Journal of Mammalogy, 85(4):781–787, 2004

EFFECTS OF FEMALE IMMIGRANTS ON DEMOGRAPHY AND SOCIAL ORGANIZATION OF PRAIRIE VOLE (*MICROTUS OCHROGASTER*) POPULATIONS

Y. KIRK LIN,* LOREN D. HAYES, AND NANCY G. SOLOMON

Department of Zoology, Miami University, Oxford, OH 45056, USA
Present address of YKL: Department of Biological Sciences, California State University, Sacramento, CA 95819-6077, USA

We experimentally investigated effects of female immigrants on demography and social organization of prairie vole (*Microtus ochrogaster*) populations. We tested the hypothesis that increased immigrant pressure by unrelated adult females would decrease the survivorship of juveniles and indirectly decrease the proportion of communal groups in the populations. We established prairie vole populations in 8 enclosures (32 × 32 m). Four populations were supplemented with adult female immigrants, and the other 4 served as control populations in which no females were introduced. The results showed that adult female immigrants reduced the proportion of females and the proportion of juveniles in resident populations but did not change the social organization. We concluded that adult female immigrants did negatively affect resident populations. However, the direct numerical input and subsequent reproduction by immigrants would compensate for their negative effect on resident populations.

Key words: demography, dispersal, immigration, infanticide, *Microtus*, prairie voles, social organization

Although analyses of immigration have tended to focus on positive effects, such as reducing the probability of local extinction (Brown and Kodric-Brown 1977; Levins 1970; Pulliam 1988) and inbreeding depression (Keller et al. 2001), immigration can bring negative consequences to residents, including pregnancy disruption (i.e., Bruce effect—Bruce 1959, 1960), infanticide (Hrdy 1979; Wolff 1993), increased intensity of competition for resources (Lambin and Krebs 1991), increased social stress (Christian 1980), increased risk of predation (Banks et al. 2002), and disruption of a local genetic complex (Shields 1987). Few empirical studies, though, explore negative consequences of immigration on local populations. For example, increased survivorship of preweaning young animals was associated with removal of immigrants from populations (Lambin and Yoccoz 1998). Similarly, Wolff and Schauber (1996) found that juvenile mortality was positively correlated with number of unrelated female immigrants in a habitat patch. These studies suggest that juveniles are vulnerable to negative effects of immigration. Slight decreases in juvenile performance (survivorship and age at 1st reproduction), however, can profoundly reduce the growth of a population.

The presence of immigrants can also induce changes in local social organization, especially the formation of communal groups in social species. Communal groups (social units that contain more than 2 adults of the same sex) usually occur when juveniles delay dispersal due to environmental factors (Koenig et al. 1992), including intrusion pressure (Ebensperger 2001; Manning et al. 1995). Thus far, the effect of immigrant (intruder) pressure on social organization has not been investigated. In the field, immigrants likely reduce juvenile survivorship (Lambin and Yoccoz 1998) and curtail the subsequent formation of communal groups. Alternatively, immigrants might saturate suitable habitats (Brown 1969), force young animals to delay dispersal, and lead to the development of communal groups. Delaying dispersal could also help parents deter intruders from committing infanticide or disrupting pregnancy while conserving reproductive efforts that would otherwise be reduced by immigrants if they compete for opportunities of independent breeding.

Given the potential opposing effects by immigrants on resident populations, more research on immigration is clearly needed. Therefore, the objective of this study was to use the prairie vole (*Microtus ochrogaster*) as a model species to evaluate effects of female immigrants on demography and social organization of resident populations. We focused on female immigrants because females are the territorial sex in most small mammals and thus could have greater effects on resident populations. The effects of male immigrants could be completely different from those of female immigrants due to differential breeding strategies and might obscure the effects of

---

* *Correspondent: kirkohio@yahoo.com*

females. Prairie voles form 3 types of social units, including male–female pairs, single-female units, and communal groups (Getz and McGuire 1997). We hypothesized that increased immigrant pressure by unrelated adult females would decrease the survivorship of juveniles and indirectly decrease the proportion of communal groups in resident populations.

MATERIALS AND METHODS

Study site.—The experiment was conducted from 16 July through 15 November 2000 (16 weeks) at Miami University's Ecology Research Center, Oxford, Ohio. We established prairie vole populations in eight 0.1-ha enclosures (32 × 32 m) constructed of galvanized steel panels extending 45 cm below and 60 cm above ground. All enclosures were seeded with blue grass (*Poa*), clover (*Trifolium*), fescue (*Festuca*), timothy (*Phleum*), and ryegrass (*Elymus*) in April 1994. These plants remained in enclosures during the study. Other common plants included bromegrass (*Bromus*), goldenrod (*Salidago*), blackberry (*Rubus*), and milkweed (*Asclepias*). We maintained a 1-m-wide area of bare soil around enclosure walls to discourage voles from escaping. Within each enclosure were permanent trapping stations at 5-m intervals in a 5 × 5 grid with 1 Sherman live trap at each station.

