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SIMILARITY OF RESIDENCE TIMES AMONG MICROTUS LITTERMATES: IMPORTANCE OF SEX AND MATURATION¹

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Dispersal seems to be necessary for microtine population regulation (Gaines and McClenaghan 1980, Stenseth 1983, Lidicker 1985). Dispersing voles are not a random subset of the population, and selective dispersal may alter the genetic composition of the population. If dispersal has a genetic basis, duration of stay in a population may vary more among than within litters. Both Hilborn (1975) and Beacham (1979) concluded that litters differed significantly in dispersal tendency in various species of *Microtus*, though Hilborn measured only duration of stay in the population, whereas Beacham measured both duration of stay and dispersal tendency. Both analyses implicitly assumed that male and female littermates were alike in dispersal tendencies. Anderson (1975) reached conclusions similar to those of Hilborn and Beacham after she introduced littermates into enclosed and unenclosed populations, but she, also, ignored sex differences. In most mammals, including microtines, males tend to disperse from the natal site and females to remain near it (Greenwood 1980, Boonstra et al. 1987); thus the assumption of Anderson, Beacham, and Hilborn may be invalid.

If a large number of the litters obtained by Hilborn and Beacham were single-sex litters, the apparent similarity in length of stay within litters might have been caused by sex-dependent rather than litter-dependent factors. In addition, one of the components of life history that affects genetic change within the population is that portion spent during maturity. In this analysis, we examine data collected on two *Microtus pennsylvanicus* populations. To test the hypothesis that duration of stay in a population varies less within than among litters (independent of sex composition), we also examine whether these effects occur both in immature and mature animals.

Methods

The study was carried out on two control grids near Toronto, Ontario (Boonstra and Rodd 1984). Each

trapping grid covered 0.7 ha and had 100 trap points spaced 7.6 m apart. One or two Longworth live traps and one pitfall trap were placed at each trap point and locked open when not in use. Longworth traps were only slightly less effective than pitfalls in capturing young voles (Boonstra and Rodd 1984). When first caught, voles were ear tagged, and on all occasions tag number, location, mass, sex, and sexual condition were noted. Live traps and pitfalls were set for 2 d every 2nd wk in summer; only Longworth traps (which contain a nesting space) were set in winter (usually every 2 wk, weather permitting). Each area was trapped on alternate weeks.

Littermates were defined as new voles ≤ 23 g caught in the same week in either type of trap at the same or immediately adjacent trap points (within 7.6 m) and differing in mass by no more than 3 g. These criteria were based on the observations that known littermates that entered traps in the same week differed by no more than 3.3 g (Craine 1987) and that most juveniles at these masses that entered traps were within two trap stations of the nest site (Boonstra et al. 1987). We measured residence time in the trappable population, recognizing that voles that disappeared from the grid may have died or dispersed. Total residence time was partitioned into time spent as an immature and as a mature animal. The immature period lasted until the individual first became reproductive (as judged from males having scrotal testes or females having a perforate vagina, active nipples, an open pubic symphysis, or an obvious pregnancy). For the analysis of variance, the data from the two grids were partitioned as follows: for grid A (Aurora) 1978 and 1982 data were excluded because the sample sizes were small and only a portion of the breeding season was covered; for grid F (International Airport) 1978, 1981, and 1982 data were excluded because only a small portion of the breeding season was covered or the density was too low. Both populations were judged as increasing in 1979 and being at a peak in 1980; the Aurora population had a second peak in 1981 (Krebs and Myers 1974, Boonstra 1985).

We used two analyses. The first (see Table 2), on total residence time, examined whether duration of stay within a population varied less within than among litters when the variation due to sex, area, and week of capture was removed. We used a partially nested two-way analysis of variance employing the SAS procedure GLM (1982). Litters were nested within weeks,

TABLE 1. Size and composition of litters of *Microtus pennsylvanicus* derived from trapping data.

