Dispersion of adult male *Peromyscus leucopus* in relation to female reproductive status

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We studied dispersion of adult male *Peromyscus leucopus* in relation to the stage of pregnancy of adult females in natural populations monitored with Longworth live traps. Because postpartum mating is common in *P. leucopus* and days to parturition measures how far a female is from her next mating, we predicted that a female in early pregnancy (many days to parturition) would have fewer adult males in her neighbourhood than a female in late pregnancy (few days to parturition). Number of adult males caught within 30 m of each adult female was recorded and number of days to parturition for each female was obtained by bringing females back to the laboratory and allowing them to give birth. A negative relationship was found between number of adult males in a female's neighbourhood and days to parturition of the female ($r = -0.419, p < 0.01$), with the latter accounting for 8.8% of the variance in the former. These results support the hypothesis of a promiscuous mating system in *P. leucopus*.

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La dispersion des mâles adultes de *Peromyscus leucopus* a été étudiée en fonction du déroulement de la grossesse des femelles adultes chez des populations naturelles échantillonnées au moyen de pièges Longworth. Les accouplements postpartum sont fréquents chez *P. leucopus* et le nombre de jours avant la parturition permet d'évaluer l'intervalle de temps avant le prochain accouplement chez une femelle; ces constatations nous ont permis de prédire qu'une femelle au début de sa grossesse (plusieurs jours avant la parturition) aura moins de mâles adults dans son entourage qu'une femelle qui arrive au terme de sa grossesse (quelques jours avant la parturition). Le nombre de mâles adultes capturés à moins de 30 m de chaque femelle adulte a été déterminé et le nombre de jours avant la parturition a pu être compté car les femelles ont été rapportées au laboratoire et gardées jusqu'à ce qu'elles mettent bas. Il y a une corrélation négative entre le nombre de mâles adultes dans l'entourage d'une femelle et le nombre de jours jusqu'à sa parturition ($r = -0,419, p < 0,01$) et ce dernier paramètre explique 8,8% de la variance du premier. Ces résultats indiquent que la promiscuité fait partie intégrante du système d'accouplements de *P. leucopus*.

[Traduit par la revue]

Introduction

Direct observation of *Peromyscus leucopus* in the wild is impossible because of their nocturnal habits and secretive nature. As a result, their mating system and social behaviour have been studied primarily through laboratory observations of behavioural patterns and field investigations of spacing patterns. Male *P. leucopus* exhibited paternal behaviour in confined cages (Horner 1947; McCarty and Southwick 1977; Hartung and Dewsbury 1979) and radiotelemetry studies indicated either pair activity in adults of opposite sexes (Mineau and Madison 1977) or male–female association (Wolff and Hurlbutt 1982). These studies seem to indicate that *P. leucopus* is a monogamous species with paternal care. Nicholson (1941), however, found that adult males did not associate with young unless they were near weaning age. Of 64 nest boxes with young and at least one adult, a single adult male was found with young in five cases, and an adult male and an adult female were found with young in 11 cases. In all 16 cases, young were at least 18 days old. Xia and Millar (1988) argued that the paternal behaviour exhibited by males in confined cages was an artifact because paternal behaviour disappeared in an enclosure that did not confine the adult pair to the same nest. They also observed that males were associated with females only when they were approaching postpartum estrus. Estrous females in enclosures readily accepted multiple matings from more than one male (personal observation). Thus the mating system of *P. leucopus* appears to be promiscuity rather than monogamy, and the finding of pair activity based on a radiotelemetry study (Mineau and Madison 1977) may represent only a rare case. All radiotelemetry studies involved ... radiotelemetered males and females of

unknown reproductive status. Consequently, none of them provided any definite answer as to the general pattern of spatial relationship between adult males and females. Here we studied the dispersion of adult males in relation to reproductive status (days to parturition) of adult females. Female *P. leucopus* are usually receptive immediately after the birth of a litter (Svihla 1932; personal observation). If females mate promiscuously and males are only interested in females approaching estrus, we hypothesized that a female near parturition should attract more adult males than a female in early pregnancy.