Monitoring vole populations.—All individuals used in this experiment originated from Lawrence, Kansas, and were held in a laboratory colony at Miami University for 1 month prior to experimentation. Females were separated from males so they would not be pregnant at the time of release. All voles were toe-clipped (no more than 1 toe per foot) for individual identification. Prior to the beginning of the experiment, we trapped all enclosures for 3 weeks to remove resident small mammals. We randomly divided the 8 enclosures into 2 treatment groups—immigrant-supplemented (treatment populations, hereafter) and control enclosures—with 4 replicates per treatment. In mid-July, 4 adult prairie voles of each sex were randomly assigned and released into each enclosure. This created a density of 80 voles/ha.

Founders were given 30 days to establish residency. On the 31st day, 2 additional adult females (immigrants) were added to each treatment population. At that time, female founders had already established mutually exclusive home ranges, and almost all of them were lactating or pregnant. Immigrants were removed and replaced every 2 weeks to reduce the probability of reproduction (prairie voles have a 3-week gestation period) by immigrants inside enclosures. The purpose of the manipulation was to create an influx of immigrants into treatment populations every 2 weeks at a rate within the ranges observed in a more natural setting (Lin and Batzli 2001). The experiment was designed to investigate the potential negative effect of immigrants during their initial attempts to be assimilated into resident populations. We removed and replaced immigrants every 2 weeks because, once successfully assimilated, immigrants would become residents, and their subsequent reproduction would have confounded any initial negative effects. After immigrants were removed from enclosures, they were housed individually for 3 weeks to determine whether they were pregnant.

Livetrapping began 2 weeks following the release of founders and continued for 16 weeks. We recorded trap location, individual identification, body weight, sex, reproductive status (e.g., scrotal testes, perforated vagina), and general condition (e.g., level of wounding) for each captured vole. We quantified the level of wounding by counting the number of scars on voles: 0 for no scars, 1 for 1–2 scars, 2 for 3–4 scars, and 3 for ≥5 scars. Newly captured voles recruited to the population were toe-clipped for individual identification. Females in late pregnancy (with palpable embryos) or lactating (enlarged teats with hair removed) were tracked to their putative burrows or surface nests with the use of fluorescent powder (Lemen and Freeman 1985) or radiotransmitters (PD-2C radiocollars, Holohil Systems Ltd., Ontario, Canada). We tracked voles as needed until nests were located. After locating a nest, 4 multiple-capture traps (Getz and McGuire 1997) were placed near the burrow entrances.

A trapping regime similar to that used by Getz et al. (1993), which included both grid trapping (trapping at 5 × 5 grids) and burrow trapping (trapping around burrows), was followed. Grid trapping, designed to estimate animal density, was conducted once every 2 weeks. Grid traps were opened at 1900 h on Sundays; checked at 0700, 1300, and 1700 h during the next 2 days; and closed at 0700 h the 4th day, for a total of 7 trap checks per trapping period. Burrow trapping, designed to determine residents of burrows, was conducted 3 times every 2 weeks. Burrow traps were opened at 1900 h on Sundays and Wednesdays; checked at 0700, 1300, and 1700 h the next day; and checked at 0700 h and closed at 1300 h the 3rd day, for a total of 5 trap checks per trapping period. Only 1 burrow trapping period was conducted during every other week that grid traps were set. In short, a grid trapping period was followed by 3 burrow trapping periods every 2 weeks from week 2 to 15. All traps were baited with cracked corn during trapping, and remained in place, locked open, between trapping periods. The membership of social units was determined with burrow trapping data from weeks 12–15. We assigned an individual to a nest if it was captured $>50\%$ of times at that nest during the 4 weeks. Only individuals that survived >10 days during weeks 12–15 were included as members of social units. At the end of the field season, the final population densities were determined by a grid trapping period at week 16, followed by 3 weeks of removal trapping to remove all individuals from enclosures.

Because vegetative cover strongly affects population parameters of voles (Lin and Batzli 2001), we assessed total vegetative cover by clipping 0.2-m^2 quadrats at 6 randomly chosen sites within each enclosure. Samples were collected in the 1st week of the experiment (late July), air-dried for 1 week, and weighed to the nearest 0.1 g.

Data analyses.—The trappability of vole populations every 2 weeks was high: 96 ± 2% and 93 ± 3% in treatment and control populations, respectively. Because of high trappability, we used enumerations (minimum number known alive) to estimate population size (Boonstra 1985). Because immigrants were not introduced until week 4, we expected to see responses by individuals and populations after week 4 and analyzed responses from weeks 6 to 16. We excluded immigrants from analyses to determine whether they had a net effect on resident populations.

