase and 226/ha during the peak. The final population densities on the Friends and Strangers grids of approximately 150 animals per enclosure are equivalent to 1034/ha. This is about two to three times the peak densities reported in unenclosed peak populations for this species (Taitt and Krebs 1985).

The two populations showed similar growth curves (Fig. 1). After an initial lull in growth and a loss of a number of animals, both populations grew rapidly: the Friends grid had a rate of population increase (r) of 0.101 per week and the Strangers grid of 0.097 per week. On the Friends grid we tagged and/or toe-clipped 254 animals compared with 250 on the Strangers grid. At the end of the study in November we removed 156 voles from the Friends grid and 154 from the Strangers grid.

Reproduction

The percentage of adults reproducing was similar on both grids. All adult males and one subadult male on both grids were in breeding condition until early September. Testes then started regressing so that by the end of the study, no males were in breeding condition on either grid. The same pattern occurred amongst females, but because of the lag times introduced by pregnancy and lactation, some females were still suckling young into October. By the end of the study, we caught only one lactating female on the Friends grid and none on the Strangers grid.

Fig. 1. Changes in *Microtus pennsylvanicus* populations from two enclosures: one started with related females (Friends grid) and one started with unrelated females (Strangers grid). Population estimates calculated by Jolly-Seber methods

Table 1. Summary of reproduction by female *Microtus pennsylvanicus*. Pregnancy success is defined in the text

	Friends grid	Strangers grid
Number of mothers	29	25
Number of litters	65	58
Percentage of litters born to original females	61.5%	63.8%
Mean number (± 1 SE) of litters per mother	2.1 (0.28)	2.3 (0.27)
Pregnancy success (N = number of obvious pregnancies)	93.7% ($N=32$)	77.8% ($N=36$)

We calculated the minimum number of litters that each female had by examining her capture history for weight changes, obvious pregnancy, and presence of lactational fat with the limitation that each litter had to be separated by at least 21 days. Table 1 shows that the number of females that had litters, the number produced by the original females, and the total number of litters produced was similar on both grids. On the Friends grid, female 5765 and her daughters produced a minimum of 23 litters; female 5768 and her daughters a minimum of four litters; and female 5770 and her daughters a minimum of 13 litters. In addition, 19 females born into the population had a minimum of 25 litters. On the Strangers grid, the three females originating from the lab produced a minimum of seven litters; the six airport females a minimum of 16 litters; and the six station females a minimum of 15 litters. In addition, 13 females born into the population had a minimum of 20 litters. Thus, production of litters was shared amongst many females in both populations. However, these data do not tell us whether young from these litters actually entered the trappable populations. The same general picture emerges when we examine only young from litters found by spooling which subsequently entered the population: 15 and 11 different females produced young that entered the trappable populations on the Friends and Strangers grid respectively.

Some litters disappeared shortly after birth and thus the reproductive bout was unsuccessful. We calculated an index of pregnancy success which was the percentage of females obviously pregnant in one trapping session which were subsequently lactating in the next. Table 1 indicates that the pregnancy success was about 16% higher on the Friends grid.

Survival

We used three different measures to compare survival of animals. We calculated the average Jolly-Seber survival estimate according to the method of Carothers (1973) for all animals in the trappable population to mid-October. Males had an average survival rate per 2 weeks (± 1 SE) on the Friends grid of 0.95 (0.036) compared with a rate of 0.85 (0.061) on the Strangers grid; females had values of 0.90 (0.028) and 0.92 (0.022) respectively. Thus, though males survived slightly worse on the Strangers grids, females showed no difference.

Table 2. Success of lactating females spooled to locate nests and the fates of their young

	Friends grid	Strangers grid
Number of lactating females spooled	39	37
Number of litters found	24	19
Mean litter size (SE)	5.4 (0.34)	4.8 (0.37)
Average age - days (SE)	6.2 (0.57)	6.2 (0.79)
Sex ratio of nestlings (males/female)	1.02	1.42
Mean number of young per litter (SE) subsequently entering traps	3.5 (0.40)	2.2 (0.54) ^a
Sex ratio of young entering traps	1.24	1.16

^a $P < 0.05$

To obtain an index of survival of young per pregnancy, we calculated what proportion of young found in nests through the spooling technique were subsequently caught in traps. On the Friends grid this value was 65% ($N=132$ young) versus 45% ($N=92$) ($\chi^2 = 7.87$, $P < 0.01$) on the Strangers grid. Table 2 echoes this result indicating that about 1.3 more young per litter entered the Friends grid than entered the Strangers grid. A second index of survival of young involved determining the total number of young entering the trappable population (assuming that no animals entered or escaped from the enclosures) and dividing this by the total number of litters produced (see Table 1). In contrast to the previous index, this one indicated similar survival per litter on both grids: on the Friends grid 3.18 young/litter ($N=207$ young trapped) entered traps compared to 3.43 young/litter ($N=199$) on the Strangers grid. We conclude that there were no major differences in survival between grids and that the higher survival of the young from the spooled females on the Friends grid was due to chance.