Materials and methods

Mouse populations in five forests near London, Ontario, Canada, were monitored using grids and lines of Longworth live traps from May 15 to August 26, 1987 (Table 1). All habitats sampled had similar physiognomic features. Traps were placed 10 m apart within lines, and lines were 15 m apart in grids. A trapline or grid was considered as a sampling unit if traps from other lines or grids were at least 60 m away from this line or grid. The number of sampling units in each of the five forests is also included in Table 1. Sampling units differed much in size among, but not within, the five forests. All traps were baited with sunflower seeds, provided with cotton batting, and checked daily for at least 5 days. Animals caught were ear tagged, and sex, age (adult or juvenile), and location were recorded. Adult females were brought back to the laboratory and checked for parturition every 3–4 days. Number of days to parturition was recorded for each female. Traps within 30 m of the trap where each female was caught were arbitrarily defined as her neighbourhood traps. Fig. 1 illustrates the number of neighbourhood traps for two females (F1 and F2) in one sampling unit which is a grid of six lines (A–F) each with 13 traps. The female F1 has 22 neighbourhood traps while female F2 has only eight neighbourhood traps. Females caught on traplines had

TABLE 1. Monitoring scheme of *Peromyscus leucopus* in the five forests

Forest	Monitoring period	No. of pregnant females caught	No. of sampling units	Total no. of traps
Arva	May 15 – June 3	8	6	108
Weldon	June 3 – June 10	6	2	100
McLarty's	June 15 – July 5	5	1	78
Burm's	July 5 – July 26	8	3	140
Highway 16	July 27 – Aug. 26	8	2	90

NOTE: Sampling units were traplines in Arva and grids in the other four forests. The size of the sampling units differed much among, but not within, the five forests.

FIG. 1. A grid of traps with six lines (A–D) each with 13 traps, illustrating the assignment of neighbourhood traps to different females. The neighbourhood traps for female F1 and F2 are numbered.

a maximum of six neighbourhood traps. If two females (e.g., F1 and F3 in Fig. 1) were caught within 60 m, some neighbourhood traps were common to both females. Such a "common" trap was counted as 0.5 traps for each female. Adult males caught in a neighbourhood trap of a female were recorded as her neighbourhood males. A male caught in a "common" trap was counted as 0.5 neighbourhood males for each female. Because the movement of males may be influenced by the removal of their neighbouring females, only males caught up to the night when their neighbouring females were caught were included in the analysis. The variables recorded were (*i*) days to parturition (D_p) of each female, (*ii*) the distance of a female to her closest adult female (FDF), (*iii*) the number of neighbourhood males for each female (N_m), (*iv*) the total number of adult males caught in the sampling unit (N_t), (*v*) the number of neighbourhood traps for each female (N_{nt}), and (*vi*) the total number of traps in the sampling unit (N_{tt}).

Results

Altogether 45 adult females were caught in the field, of which 35 gave birth in the laboratory. Thus most adult females in the field were pregnant. Mean and standard deviation of the six variables for the 35 females are displayed in Table 2.

Three factors may have influenced the number of adult males (N_m) caught in a female's neighbourhood. First, a female with many neighbourhood traps (a large N_{nt}) should have had greater N_m than a female with few neighbourhood traps. For example, female F1 in Fig. 1 had greater N_m than female F2. If the distribution of adult males is random, then the expected number of neighbourhood males (N_e) is simply a function of N_t, N_{nt}, and N_{tt}, i.e.,

TABLE 2. Some descriptive statistics for the six variables and N_e, the expected number of neighbourhood males

Variables	N	Mean	SD
D_p	35	11.29	5.79
N_m	35	1.09	1.09
N_t	35	3.88	2.49
N_{nt}	35	9.86	4.56
N_{tt}	14	36.86	9.81
FDF	35	66.97	55.60
N_e	35	0.99	0.59

NOTE: See text for definitions of variable names and the calculation of N_e.