We classified voles into 3 age classes on the basis of mean weekly body mass (Desy and Batzli 1989): juveniles (<22 g for both sexes), subadults (22–30 g for males and 22–28 g for females), and adults (>30 g for males and >28 g for females). Because we trapped voles for 5 days each week, we could accurately estimate the date of parturition for each female by examining changes in body weight and reproductive condition (palpable embryos, opened pubic symphysis, enlarged nipples). We determined number of females that gave birth, mean number of litters per reproductive female, and mean number of young per litter that survived to trappable age for each population. We determined the mean body growth rate of male and female young that were captured in more than 2 (grid or burrow) trapping periods when their body weight was <25 g.

We used fixed-factor, repeated measures 1-way analyses of variance (ANOVAs) to test for immigration effects on population size, population growth rate (population size at week t divided by population size at week $t - 2$), sex composition, and age structure estimated every 2 weeks. Fixed-factor, 1-way ANOVAs were used to test for differences in female reproductive performance (number of reproductive females, number of litters per reproductive female, and litter size), social organization, and amount of vegetative cover between treatments. For comparisons between sexes (such as mortality of founders and new recruits) and mean body growth rates of young, we used a 2-way ANOVA with immigration treatment and sex as the fixed factors. We used arcsine–square root transformation on proportion data, such as mortality, and natural log transformation on population size and population growth rate before analyses to stabilize variances. All values are expressed as $\bar{X} \pm 90\%$ confidence limits.

RESULTS

The introduction of 2 adult females every 2 weeks to treatment populations created per capita immigration rates ranging from 28 ± 9% at week 6 to 19 ± 7% at week 14. The rates gradually declined with time due to in situ population growth of resident populations. Extinction of resident populations occurred in 2 treatment populations at weeks 6 and 7. Similarly, the size of 1 control population declined to a single individual, near extinction, by week 10. The reason for local extinction was not clear. We excluded the 3 extinct populations from our analyses. In short, the replicates for treatment and control populations became 2 and 3, respectively. Because of the loss of replicates, we report differences that reach a significance level of $P < 0.10$ to compensate for the low power (power <65% for all tests with $0.05 < P < 0.10$, given $\alpha = 0.05$) in order to detect biologically meaningful results (Schauber and Edge 1999; Steidl et al. 1997; Yoccoz 1991).

Habitat characteristics.—The amount of vegetative cover was not different between treatment and control populations (608.6 ± 40.4 and 533.5 ± 66.2 g/m^2, respectively; $F = 1.19$, *d.f.* = 1, 3, $P = 0.35$).

Population parameters.—In situ recruitment was 1st detected at week 4. The sizes of resident populations grew from 11.0 ± 4.7 to 20.5 ± 4.1 individuals (weeks 6–16) in treatment populations and 15.0 ± 1.5 to 32.7 ± 8.5 individuals in control populations (Fig. 1A; time effect, $F = 12.8$, *d.f.* = 5, 15, $P = 0.0001$). The difference in population sizes between treatments was not significant over the course (weeks 6–16, $F = 0.68$, *d.f.* = 1, 3, $P = 0.47$) or at the end (week 16, $F = 1.90$, *d.f.* = 1, 3, $P = 0.26$) of study, nor was there significant interaction between treatment and time ($F = 0.42$, *d.f.* = 5, 15, $P = 0.83$). Including immigrants in the analyses did not increase the total population size ($F = 0.03$, *d.f.* = 1, 3, $P = 0.87$) or the number of adult females ($F = 3.95$, *d.f.* = 1, 3, $P = 0.14$) in treatment populations over control populations. Population growth rates (lambda) in both treatment and control populations were greater than unity (weeks 6–16) and remained relatively constant throughout most of the experiment (Fig. 1B; time effect, $F = 0.91$, *d.f.* = 5, 15, $P = 0.50$). The difference between treatments was not significant ($F = 0.56$, *d.f.* = 1, 3, $P = 0.51$), nor was there significant interaction between treatment and time ($F = 0.52$, *d.f.* = 5, 15, $P = 0.76$). The sex ratio of resident populations was skewed toward males when immigrants were present. The proportion of females was higher in control than in treatment populations (Fig. 2A; immigrant effect, $F = 11.0$, *d.f.* = 1, 3, $P = 0.05$). The effect of time ($F = 0.42$, *d.f.* = 5, 15, $P = 0.83$) and interaction between treatment and time ($F = 0.76$, *d.f.* = 5, 15, $P = 0.59$) were not significant. In addition, the proportion of juveniles (age structure) was higher in control than in treatment populations (Fig. 2B; immigrant effect, $F = 7.23$, *d.f.* = 1, 3, $P = 0.07$), although there was no significant effect of time ($F = 2.17$, *d.f.* = 5, 15, $P = 0.11$) or interaction between treatment and time (F