Litters located by spooling

We spooled 76 lactating females during the experiment (five were spooled twice during a trapping session, as the first search for a nest was unsuccessful). We found 61% and 51% of the females spooled on the Friends and Strangers grid, respectively (Table 2). Litter age ranged from 1 to 13 days old and litter size ranged from 1 to 9 young. On the Friends grid, 4 litters recruited to the trappable population in their entirety and 3 litters failed to recruit any members to the trappable population; on the Strangers grid these values were 5 and 6 litters, respectively. There was no relationship between estimated age of the litter in the nest and litter size when the data from both grids were combined ($r = -0.14$, $N=43$) nor between litter age and percentage of the litter subsequently entering traps ($r = 0.26$).

In the autumn we discovered 3 cases in which two litters of different ages were occupying the same nest. On the Friends grid on 18 September a nest of 8 babies was found: six were about 8 days old and two about 6 days old. Subsequently, all but one individual from the older litter were caught in traps. On the Friends grid on 2 October, a nest with 10 babies was found: five were about 9 to 10 days old (eyes open) and five were about 6 days. Subsequently, three individuals from each litter were caught in traps. On

the Strangers grid on 2 October, a nest with 10 babies was found: four were about 10 days old and six were about 5 days old. Subsequently one individual from the older litter and four from the younger were caught in traps. Thus, this pooling of litters occurred occasionally in both populations, though we were not able to establish the identity of the second mother in any of the cases and therefore could not determine whether related females were engaging in this practice. Since members of both litters subsequently entered the live-traps, there did not appear to be an obvious survival cost to the younger litter.

Only one instance of parasitism by the grey flesh fly was found. On the Friends grid on 22 July a litter of four about 9 days old (eyes open) was all found with large fly larvae. Two young were already dead and two were dying.

Two instances of possible infanticide were found, both on the Friends grid. On 20 August, a litter of three about 2 days old was located, two with bite wounds on the hind quarters; none was subsequently captured in traps. On 27 August, a litter of three about 4 days old was found: two were found dead about 5 feet from the nest on the runway and one was found at the nest mouth with a bite wound on her shoulder. It was not caught subsequently in a trap.

Discussion

The two populations showed very similar demography for virtually all indices examined and thus we conclude that relatedness among females had no effect on demography. Kawata (1987) also found no effect of relatedness on the number of red-backed voles that established home ranges nor on the number of females that subsequently gave birth in the lab. However, in Kawata's study the field experiment was terminated shortly after the females were impregnated, and thus the long-term effect on demography was not determined. There are a number of possible explanations for our results. First, if densities in our initial populations were low relative to what is normally found, then conflict between unrelated neighbors might not occur. However, our densities were initially intermediate to those found in adjacent grassland and rapidly exceeded them.

Second, lack of dispersal openings (one-way exits – e.g. Johnson and Gaines 1987) constrained all animals to remain and this may have affected our results. The design may have been strengthened by adding exits, but we wished to see the effects under the extreme of totally confined conditions. Inherent in the argument for exits is the assumption that the main mechanism for disappearance is dispersal. A number of recent studies have found that dispersal may be minimal from vole populations (Tamarin et al. 1984; Verner and Getz 1984). As well, Krebs (1988) has argued that infanticide may be a major mortality factor accounting for population declines. Caley and Boutin (1985), McShea and Madison (1987), and now we report possible instances of infanticide in this species. However, in our study, infanticide was only detected on the Friends grid.