[1] $\quad N_e = N_t \cdot N_{nt}/N_{tt}$

For example, if five males were caught in the grid depicted in Fig. 1, then the N_e for female F1 is 1.41 ($= 5 \times 22/78$) males. N_e was calculated in this way for all 35 females. Mean and standard deviation of N_e are also included in Table 2. A truly random distribution of males in space implies that mean N_m equals mean N_e, and N_m increases with N_e with slope equal to 1 and intercept equal to 0. Two biases, however, tend to draw N_m away from N_e. One is that males and females may be spatially associated. For example, both males and females may be spatially associated with favourable microhabitats. This will result in N_m increasing with N_e with a slope larger than 1, i.e.,

[2] $\quad N_m = (1 + b_{Asn})N_e$

where b_{Asn} measures the degree and type of association between males and females. b_{Asn} larger than 0 indicates a positive association, b_{Asn} smaller than 0 indicates a negative association, and b_{Asn} equal to 0 indicates that the distribution of males is independent of females. The intercept will still be 0 because $N_m = 0$ when $N_e = 0$. The observed relationship between N_e and N_m is shown in Fig. 2. The other force that may influence N_m is the male's spatial response to the female's reproductive status. For example, a female with D_p of 2 may attract more males than a female with D_p of 20 because males only have to wait for 2 days to mate in the former and 20 days in the latter. In short, we predicted that females close to their parturition date should have more males nearby than females in early pregnancy. A regression model used to test our prediction is as follows:

[3] $\quad N_m = b_0 + (1 + b_{Asn})N_e + b_{D_p} \cdot D_p$

where b_0 is the intercept and b_{D_p} measures the type of male
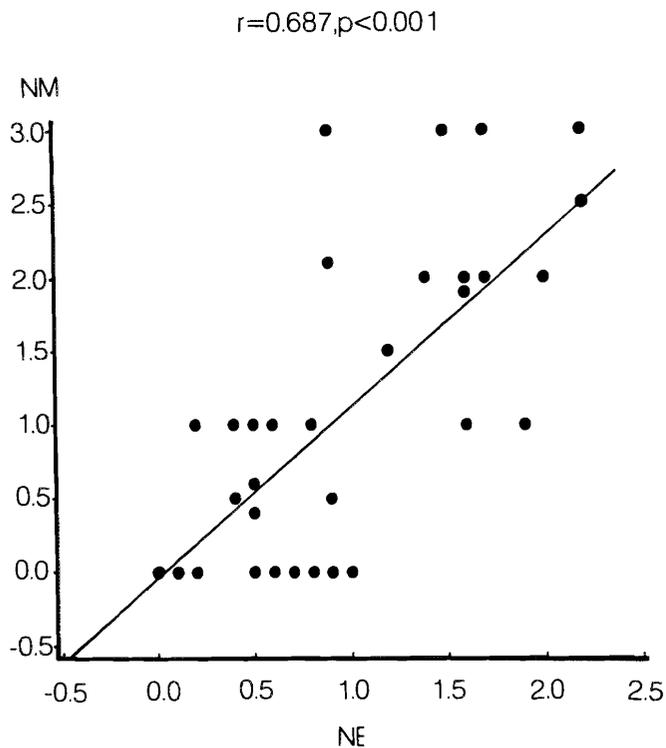
$r=0.687, p<0.001$

FIG. 2. Relationship between observed number of neighbourhood males (NM) and its expected value (NE). A simple linear regression line is shown as a solid line across the scatter plot.

spatial response to the female's reproductive status. Our prediction was that N_m should increase with a decrease in D_p, i.e., $b_{D_p} < 0$.