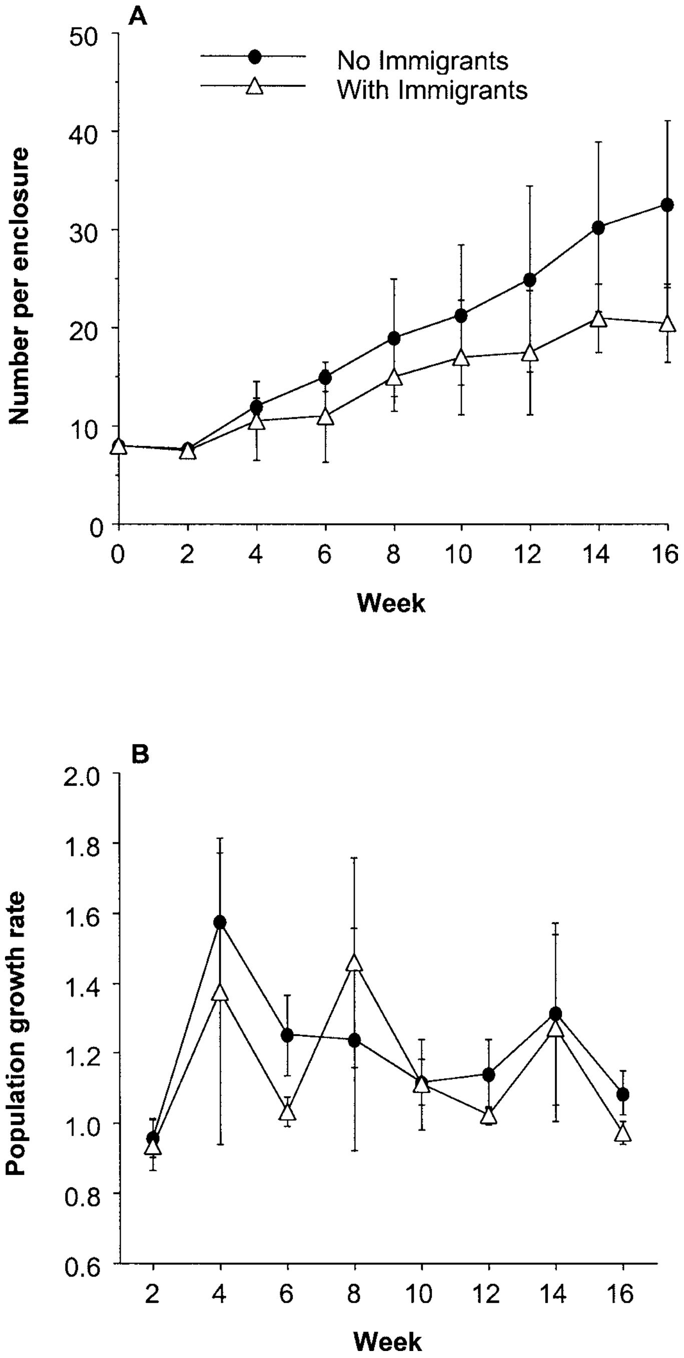

FIG. 1.—A) Population densities and B) population growth rates (population size at week t divided by population size at week $t - 2$) of prairie voles in the control and immigrant-supplemented populations. Values are mean ± 90% *CL*.