Litter size	Grid A				Grid F			
	Males only	Females only	Mixed sex	Total	Males only	Females only	Mixed sex	Total
2	44	48	121	213	32	38	61	131
3	7	24	59	90	10	6	48	64
4	2	4	42	48	1	0	29	30
5	0	0	23	23	1	0	9	10
6	1	0	6	7	1	0	11	12
7	0	0	3	3	0	0	3	3
8	0	0	1	1	0	0	3	3
9	0	0	1	1	0	0	0	0
Totals	54	76	256	386	45	44	164	253
Litter size ($\bar{X} \pm \text{SE}$)	2.78 $\pm$ 0.06				2.93 $\pm$ 0.07			

which were nested within grids; the factor sex was common to all levels. Variation due to interaction effects between sex and grid, sex and week, and sex and litter was also determined. The sex source of variation removed variability resulting from litters having different compositions of males and females. The grid source of variation removed variability resulting from litters on one grid living longer than on the other. The weeks source of variation removed variability resulting from litters living longer if born at one time of the year than at another. The interaction effects between sex and the other factors removed variability resulting from a particular combination of sex and the other factors. To determine appropriate *F* values and degrees of freedom, we used the procedure outlined in Zar (1984: 470–473) (factors sex, grid, and week were fixed effects and litter was a random effect).

In the second analysis (see Table 3 and Results and Discussion) we examined whether sexes differed in their residence time and whether littermates of the same sex showed similar duration of stay after reaching maturity. We used a fully nested analysis of variance (NEST-AN: Rohlf 1985; see Sokal and Rohlf 1981 for a description of the method). Litters of the same sex were nested within weeks, which were nested within grids. Because of unequal sample sizes, we used Satterthwaite's approximation (Sokal and Rohlf 1981:300) where appropriate. Increase and peak periods were analyzed separately. Variance in residence time among litters is unlikely to be homogeneous as assumed by the analysis of variance because residence time is a highly truncated distribution, with numerous individuals disappearing after their first capture. The $\log(\bar{X} + 1)$ transformation most closely approximated the homogeneity assumption (program HOMOV: Rohlf 1985).

Results and Discussion

Our mass criterion was more conservative than that of either Hilborn (<35 g) or Beacham (<40 g). We

obtained 639 litters over the whole study. These litters accounted for 69.4% of all young caught ≤ 23 g ($N = 2630$). No significant overall sex ratio deviation from 1:1 was found (Grid A: 551 males, 532 females; Grid F: 376 males, 365 females). Litter size ranged from 2 to 9, with an overall mean ($\pm \text{SE}$) of 2.80 ± 0.07 individuals (Table 1), which is smaller than the mean litter size at birth in the laboratory (5.60 ± 0.21 individuals, $N = 80$: R. Boonstra and P. Boag, *personal observation*) or in nests in the field (5.65 ± 0.28 individuals, $N = 29$: I. Craine and R. Boonstra, *personal observation*). The difference between our derived litter sizes and those determined directly may represent the conservatism of our allocation procedure, differential

TABLE 2. Two analyses of variance testing differences in residence times among *Microtus pennsylvanicus* litters. Residence time was defined as the time between first and last captures.

Source*	df	ss	ms	F	P†
Population increase period					
Grid	1	679.4	679.4	1.35	
Sex	1	218.4	218.4	0.62	
Grid $\times$ sex	1	32.6	32.6	0.09	
Week	10	3 781.0	378.1	0.75	
Sex $\times$ week	14	4 627.7	330.6	0.93	
Litter	74	37 120.4	501.6	1.66	<.01
Sex $\times$ litter	14	4 964.9	354.6	1.17	
Error	225	68 002.0	302.2		
Total	340	119 426.4			
Population peak period					
Grid	1	1 437.0	1437.0	5.56	<.05
Sex	1	898.2	898.2	2.97	
Grid $\times$ sex	1	49.9	49.9	0.16	
Week	8	4 201.6	525.2	2.03	<.05
Week $\times$ sex	28	3 846.0	137.4	0.45	
Litter	240	61 965.5	258.2	1.24	<.02
Litter $\times$ sex	32	9 677.2	302.4	1.45	<.10
Error	664	138 107.5	208.0		
Total	975	220 182.9			

* See Methods for description of nesting of variables.

† All absent probability values are nonsignificant.

TABLE 3. Duration of residence (weeks) of litters used in the analysis during the increase and peak periods*†. Littermates were separated by sex. *N* = number of litters.

Sex	Population increase period				Population peak period			
	Immature		Mature		Immature		Mature	
	$\bar{X} \pm SE$	(<i>N</i>)	$\bar{X} \pm SE$	(<i>N</i>)	$\bar{X} \pm SE$	(<i>N</i>)	$\bar{X} \pm SE$	(<i>N</i>)
Males	8.0 ^a ± 0.8	(114)	2.8 ^b ± 0.7	(114)	9.3 ^a ± 0.6	(286)	1.5 ^c ± 0.3	(286)
Females	6.4 ^a ± 0.7	(114)	11.3 ^a ± 1.5***	(114)	8.7 ^a ± 0.6	(292)	4.9 ^b ± 0.6***	(292)

* Significance of differences between sexes tested within a group (e.g., mature males vs. mature females in increase period) using $\log(X + 1)$ transformation.