Because the five areas sampled differed in density and in size of sampling units, the area effect was coded with four dummy variables and incorporated in the regression model (Berenson et al. 1983). The final model fitted to the data was

[4] $N_m = b_0 + 1.038N_e - 0.056D_p,$

where $b_0 = 0.491$ for Hwy. 16, 0.460 for Arva, 1.128 for Weldon, 0.501 for McLarty's, and 0.914 for Burm's (Table 3). The model accounts for 57.1% of the total variance in N_m, with N_e accounting for 23% of the total variance and D_p accounting for 7%, using sequential sum of squares (Kim and Kohout 1975; Tabachnick and Fidell 1983). The value of b_{Asn} (1.038 − 1) is close to 0, indicating little association between males and females. b_{D_p} (−0.056) is significantly smaller than 0 (Table 3, $t = -2.16$, df = 28, $p = 0.021$, one-tailed test), indicating that adult males indeed adjust their position in relation to the stage of pregnancy of adult females.

Although the above results support our hypothesis, one experimental constraint remains unconsidered. The neighbourhood area of a female in our study is defined as the area with a radius of 30 m from the trap where the female was caught. If two females were caught close to each other, then each male caught in "common" traps was counted as 0.5 for each female; but if only one was caught, then all males caught in those potentially "common" traps were counted as her neighbourhood males. This would yield an overestimate of N_m for the single female relative to the situation when both females were caught. The degree of this overestimation will horoughness of trapping, which is, unfor-
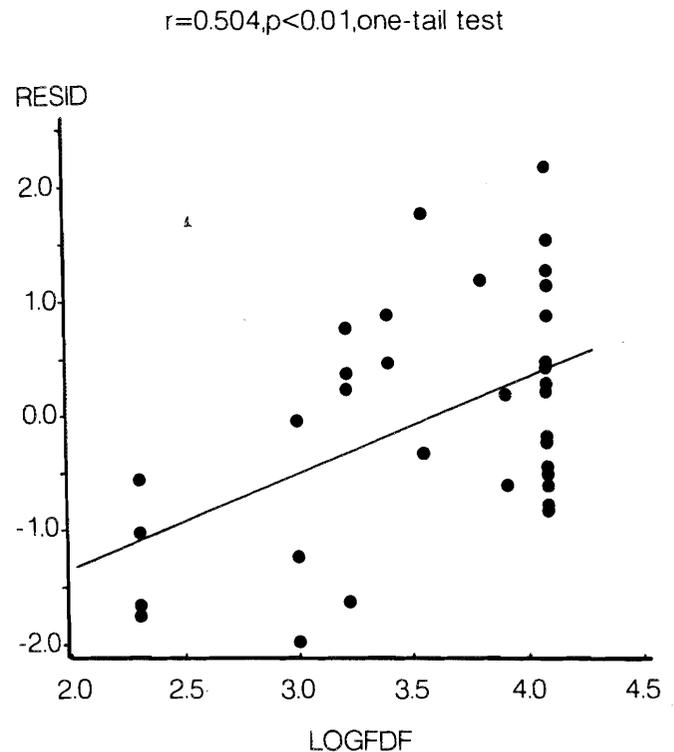
$r=0.504, p<0.01$, one-tail test

FIG. 3. The influence of FDF on N_m: a plot of the residual of the model (RESID) $N_m = b_0 + (1 + b_{Asn})N_e + b_{D_p} \cdot D_p$ versus LOGFDF (natural logarithm of FDF). A simple linear regression line is shown as a solid line across the scatter plot.

tunately, difficult to estimate. Assuming that density is equal within a forest, then the trapping is likely more thorough in situations in which several females were caught close to each other than in situations where only single females were caught. The distance from a female to her closest female neighbour (FDF) is smaller in the former situation than in the latter. Therefore the smaller the FDF, the more thorough the trapping was and the less likely that N_m was overestimated. This relationship should hold until FDF is as large as 60 m, but no larger. To illustrate the last point, consider female F1 in Fig. 1. F1 has 22 neighbourhood traps. If another female was caught in location E6, then 14 of the 22 traps are "common" traps and only half of the males caught in these "common" traps can be counted as F1's neighbourhood males. If no other female is caught within 60 m, then all males caught in the 22 traps are F1's neighbourhood males. But if no other female is caught within 120 m, the number of neighbourhood males that F1 has will still be the same as when there is no other female caught within 60 m, i.e., the number of adult males caught in those 22 traps. Thus the effect of FDF on N_m disappears when FDF is larger than 60 m. For this reason, all FDF values larger than 60 m were recoded to 60 m. Figure 3 shows the relationship between N_m and FDF under these conditions. FDF does seem to influence N_m (Fig. 3) and it is appropriate to incorporate FDF into the regression model:

[5] $N_m = b_0 + b_{FDF} \cdot \ln FDF + (1 + b_{Asn})N_e + b_{D_p} \cdot D_p$

The model fitted to the data is

[6] $N_m = b_0 + 0.719(\ln FDF) + 0.988N_e - 0.062D_p$

Detailed results are presented in Table 4. The error variance is

TABLE 3. Regression coefficients and significance tests for the regression model $N_m = b_0 + (1 + b_{Asn})N_e + b_{D_p} \cdot D_p$

Variables	Coefficient	SD of coefficient	T	P*	95% CI
Intercept	0.491	0.426	1.15	ns	
Dummy 1	−0.031	0.399	−0.08	ns	
Dummy 2	0.637	0.429	1.49	ns	
Dummy 3	0.010	0.460	0.02	ns	
Dummy 4	0.423	0.416	1.02	ns	
N_e	1.038	0.261	3.98	0.001	0.59 to 1.48
D_p	−0.056	0.026	−2.16	0.021	−0.10 to −0.01

Analysis of variance

Source of variation	df	SS	MS	F	P
Regression	6	20.73	3.45	6.22	<0.01
Residual	28	15.56	0.56		
Total	34	36.29			

NOTE: CI, confidence interval. Dummy variables 1 to 4 are for Arva, Weldon, McLarty's, and Burm's, respectively. Their corresponding coefficients change the intercept of the model. The intercept for Hwy. 16 is 0.491. Intercepts for the other areas are the sum of 0.491 and the respective coefficients.

*H_0: $b_{dummy\ var.} = 0$, $(1 + b_{Asn}) = 0$, $b_{D_p} \geq 0$.

TABLE 4. Regression coefficients and significance tests for the regression model $N_m = b_0 + b_{FDF} \cdot FDF + (1 + b_{Asn})N_e + b_{D_p} \cdot D_p$

Variables	Coefficient	SD of coefficient	T	P*	95% CI
Intercept	−1.885	0.714	−2.64	0.016	
Dummy 1	−1.551	0.359	−1.53	ns	
Dummy 2	0.551	0.356	1.55	ns	
Dummy 3	−0.258	0.388	−0.67	ns	
Dummy 4	0.473	0.345	1.37	ns	
FDF	0.719	0.194	3.71	0.001	0.39 to 1.32
N_e	0.988	0.217	4.56	0.001	0.62 to 1.36
D_p	−0.062	0.021	−2.89	0.005	−0.10 to −0.03

Analysis of variance

Source of variation	df	SS	MS	F	P
Regression	7	25.984	3.712	9.733	<0.001
Residual	27	10.299	0.381		
Total	34	36.283			

NOTE: CI, confidence interval. Dummy variables 1 to 4 are for Arva, Weldon, McLarty's, and Burm's, respectively. Their corresponding coefficients change the intercept of the model. The intercept for Hwy. 16 is −1.885. Intercepts for other areas are the sum of −1.885 and the respective coefficients.