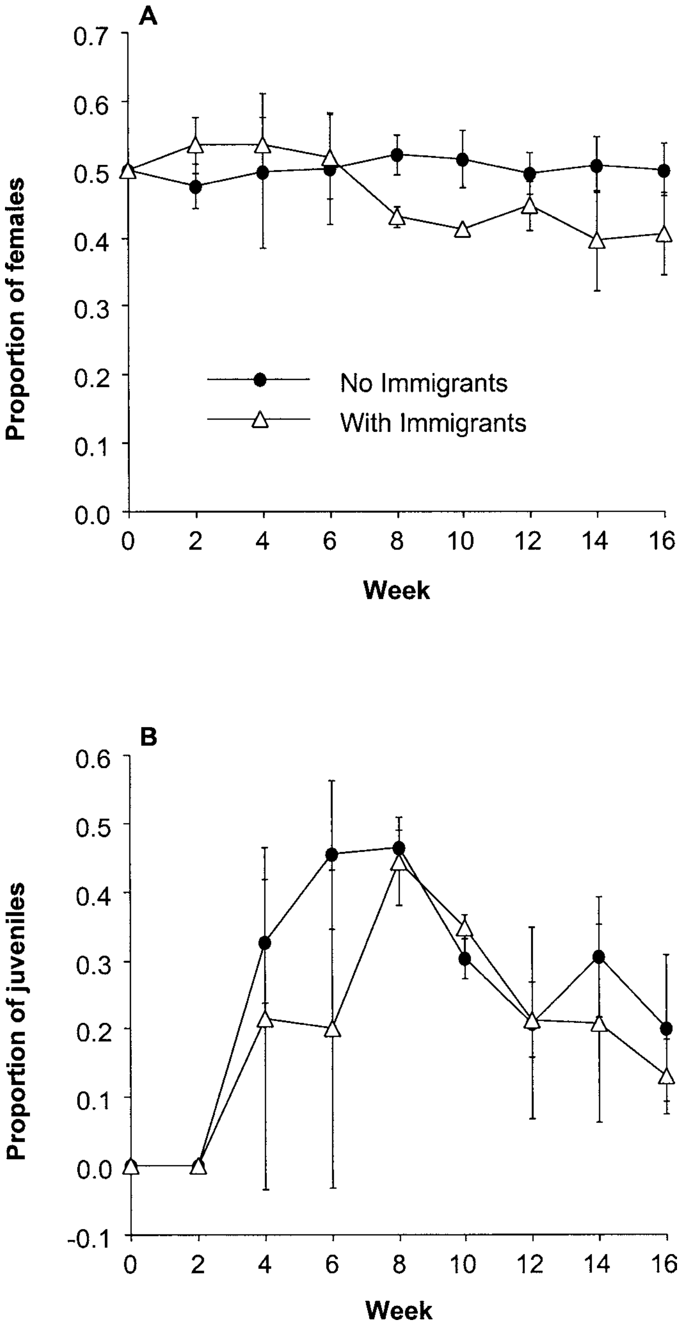

FIG. 2.—A) Sex composition and B) age structure of prairie voles in control and immigrant-supplemented populations. Values are mean ± 90% *CL*.

= 0.72, *d.f.* = 5, 15, *P* = 0.62). The sex ratio of young recruited into populations was not different between treatments (*G*-test of independence with Williams' correction; *G* = 0.33, *P* > 0.5). The average numbers of new recruits were 7.0 ± 4.7 females and 10.5 ± 0.6 males in treatment populations and 14.7 ± 4.5 females and 16.3 ± 3.1 males in control populations.

Mortality of founders over the 16 weeks was similar between treatment (25 ± 0% and 29 ± 5% for female and male, respectively) and control (19 ± 13% and 42 ± 30% for female and male, respectively) populations (*F* = 0.01, *d.f.* = 1, 6, *P* = 0.93 for immigrant effect; *F* = 1.60, *d.f.* = 1, 6, *P* = 0.53 for sex effect; *F* = 0.18, *d.f.* = 1, 6, *P* = 0.69 for treatment × sex interaction). The mortality of new recruits was also similar between treatment (14 ± 16% and 10 ± 1% for female and male, respectively) and control (9 ± 9% and 10 ± 10% for female and male, respectively) populations (*F* = 0.41, *d.f.* = 1, 6, *P* = 0.55 for immigrant effect; *F* = 0.06, *d.f.* = 1, 6, *P* = 0.81 for sex effect; *F* = 0.03, *d.f.* = 1, 6, *P* = 0.87 for treatment × sex interaction).

Resident female reproduction.—In treatment populations, on average, 5.0 ± 1.2 females gave birth over the 16 weeks. They gave birth 2.8 ± 0.2 times per female to 1.2 ± 0.2 young per litter that survived to a trappable age. In control populations, on average, 8.0 ± 2.3 females gave birth. They gave birth 2.6 ± 0.5 times per female to 1.5 ± 0.1 young per litter. None of the above parameters differed significantly between treatments (*F* = 1.62, *d.f.* = 1, 3, *P* = 0.29 for number of females that gave birth; *F* = 0.16, *d.f.* = 1, 3, *P* = 0.71 for number of litters per female; *F* = 3.13, *d.f.* = 1, 3, *P* = 0.18 for number of young per litter). Interbirth interval was not different between females in treatment and control populations (22.1 ± 0.9 and 23.6 ± 1.3 days, respectively; *F* = 1.24, *d.f.* = 1, 3, *P* = 0.35). The cumulative number of young recruited into populations reached 17.5 ± 5.2 in treatment and 31.0 ± 7.5 in control populations by week 16 (*F* = 2.90, *d.f.* = 1, 3, *P* = 0.19). Body growth rates of young were marginally greater in males than females (sex effect, *F* = 3.70, *d.f.* = 1, 6, *P* = 0.10); however, they were not different between treatment (0.42 ± 0.06 and 0.65 ± 0.10 g/day for female and male, respectively) and control (0.64 ± 0.06 and 0.73 ± 0.14 g/day for female and male, respectively) populations (immigrant effect, *F* = 2.95, *d.f.* = 1, 6, *P* = 0.14; treatment × sex interaction, *F* = 0.71, *d.f.* = 1, 6, *P* = 0.43). Twenty-six ± 9 and 26 ± 13% of female new recruits in treatment and control population, respectively, became pregnant and gave birth.

