RELATIONSHIP OF PREVIOUS TRAP OCCUPANCY TO CAPTURE OF WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*)

**Moshe Wolf** and **George O. Batzli**

*Department of Animal Biology, University of Illinois at Urbana–Champaign, Urbana, IL 61801*

Adult white-footed mice (*Peromyscus leucopus*) were more likely to be captured in traps previously occupied by conspecific individuals of the opposite sex than in traps previously occupied by the same sex, especially during breeding season. Sex of a mouse in the 3rd capture by a particular trap appeared related to the sexes of mice in both the 1st and 2nd captures. Breeding females were more likely to be captured in traps previously containing males than nonbreeding females. Breeding individuals occurred more often than expected in traps that previously held other breeding mice of the same sex rather than nonbreeding mice. Captures of juveniles were more likely to follow previous captures of juveniles than of adults, probably because members of the same litter were being captured. Finally, white-footed mice were less likely to be captured in traps that previously held a potential predator, short-tailed shrew (*Blarina brevicauda*).

Key words: livetrapping bias, *Peromyscus leucopus*, predator avoidance, sex-biased capture, white-footed mice

A variety of factors can affect the success of live traps in capturing small mammals. For instance, previous use of live traps by conspecific individuals often increases capture rates (Boonstra and Krebs 1976; Daly and Behrends 1984; Gurnell and Little 1992). This is not always the case (Tew 1987), however, and results may depend on the sex and age of individuals involved (Daly and Behrends 1984; Gurnell and Little 1992; Heske 1987). Adult white-footed mice, *Peromyscus leucopus*, and house mice, *Mus domesticus*, appear more likely to enter traps that have odor of the opposite sex than traps with odor of the same sex (Drickamer 1984, 1995; Mazdzer et al. 1976), a phenomenon called heterosexual bias. Other species (*Apodemus sylvaticus*, *Apodemus flavicollis*, *Clethrionomys glareolus*, *Peromyscus eremicus*, *Dipodomys agilis*, and *Perognathus fallax*), on the other hand, may show preference for traps with conspecific scents without heterosexual bias (Daly et al. 1980; Gurnell and Little 1992; Stoddart and Smith 1986). Breeding condition can also influence trap response of mice; odor of house mice in breeding condition may be more attractive to the opposite sex than that of nonbreeding mice (Drickamer 1995). Finally, previous capture of potential predators, such as short-tailed shrews (*Blarina brevicauda*), could influence the success of trapping mice. Meadow voles (*Microtus californicus*) avoid traps that previously contained shrews, although no more so than traps that contained other species of rodents (Boonstra et al. 1981).

Whatever the effects of previous captures may be, documenting them should aid in the planning and interpretation of field studies that use livetrapping. In this study, we examined the relationships of sex, age, breeding condition, and species of previously captured small mammals to subsequent capture of white-footed mice. Earlier results led us to expect more male captures after a female capture and vice versa (het-
erosexual trap bias), and we expected this trend to be intensified for breeding individuals. We also expected that previous captures of a shrew in a trap would lower the probability of capturing white-footed mice, particularly for females because of the vulnerability of their young (Getz et al. 1992).

**Materials and Methods**

White-footed mice were trapped in fragments of eastern deciduous forest at 4 sites in east-central Illinois: Trelease Woods, a 24-ha patch of forest in central Champaign County; Patton Woods, a 6-ha fragment in northern Champaign County; Allerton Park 1, a site adjacent to agriculture on the edge of a 610-ha forest in central Piatt County; and Allerton Park 2, a site adjacent to tall-grass prairie on an edge of the same forest but across a paved road and about 3 km from Allerton Park 1. These sites were chosen because of accessibility and low levels of human disturbance (as all are protected areas). All sites contained mature, upland eastern deciduous forest dominated by oak–hickory–maple associations.

At each of the 4 sites, we established an 8-by-11 trapping grid with stations at 15-m intervals, 150 m along a forest edge, and reaching 105 m into the interior of the forest. A map of the general plan for these grids is shown in Wolf and Batzli (2002). At each station we set a single Sherman trap (7.6 by 8.9 by 22.9 cm) baited with black sunflower seeds and provided with cotton nesting material during cold seasons (November and March). Traps were set for 4 consecutive nights and checked the following dawn during each of 5 trapping sessions at each site, during September, November, March, May, and July 1997–1998 at Trelease Woods and at the Allerton Park sites and during March, May, July, September, and November 1998 at Patton Woods. We marked white-footed mice with Monel ear tags (National Band and Tag Co., Newport, Kentucky) and released them at the point of capture. Date, location, tag number, weight, sex, age, and reproductive condition were recorded at each capture. Presence of other species was noted, but no other data were taken for them.