*H_0: $b_{FDF} \leq 0$, $b_{dummy\ var.} = 0$, $(1 + b_{Asn}) = 0$, $b_{D_p} \geq 0$.

much reduced relative to the previous model and this model accounts for 71.6% of the total variation in N_m, with FDF accounting for 15.2%, N_e accounting for 20.5%, and D_p accounting for 8.8%, using sequential sum of squares (Kim and Kohout 1975; Tabachnick and Fidell 1983). b_{D_p} is much smaller than 0 (Table 4, $t = -2.89$, df = 27, one-tailed test, $P = 0.005$), indicating a strong negative relationship between D_p and N_m. The b_{Asn} (1 − 0.988) is still very close to zero, implying no association between adult males and females given that other variables are controlled. Figure 4 shows the relationship between D_p and N_m as follows. D_p was removed from the last model and the residual of that model without D_p represents variation in N_m that cannot be explained by differences in area, FDF, and N_e. This residual was plotted as a function of D_p in Fig. 4 to see if more "extra N_m" corres-

ponds to smaller D_p. The graphic presentation supported in a much simpler way our conclusion that the closer a female is to her postpartum estrus, the more males are found in her neighbourhood.

Discussion

The percentage of the total variance accounted for by D_p was small (7.2 and 8.8% for the first and second regression models, respectively), which was expected because of the many sampling assumptions involved. For example, the trap where the female was caught may not have been the center of her home range, which would result in the misassignment of neighbourhood traps and, consequently, the misassignment of neighbourhood males. In addition, when two females of very
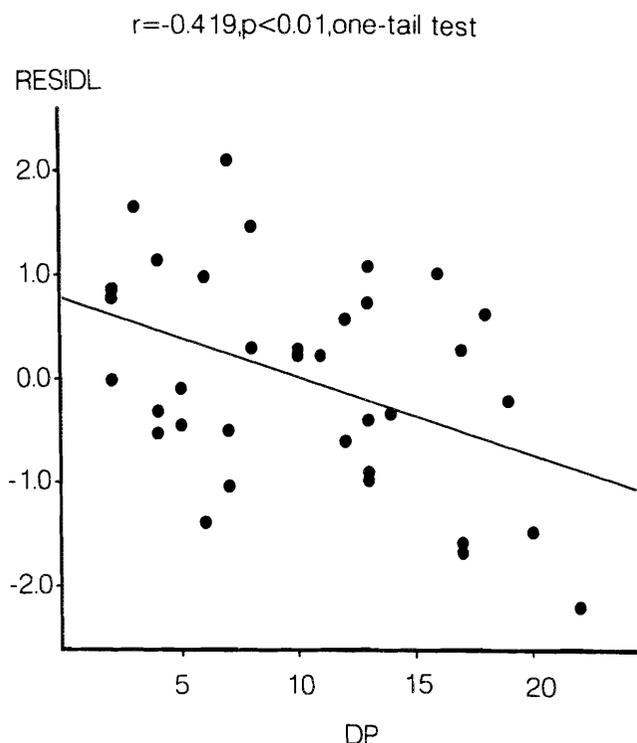
r=-0.419,p<0.01,one-tail test

FIG. 4. The influence of D_p on N_m: a plot of the residual of the model (RESIDL) $N_m = b_0 + b_{FDF} \cdot FDF + (1 + b_{Asn})N_e$ versus D_p (DP). A simple linear regression line is shown as a solid line across the scatter plot.

different reproductive status were caught close to each other, there were many "common" traps and each male caught in these "common" traps was counted as 0.5 for each female. In that case, the effect of D_p on N_m, no matter how great, is much obscured.

The b_{D_p} showing the numerical relationship between N_m and D_p was also small (-0.056 for the first model and -0.062 for the second), but this is a minimal estimate. The model is based on the number of males caught, not on the number of males actually present. If only one quarter of the males actually present were caught, then each term in the final model should have been multiplied by 4 to reflect the real situation and the b_{D_p} would have been -0.248. Also, D_p may not have been estimated accurately because females were not checked daily. This error will result in an underestimate of b_{D_p} (Sokal and Rohlf 1981; Snedecor and Cochran 1980). What is important is the establishment of a negative relationship between N_m and D_p.