Social organization.—During weeks 12–15, neither the percentage of social units that were communal groups (67 ± 39% and 56 ± 39%, respectively; *F* = 0.08, *d.f.* = 1, 3, *P* = 0.79) nor the number of adults per group (3.8 ± 1.0 and 4.0 ± 0.5, respectively; *F* = 0.02, *d.f.* = 1, 2, *P* = 0.91) differed between treatment and control populations.

Performance of immigrants.—Twelve adult females were added to each treatment population. The 2-week survivorship of immigrants was relatively high (92 ± 4%) and was not significantly different from that of resident adult females (96 ± 4%, *F* = 0.08, *d.f.* = 1, 2, *P* = 0.80). Among immigrants, 18 ± 1% subsequently gave birth in the animal colony after they were removed from resident populations. On the basis of burrow trapping data, immigrants visited the burrows of residents 0.47 ± 0.1 times/burrow/week. The overall visitation rates by non–burrow member adult females (including residents) were not different between treatment and control populations (0.79 ± 0.63 and 0.10 ± 0.14 times, respectively; *F* = 1.45, *d.f.* = 1, 3, *P* = 0.31). However, weekly visitation rates should be regarded as only an index because traps at burrows were active only 130 h every 2 weeks. The level of wounding was significantly higher in immigrants than in residents (1.86 ± 0.10 and 0.35 ± 0.25, respectively; $F = 42.12$, $d.f. = 1, 2$, $P = 0.02$), but there was no difference between wounding of residents in the 2 treatments (0.13 ± 0.03 for residents in control enclosures; $F = 1.83$, $d.f. = 1, 3$, $P = 0.27$).

DISCUSSION

Overall, the presence of adult female immigrants was associated with change in 2 demographic parameters: sex ratio and age structure of resident populations. The proportions of females and juveniles were lower in treatment populations into which immigrants were introduced. The demographic processes that contributed to the low proportion of females might include female-biased mortality of founders, new recruits, or both, as well as male-biased recruitment. However, none of these parameters showed a significant difference between treatment and control populations. On the other hand, the demographic processes associated with the low proportion of juveniles might involve lower female reproductive output, higher mortality of juveniles, and lower mortality of adults in treatment than in control populations. Similarly, none of these parameters showed a significant difference between treatment and control populations. Furthermore, the lowered proportions of females and juveniles did not lead to a significant decline in population growth rate or population size by the end of the study. Evidently, the loss of several replicates reduced our statistical power to pinpoint demographic mechanisms that led to the lower proportions of females and juveniles. One needs to be cautious that some biologically significant effects might have been missed due to the small sample sizes (Steidl et al. 1997).

Our experimental manipulation created a 19–28% per capita immigration rate. Mechanisms that caused the observed immigration effects might include increased intensity of competition for resources, infanticide, increased risk of predation, pregnancy disruption, and disruption of a local genetic complex. The latter 2 mechanisms would not have occurred in this study because we did not add adult males and because we did not allow immigrant reproduction. Immigrants could increase the risk of predation for residents if they attract predators to the populations. Reported elsewhere (Hayes et al. 2004), we found that immigrants had larger home ranges and were more active at night than residents. The use of space and time that exposes immigrants to a greater risk of predation might have brought predators to resident populations.

The addition of immigrants could directly increase population density and increase intensity of competition for resources. However, the total and breeding densities in treatment populations were not higher than control populations when immigrants were included in the analyses, suggesting that density alone did not cause the lowered proportions of females and juveniles in treatment populations. It was probably the addition of strange females that considerably increased the intensity of competition for resources (Wolff 1995). Adult females are strongly territorial in most small mammal species (Wolff 1993) and are aggressive toward other conspecific females (Boonstra and Rodd 1983; Wolff 1997). Wolff (1993) proposed that female small mammals were territorial in order to defend juveniles from infanticidal females (but see Ostfeld 1985; Tuomi et al. 1997). Several studies (Boonstra 1978; Galindo and Krebs 1985; Lambin 1994; Rodd and Boonstra 1988; Wolff et al. 2002, and references therein) have linked adult females to reduced survival and recruitment of juveniles in the field. Adult female immigrants might commit infanticide as a form of resource competition (Wolff 1995). Although field evidence is sparse, removal of immigrants from resident populations has been shown to increase survivorship of preweaning young in small mammals (Lambin and Yoccoz 1998—Townsend's vole, *Microtus townsendii*). Likewise, Wolff and Schauber (1996—gray-tailed vole, *Microtus canicaudus*) found that juvenile mortality was positively correlated with the number of unrelated female immigrants in a habitat patch (but see de la Maza 1999).