We determined the age of white-footed mice by dorsal pelage: gray for juveniles, brown for adults, and mixed (molting) for subadults. Adults were classified as breeding if males had scrotal testes and if females were pregnant (weight gain and enlarged teats) or lactating (large teats with nearby hair removed).

To investigate the relationship of short-tailed shrews to the success in trapping mice, we compared the frequency of capture for traps that captured mice after capture of a shrew to the frequency of capture for traps that captured mice after capture of a mouse. We excluded data from traps that were subsequently occupied by the same individual or by other species because such captures reduced the access of other white-footed mice to these traps.

Likelihoods of observed relationships occurring by chance (tests of independence) were calculated using contingency tables on the basis of frequencies of mice in different categories during 1st and 2nd (or 3rd) captures. For 2-dimensional contingency tables we used Haber’s correction for continuity if $d.f. = 1$, except for tests of homogeneity (also called heterogeneity) between data sets (Zar 1999). For multidimensional contingency tables we used log-linear models (Fienberg 1980). To find significant trends in multidimensional tables we used a hierarchical approach, 1st establishing nonindependence at the highest dimension (4 in our case), then at succeeding levels (3 and 2 in our case). To reduce confusion, we only report salient details of the full analysis.

**Results**

**Overall trap use.**—We trapped 740 white-footed mice (1,765 captures) in 9,860 trap-nights. Numbers of mice and number of captures (in parentheses) were: 231 (486) for Allerton Park 1, 182 (514) for Allerton Park 2, 199 (497) for Patton Woods, and 128 (268) for Trelease Woods. Most individuals (86%) and captures (91%) were adult, and we caught about twice as many juveniles (9% of individuals and 5% of captures) as subadults (5% of individuals and 3% of captures). Sex ratios of adults, subadults, and juveniles did not differ significantly from a 1:1 ratio at any site, although more males than females were caught summing over all sites (Wolf and Batzli 2002).

Other species were also captured. We had 106 captures of short-tailed shrews, but we
**Table 1.**—Heterosexual bias in frequency of consecutive captures of *Peromyscus leucopus* of both sexes during breeding (May, July, September) and nonbreeding (March, November) seasons. Observed frequencies differ significantly from expected frequencies—see text.

| 2nd capture | Male | Female |
|-------------|------|--------|
| Observed    | Expected | Observed | Expected |
| Breeding season | | | |
| 1st capture male | 109 | 130.3 | 108 | 86.7 |
| 1st capture female | 103 | 81.7 | 33 | 54.3 |
| Nonbreeding season | | | |
| 1st capture male | 26 | 33.2 | 44 | 36.8 |
| 1st capture female | 46 | 38.8 | 36 | 43.2 |

**Table 2.**—Heterosexual bias in frequency of male and female *Peromyscus leucopus* found in 3rd consecutive capture after 1st and 2nd captures of either a male or a female. Observed frequencies differ significantly from expected frequencies—see text.

| 3rd capture | Male | Female |
|-------------|------|--------|
| Observed    | Expected | Observed | Expected |
| 1st capture male | | | |
| 2nd capture male | 8 | 14.2 | 22 | 15.8 |
| 2nd capture female | 27 | 20.8 | 17 | 23.2 |
| 1st capture female | | | |
| 2nd capture male | 17 | 21.4 | 16 | 11.6 |
| 2nd capture female | 16 | 11.6 | 2 | 6.4 |

We did not know how many individuals these captures represented because shrews were not marked. We captured only a few individuals of additional species: 1 eastern chipmunk (*Tamias striatus*), 2 meadow voles (*Microtus pennsylvanicus*), 1 long-tailed weasel (*Mustela frenata*), 3 house wrens (*Troglodytes aedon*), and 2 deer mice (*Peromyscus maniculatus*). Only the relationship of shrews to white-footed mice was included in our analyses because of small sample sizes of the other species.

**Response to conspecific mice.**—When testing for heterosexual bias we combined data across sites to increase sample size; the assumption of homogeneity among sites could not be rejected ($\chi^2 = 4.29$, $d.f. = 3$, $P = 0.23$). Both sexes showed heterosexual bias. During the breeding season, males were captured 26% more often than expected after females had been in the trap and females were captured 25% more often than expected after males had been trapped ($\chi^2 = 22.0$, $d.f. = 1$, $P < 0.001$; Table 1). During the nonbreeding season, 18% more males than expected were captured after females and 20% more females than expected were captured after males ($\chi^2 = 5.20$, $d.f. = 1$, $P = 0.02$; Table 1). Heterosexual bias was significantly stronger during the breeding season (chi-square test for homogeneity of tables, $\chi^2 = 5.25$, $d.f. = 1$, $P = 0.02$; Table 1).