Our study shows that a female approaching her postpartum estrus may have several males in her neighbourhood. This may provide an explanation for the pair activity claimed in Mineau and Madison (1977). One female in her late pregnancy and one of several males in her neighbourhood may happen to be radio-telemetered; this situation would appear to the observer with a radio signal detecter as nothing but nice and clear pair bonding, simply because all the other nonradiotelemetered males are undetectable. On the basis of our results, we conclude that pair activity is not the true pattern in *P. leucopus* and the spacing pattern of males in relation to a female's reproductive status, as revealed in this study, suggests a promiscuous mating system.

Myton (1974) suggested that *P. leucopus* are arranged in "family" groups consisting of one adult female and several adult males. She did not say whether this "family" grouping is common throughout the whole year or just in a specific season, but this social grouping certainly would require a very male-biased sex ratio, with at least two adult males to every adult female. Such a biased sex ratio has rarely been documented in natural populations or laboratory colonies. Terman (1968) reviewed 10 trapping studies and found a total of 2484 males and 1951 females; the percent males (56%) was significantly greater than 50%. Because males travel more extensively (Stickel 1968), estimates of sex ratio based on trapping may be male biased. But even given that 56% of animals are males, Myton's (1974) observation that some adult females have several adult males nearby necessarily implies that there must be some adult females that have just one male nearby or even no male at all. Our hypothesis explains why some adult females have more males nearby than others in terms of D_p, and Myton's "family" groups may just be temporary associations of several adult males with an adult female close to estrus.

From our results, it appears that males adjust their positions in relation to female's reproductive status. This may also contribute to the differential dispersal among juveniles whereby juvenile males, upon weaning, disperse while juvenile females remain in the maternal home range. This differential dispersal is traditionally explained in terms of avoiding close inbreeding (Krohne et al. 1984; Wolff and Lundy 1985; Goundie and Vessey 1986; Wolff et al. 1988). However, the dipersal time of juvenile males is the time when they are weaned, which is much earlier than the time when they are approaching sexual maturity. Weaning corresponds to the time when the second litter is about to be born, i.e., the time when several adult males are attracted to the dam. Juvenile males may simply be driven out of their maternal home range by these adult males. Wolff et al. (1988) argued that aggression from adult males was not responsible for dispersal of juvenile males because only a small percentage (26 and 28% in two series of trials) of adult males showed aggression toward juveniles. Wolff et al. (1988) however, did not observe behaviour of adult male *P. leucopus* towards juvenile males with an estrous female nearby. Thus adult aggression cannot yet be completely ruled out as an explanation for the differential dispersal. Adult aggression has been indicated in several studies involving a congeneric species, *P. maniculatus* (Sadleir 1965; Healey 1967; van Horne 1981).

We should finally mention that our results could have a different interpretation. The negative relationship between D_p and N_m could well be explained by varying degrees of female aggression during pregnancy. Females in early pregnancy (large D_p) may have a recently born litter, i.e., early lactation. It is known that females during the early lactation period are the most aggressive toward males (Layne 1968; Gleason et al. 1980; Wolff 1985), and we observed in enclosures that females with newborn young kill adult males that blundered into the nest containing those young. Because this female aggression decreases with the progress of lactation (or the decrease of D_p, in other words), the large N_m associated with small D_p may have nothing to do with the attractiveness of the females in terms of potential mating, but may occur simply because males avoid aggressive females in early lactation (large D_p). An analysis discriminating between the two possible explanations for

the negative relationship between D_p and N_m is currently underway.

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BERENSON, M. D., LEVINE, M., and GOLDSTEIN, M. 1983. Intermediate statistical methods and applications. A computer package approach. Prentice-Hall, Englewood Cliffs, NJ.

GLEASON, P. E., MICHAEL, S. D., and CHRISTIAN, J. J. 1980. Aggressive behavior during the reproductive cycle of female *Peromyscus leucopus*: effects of encounter site. Behav. Neural Biol. **29**: 506–511.

GOUNDIE, T. R., and VESSEY, S. H. 1986. Survival and dispersal of young white-footed mice born in nest boxes. J. Mammal. **67**: 53–60.