The addition of immigrants could affect the social organization of resident populations because immigrants can saturate suitable habitats (Brown 1969), forcing young animals to delay dispersal and leading to the development of communal groups. Communal groups also might become prevalent if, under the threat of infanticide, young delay dispersal to help parents deter intruders from committing infanticide. Alternatively, the number of communal groups could be reduced simply because immigrants reduce juvenile survivorship. Neither hypothesis is consistent with the results from this study. Adult female immigrants did not change the social organization in resident populations. The proportions of social units that were communal were not different between treatment and control populations.

The immigration rates in this study declined with time as resident populations grew from 80 to ~210 voles/ha during the course of study. Inversely density-dependent immigration rates have been observed in previous studies (Gundersen et al. 2002; Lin and Batzli 2001). Territorial females, particularly at high densities, can form a social fence that impedes immigration (Hestbeck 1982). The probability of successful assimilation by immigrants has been shown to decrease with increasing resident population density (Gundersen et al. 2002) and to increase with increasing immigrant density (Seamon and Adler 1997). In this study, the wounding rates of immigrants were significantly higher than those of residents, suggesting that residents actively resisted the assimilation of immigrants (also see Montgomery et al. 1997). However, the immigrants seemed to do well in the face of active resistance. There was no difference in 2-week survivorship between immigrants and residents, suggesting that assimilation of most immigrants would be successful if they were allowed to remain in populations.

The net effects of immigrants on resident populations will probably be determined by the reproductive performance of immigrants. Lin (1999) found that female immigrants generally had higher reproductive rates than residents after they arrived in new habitats (also see Dueser et al. 1981, but see Krohne and Burgin 1987; Pugh and Tamarin 1990; Wauters et al. 1994). In this study, 18% of immigrants became pregnant in 2 weeks. In addition, we observed that at least 2 immigrants established underground nests during the 2 weeks in the field. Hence, we concluded that adult female immigrants did have notable negative effects on resident prairie vole populations. However, the direct numerical input and subsequent reproduction by immigrants could probably compensate for their negative effect on resident populations. Finally, we recognize that we only investigated the effects of adult female immigrants of a territorial species. The effects of male immigrants could be completely different from those of female immigrants due to differential breeding strategies between sexes. Similarly, the negative effects of immigrants of a territorial species on resident populations might be stronger than of a nonterritorial species due to territory competition. Both situations require further investigation.

Acknowledgments

We thank A. Ayers, D. Becker, L. Beeler, E. Halbert, A. Martin, L. McGraw, M. Owen, and K. Utendorf, who assisted in the field during this study. We thank R. Stander of Ecology Research Center for logistical support. We are grateful to N. Slade at the University of Kansas for providing animals and J. Jacquot at the Grand Valley University for lending us radiocollars. We thank B. Keane and M. Spritzer for commenting on an earlier draft of this manuscript. Finally, we acknowledge the postdoctoral fellowship provided by Miami University to YKL and the financial support provided by the National Institute of Health (NIMH 57115-01A2) to NGS. The procedures of this experiment followed American Society of Mammalogists guidelines (Animal Care and Use Committee 1998).

Literature Cited

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Banks, P. B., K. Norrdahl, and E. Korpimaki. 2002. Mobility decisions and the predation risks of reintroduction. Biological Conservation 103:133–138.

Boonstra, R. 1978. Effect of adult Townsend's voles (*Microtus townsendii*) on survival of young. Ecology 59:242–248.

Boonstra, R. 1985. Demography of *Microtus pennsylvanicus* in southern Ontario: enumeration versus Jolly–Seber estimation compared. Canadian Journal of Zoology 63:1174–1180.

Boonstra, R., and F. H. Rodd. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. Journal of Animal Ecology 52:757–780.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bulletin 81:293–329.

Bruce, H. M. 1959. An exteroceptive block to pregnancy in mouse. Nature 184:184–105.

Bruce, H. M. 1960. A block to pregnancy in the mouse caused by proximity of strange males. Journal of Reproductive Fertility 1:96–103.

Christian, J. J. 1980. Endocrine factors in population regulation. Pp. 55–115 in Biological mechanisms in population regulation (M. N. Cohen, R. S. Malpass, and H. G. Klein, eds.). Yale University Press, New Haven, Connecticut.

de la Maza, H. M. 1999. Exposure to strange adults does not cause pregnancy disruption or infanticide in the gray-tailed vole. Behavioral Ecology and Sociobiology 45:107–113.

Desy, E. A., and G. O. Batzli. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. Ecology 70:411–421.

Dueser, R. D., M. L. Wilson, and R. K. Rose. 1981. Attributes of dispersing meadow voles in open-grid populations. Acta Theriologica 26:139–162.

Ebensperger, L. A. 2001. A review of the evolutionary causes of rodent group-living. Acta Theriologica 46:115–144.

Galindo, C., and C. J. Krebs. 1985. Habitat use by singing voles and tundra voles in the southern Yukon. Oecologia 66:430–436.