† Significant differences within a sex tested by ANOVA ($P < .05$) using $\log(X + 1)$ transformation. Identical superscript letters indicate means that are not different.

*** $P < .001$; others, $P > .05$.

trappability within a litter, mortality or dispersal of postweanling young in the field, or a combination of these. Differences in sex ratio were a potential source of bias (i.e., littermates could have similarity of residence times because of sex-dependent rather than litter-dependent factors), as 15.5% (99) of the litters contained only males and 18.8% (120) contained only females (Table 1).

The principal conclusion emerging from the first analysis (Table 2) is that littermates are more similar in duration of residency than are nonlittermates even when variation due to differences in sex composition are removed. Thus, the results of Hilborn (1975) and Beacham (1979) are corroborated.

However, this conclusion and its implications cannot be accepted at face value. None of these analyses distinguishes between the length of time animals spend in the population as immature and as mature, breeding animals. Recent evidence indicates that in most microtine species recruitment to the breeding population on the natal grid is heavily skewed in favor of females (Boonstra et al. 1987).

To see how similar littermates were during the mature and immature periods of life, we calculated the mean residence time for both periods for each sex in each litter. All litters in the increase and peak periods were included in the analysis. In increase and peak phases immature males had similar residence times, which were 2–5 times greater than those after maturity (Table 3). In fact, most litters had no mature, resident males (78.1% in the increase and 86.0% in the peak phase). Similar results were seen when litters with only one male were excluded. Of the litters with ≥ 2 males, 66.7% ($N = 54$) had no males resident at maturity in the increase phase and 79.5% ($N = 156$) had none in the peak phase. Residence time of immature females within a phase was similar to that of immature males, but mature females were resident 2–3 times longer than mature males. Nevertheless, 50.0 and 65.8% of litters had no mature females resident in the increase and peak phases, respectively. The corresponding figures

for litters with ≥ 2 females were 36.5% ($N = 52$) and 52.7% ($N = 148$). These highly skewed distributions in both males and females tend to produce strong similarities in residence times within litters and may explain, in part, the significance levels found in increase and peak phases (Table 2).

If microtine populations change genetically because certain families dominate the breeding population while others disappear, then littermates should have similar residence times as mature breeding animals. To remove the swamping effect of so many litters that have no resident mature members and because males and females show large differences in duration of residence as mature animals (Table 3), we separated individuals in a litter by sex. We then examined only litters containing ≥ 2 members in which at least one mature member remained in the population. Our second analysis indicates no relationship between length of residence as a mature animal and litter of birth in either males (increase: $F = 0.78$, $df\ 9,26$, $P > .50$; peak: $F = 0.94$, $df\ 18,64$, $P > .50$) or females (increase: $F = 0.64$, $df\ 17,48$, $P > .75$; peak: $F = 0.69$, $df\ 45,103$, $P > .75$). (We do not present the F values for the other levels [grid and week] from the nested analysis because they are unimportant for the question we pose.) Hence, we conclude that length of residence of each sex in the breeding population is independent of the family of birth.

Our first analysis (Table 2) indicates a differential disappearance rate among litters, but our second analysis and Table 3 indicate that this did not translate into differential residency at maturity among litters. The differential disappearance rate among litters may have been the result of differential dispersal, mortality, or both. However, even though some litters disappeared after a short residency and others after a long residency, most disappeared completely before reaching maturity. Of those that did not, there was no relationship between litter of birth and residency in the population at maturity. Thus, our evidence provides no support for the hypothesis that similarities in res-

idence time within litters is a mechanism for genetic change. Therefore, as neither Hilborn (1975) nor Beacham (1979) factored out the effect of sex or partitioned lifespan into immature and mature periods when examining longevity data, no clear interpretation of their results is possible. However, Beacham's (1979) evidence that dispersal during the peak may be a function of the litter of birth is convincing, though it could simply reflect littermates of the same sex moving simultaneously because they grow at the same rate, mature at the same time, and are driven out at the same time. It is imperative to determine if littermates are more likely than a random sample to mature and remain in a population. Our evidence indicates that in *Microtus pennsylvanicus* they are not; hence differential disappearance (dispersal and death) among families may not be necessary to produce genetic changes in fluctuating microtine populations.

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