HARTUNG, T. G., and DEWSBURY, D. A. 1979. Paternal behavior in six species of muroid rodents. Behav. Neural Biol. **26**: 466–478.

HEALEY, M. C. 1967. Aggression and self-regulation of population size in deermice. Ecology, **48**: 377–392.

HORNER, B. E. 1947. Parental care of young mice of the genus *Peromyscus*. J. Mammal. **28**: 31–36.

KIM, J., and KOHOUT, F. J. 1975. Multiple regression analysis: subprogram REGRESSION. *In* SPSS: statistical package for the social sciences. *Edited by* N. H. Nie. 2nd ed. McGraw-Hill, New York. pp. 320–367.

KROHNE, D. T., DUBBS, D. A., and BACCUS, R. 1984. An analysis of dispersal in an unmanipulated population of *Peromyscus leucopus*. Am. Midl. Nat. **112**: 146–156.

LAYNE, J. N. 1968. Ontogeny. *In* Biology of *Peromyscus* (Rodentia). *Edited by* J. A. King. Spec. Publ. Am. Soc. Mammal. No. 2. pp. 148–253.

McCARTY, R., and SOUTHWICK, C. H. 1977. Patterns of parental care in two cricetid rodents, *Onychomys torridus* and *Peromyscus leucopus*. Anim. Behav. **25**: 945–948.

MINEAU, P., and MADISON, D. 1977. Radio-tracking of *Peromyscus leucopus*. Can. J. Zool. **55**: 465–468.

MYTON, B. 1974. Utilization of space by *Peromyscus leucopus* and other small mammals. Ecology, **55**: 277–290.

NICHOLSON, A. 1941. The home and social habits of the wood-mouse (*Peromyscus leucopus nebrascensis*) in southern Michigan. Am. Midl. Nat. **25**: 196–223.

SADLEIR, R. M. F. S. 1965. The relationship between agonistic behaviour and population changes in the deermouse, *Peromyscus maniculatus* (Wagner). J. Anim. Ecol. **34**: 331–352.

SNEDECOR, G. W., and COCHRAN, W. G. 1980. Statistical methods. 7th ed. Iowa State University Press, Ames.

SOKAL, R. R., and ROHLF, F. J. 1981. Biometry. 2nd ed. W. H. Freeman and Co., San Francisco.

STICKEL, L. F. Home range and travels. *In* Biology of *Peromyscus* (Rodentia). *Edited by* J. A. King. Spec. Publ. Am. Soc. Mammal. No. 2. pp. 373–411.

SVIHLA, A. 1932. A comparative life history study of the mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool. Univ. Mich. No. 24.

TABACHNICK, B. G., and FIDELL, L. S. 1983. Using multivariate statistics. California State University, Northridge.

TERMAN, C. R. 1968. Population dynamics. *In* Biology of *Peromyscus* (Rodentia). *Edited by* J. A. King. Spec. Publ. Am. Soc. Mammal. No. 2. pp. 412–450.

VAN HORNE, B. 1981. Niches of adult and juvenile deer mice *Peromyscus maniculatus* in seral stages of coniferous forest. Ecology, **63**: 922–1003.

WOLFF, J. O. 1985. Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. Anim. Behav. **33**: 117–123.

WOLFF, J. O., and HURLBUTT, B. 1982. Day refuges of *Peromyscus leucopus* and *Peromyscus maniculatus*. J. Mammal. **63**: 668–672.

WOLFF, J. O., and LUNDY, K. I. 1985. Intra-familial dispersion patterns in white-footed mice, *Peromyscus leucopus*. Behav. Ecol. Sociobiol. **17**: 381–384.

WOLFF, J. O., LUNDY, K. I., and BACCUS, R. 1988. Dispersal, inbreeding avoidance and reproductive success in white-footed mice. Anim. Behav. **38**: 456–465.

XIA, X., and MILLAR, J. S. 1988. Paternal behavior by *Peromyscus leucopus* in enclosures. Can. J. Zool. **66**: 1184–1187.