Getz, L. L., and B. McGuire. 1997. Communal nesting in prairie voles (*Microtus ochrogaster*): formation, composition, and persistence of communal groups. Canadian Journal of Zoology 75: 525–534.

Getz, L. L., B. McGuire, and T. Pizzuto. 1993. Social organization of the prairie vole. Journal of Mammalogy 74:44–58.

Gundersen, G., H. P. Andreassen, and R. A. Ims. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. Ecology Letters 5:294–301.

Hayes, L. D., Y. K. Lin, and N. G. Solomon. 2004. Do female prairie vole (*Microtus ochrogaster*) immigrants affect the space use of conspecific female residents? American Midland Naturalist 151:88–92.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. Oikos 39:157–163.

Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethological Sociobiology 1:13–40.

Keller, L. E., et al. 2001. Immigration and the ephemerality of a natural population bottleneck: evidence from molecular marker. Proceedings of the Royal Society of London 268:1387–1394.

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology 67:111–148.

Krohne, D. T., and A. B. Burgin. 1987. Relative success of residents and immigrants in *Peromyscus leucopus*. Holarctic Ecology 10:196–200.

Lambin, X. 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles. Ecology 75:224–235.

Lambin, X., and C. Krebs. 1991. Can changes in female relatedness influence microtine population dynamics? Oikos 61:126–132.

Lambin, X., and N. G. Yoccoz. 1998. The impact of population kin-structure on nestling survival in Townsend's voles, *Microtus townsendii*. Journal of Animal Ecology 67:1–16.

Lemen, C. A., and P. Freeman. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammalogy 66:134–136.

Levins, R. 1970. Extinction. Lectures on Mathematics in the Life Sciences 2:75–107.

Lin, Y. K. 1999. The effects of food, cover and competition on demography, dispersal and density of voles. Ph.D. thesis, University of Illinois at Urbana-Champaign, Champaign.

Lin, Y. K., and G. O. Batzli. 2001. The influence of habitat quality on dispersal and population densities of voles. Ecological Monograph 71:245–275.

Manning, C. J., D. A. Dewsbury, E. K. Wakeland, and W. K. Potts. 1995. Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. Animal Behaviour 50:741–751.

Montgomery, W. I., W. L. Wilson, and R. W. Elwood. 1997. Spatial regulation and population growth in the wood mouse *Apodemus sylvaticus*: experimental manipulations of males and females in natural populations. Journal of Animal Ecology 66:755–768.

OSTFELD, R. S. 1985. Limiting resources and territoriality in microtine rodents. American Naturalist 126:1–15.

PUGH, S. R., AND R. H. TAMARIN. 1990. A comparison of population characteristics and reproductive success of resident and immigrant meadow voles. Canadian Journal of Zoology 69:2638–2643.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

RODD, F. H., AND R. BOONSTRA. 1988. Effects of adult meadow voles, *Microtus pennsylvanicus*, on young conspecifics in field populations. Journal of Animal Ecology 57:755–770.

SCHAUBER, E. M., AND W. D. EDGE. 1999. Statistical power to detect main and interactive effects on small mammal population attributes. Canadian Journal of Zoology 77:68–73.

SEAMON, J., AND G. ADLER. 1997. Factors affecting immigration of adults: experimental and theoretical observations with rodents. Acta Oecologica 18:637–655.

SHIELDS, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pp. 3–24 in Mammalian dispersal patterns: the effect of social structure on population genetics. (B. D. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, Illinois.

STEIDL, R. J., J. P. HAYES, AND E. SCHAUBER. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61:270–279.

TUOMI, J., J. AGRELL, AND T. MAPPES. 1997. On the evolution stability of female infanticide. Behavioral Ecology and Sociobiology 40:227–233.

WAUTERS, L., E. MATTHYSEN, AND A. A. DHONDT. 1994. Survival and lifetime reproductive success in dispersing and resident red squirrels. Behavioral Ecology and Sociobiology 34:197–201.

WOLFF, J. O. 1993. Why are female small mammals territorial? Oikos 68:364–370.

WOLFF, J. O. 1995. Friends and strangers in vole population cycles. Oikos 73:411–414.

WOLFF, J. O. 1997. Population regulation in mammals: an evolutionary perspective. Journal of Animal Ecology 66:1–13.

WOLFF, J. O., W. D. EDGE, AND G. WANG. 2002. Effects of adult sex ratios on recruitment of juvenile gray-tailed voles, *Microtus canicaudus*. Journal of Mammalogy 83:947–956.

WOLFF, J. O., AND E. M. SCHAUBER. 1996. Space use and juvenile recruitment in gray-tailed voles in response to intruder pressure and food abundance. Acta Theriologica 41:35–43.

YOCCOZ, N. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. Bulletin of Ecological Society of America 72:106–111.

Submitted 28 April 2003. Accepted 4 August 2003.

Associate Editor was Enrique P. Lessa.