Third, implicit in the design of our experiment was the assumption that sisters and their daughters on the Friends grid should recognize that they were related even though they may have been unfamiliar with each other (daughters raised in separate cages in the lab). Thus they should have used a mechanism such as phenotype matching to identify relatives (Blaustein et al. 1987) rather than just familiarity

(Bekoff 1981). We think that this argument is implicit in the formulation of the Charnov-Finerty hypothesis (i.e. neighbors recognize each other, not because they originate from litters are raised in the same nest, which infrequently occurs [Boonstra and Rodd 1983; McShea and Madison 1984; this study], but because they are genetically related). In voles, familiarity appears to be the main mechanism reducing breeding success of pairs in the lab (Gavish et al. 1984; Boyd and Blaustein 1985). However no one has examined whether voles can recognize others of varying degrees of relatedness sufficiently to affect behaviors such as infanticide. Some small mammals are capable of kin recognition independent of familiarity [e.g. *Peromyscus* Grau (1982) and *Spermophilus* Holmes and Sherman (1982)] but similar experiments remain to be done in voles. The degree of kin recognition may be context dependent in voles, so that for mating, familiarity is used a reliable indicator of relatedness whereas for maternal and infanticidal behavior, phenotype matching is used. Males tend to disperse from their natal site at or prior to maturation and thus mating with related females is less likely; females tend to remain near the natal site (Boonstra et al. 1987). Thus female-female kin interactions are more probable and there may be stronger selection to identify these kin.

Finally, our conclusions must remain tentative because the experiment was not replicated, though we regard invoking chance as an explanation for our results as unlikely. We were unable to replicate the experiment because the enclosures had to be removed to make way for a housing development.

In contrast to our results, laboratory studies have indicated that populations originating from one pair generally show less aggression and grow more rapidly than populations originating from a number of unrelated pairs. Brown (1953) set up two populations of house mice (*Mus musculus*): one with a number of unrelated pairs and the other with only a single pair. The former had higher rates of aggression, less successful reproduction, higher rates of infanticide, and a lower final population size than the latter population. Clarke (1965) used a similar design in *Microtus agrestis* in which one enclosure was started with 6 pairs (randomly chosen from a laboratory breeding colony, though the genetic relatedness was not indicated) and the other enclosure with one pair. The former also showed higher rates of aggression, lower population growth rates, and lower rates of fertility. In the Norwegian lemming (*Lemmus lemmus*) when colonies were started with unrelated pairs, aggression developed rapidly, infanticide occurred, and the population went through a series of fluctuations (Semb-Johansson et al. 1979). In contrast, when colonies were started with one pair, little aggression occurred and very high densities were reached (De Kock and Rohn 1972). We were not able to find studies in which populations started with a number of related pairs were contrasted with populations started with unrelated pairs. Nevertheless, the above laboratory studies do suggest that relatedness among population members may promote harmony and stimulate population growth.

A crucial assumption of the Charnov-Finerty Hypothesis is that high dispersal rates characteristic of increasing populations produce lower relatedness and higher rates of aggression amongst neighbors in peak populations. Implicit in this argument is the assumption that dispersers are able to settle down elsewhere and breed. We do not interpret

the hypothesis as implying that simple movement of dispersing animals through an area is sufficient to cause increased aggression at peak populations. Field evidence in microtines indicates that the probability of animals entering and recruiting to breeding populations is low at all times because resident animals inhibit colonization by strangers (Krebs et al. 1976; Boonstra 1978; Redfield et al. 1978; Baird and Birney 1982; Boonstra and Rodd 1983; Boonstra et al. 1987; Danielson and Gaines 1987). Danielson and Gaines (1987) introduced animals to enclosures with or without residents and found that colonization was more successful in winter when reproduction of residents was less intense. It is probable that if genetic mixing of the population is to occur, it will primarily happen during the period of little or no reproduction. Whether it is sufficient to produce significant heterogeneity in relatedness remains to be determined. Since natal philopatry in microtines tends to be biased towards females, female kin clusters may be the rule (Boonstra et al. 1987). Thus many of the neighbors may be related individuals under all density conditions.

By the end of the experiment, both populations had reached extreme densities which are characteristic of enclosed populations – the Fence Effect (Krebs et al. 1969). This presumably was due to the lack of dispersal coupled with the total absence of mammalian predation because of the predator proof fence. Because of this rapid population growth, experiments of the type we report here can only last several months to gain insights into population processes before they must be terminated.

Our results suggest that populations composed of unrelated animals will not show drastic reductions in population size or fail to grow. Thus, we conclude that the Charnov-Finerty Hypothesis is unlikely to be a sufficient explanation for population fluctuations in microtines. Neighbourhood kinship groups in microtines may however confer survival and reproductive advantages to individuals as has been found in other species. Evidence to examine this must await a more detailed examination of relatedness in the field.

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