Our data set contained 125 cases with 3 successive captures of different individual white-footed mice during a trapping session. An overall test of the 3-dimensional contingency table indicated that the sexes of mice found in successive captures were not independent of one another ($G = 27.7$, $d.f. = 4$, $P < 0.001$). Furthermore, none of the captures was independent of the other 2 (tests of partial independence: $G = 16.4$, 24.0, and 20.5 for 1st, 2nd, and 3rd captures, respectively, $d.f. = 3$, $P < 0.001$).

Relationship of 2nd capture to 3rd capture differed depending on the sex of the mouse in the 1st capture. Thus, 2-dimensional contingency tables show that 44% fewer males than expected occurred in the 3rd capture after 1st and 2nd captures of males but only 21% fewer males than expected occurred in the 3rd capture after a 1st capture of a female and a 2nd capture of a male (Table 2). Similarly, 38% more males than expected occurred in the 3rd captures after 1st and 2nd captures of females, but only 30% more males than expected occurred after a 1st capture of a male and a 2nd capture of
TABLE 3.—Patterns of breeding status of captured *Peromyscus leucopus* in relation to sex or breeding status of individual previously captured in same trap. Observed frequencies differ significantly from expected frequencies—see text.

| Reproductive status of mouse in 2nd capture | Breeding | Nonbreeding |
|--------------------------------------------|----------|-------------|
|                                      | Observed | Expected    | Observed | Expected |
| Females in 2nd capture |           |             |           |           |
| Males in 1st capture | 59        | 65.1        | 49        | 42.9      |
| Females in 1st capture | 26        | 19.9        | 7         | 13.1      |
| Males in 2nd capture |           |             |           |           |
| Breeding male in 1st capture | 75        | 69.4        | 10        | 15.6      |
| Nonbreeding male in 1st capture | 14        | 19.6        | 10        | 4.4       |
| Females in 2nd capture |           |             |           |           |
| Breeding female in 1st capture | 18        | 15.5        | 2         | 4.2       |
| Nonbreeding female in 1st capture | 8         | 10.2        | 5         | 2.8       |

For samples taken during the breeding season (May, July, September) breeding status as well as sex of captured mice affected trapping frequencies \( (G = 90.1, \text{d.f.} = 11, P < 0.001) \) for the test of independence over 4 dimensions—1st and 2nd captures partitioned by sex and breeding status. In part, this nonindependence reflected the heterosexual bias already examined, but sex and breeding status of mice were not independent in the 1st and 2nd captures \( (G = 64.4, \text{d.f.} = 9, P < 0.001) \). These results reflected 3 patterns in the 2-dimensional tables (Table 3). First, breeding females occurred more than expected in traps that had held females, whereas nonbreeding females occurred more than expected in traps that had 1st caught a male \( (\chi^2 = 5.95, \text{d.f.} = 1, P = 0.02; \text{Table 3}) \). Second, breeding males occurred more than expected in traps that had previously captured a breeding male, but nonbreeding males occurred more than expected in traps that had previously held a nonbreeding male \( (\chi^2 = 9.29, \text{d.f.} = 1, P = 0.002; \text{Table 3}) \). Finally, breeding females occurred more than expected in traps that had caught a breeding female, whereas nonbreeding females occurred more than expected in traps that had held nonbreeding females, although the trend was only marginally significant \( (\chi^2 = 3.0, \text{d.f.} = 1, P = 0.09; \text{Table 3}) \). No other trends in the 2-dimensional tables were even marginally significant \( (P > 0.20 \) in all cases).

In addition to the trapping bias associated with sex and breeding condition, we looked for an effect of age on 2nd captures. Of 26 traps that 1st captured juveniles 42% subsequently captured juveniles, whereas only 5% of the traps that 1st captured adults \( (n = 593) \) subsequently captured juveniles \( (\text{chi-square test of homogeneity, } \chi^2 = 5.95, \text{d.f.} = 1, P = 0.02) \). For subadults and adults, however, age of mice in the 1st capture had no relationship to age in the 2nd capture \( (\chi^2 = 1.33, \text{d.f.} = 1, P = 0.25) \).

Response to shrews.—Seventy-eight traps that 1st caught a shrew had fewer subsequent captures of white-footed mice \( (40\% \text{ of traps}) \) than did 1,196 traps that 1st caught a mouse \( (56\% \text{ of traps, chi-square test of homogeneity, } \chi^2 = 7.96, \text{d.f.} = 1, P = 0.005) \). Female mice did not respond differently from male mice to traps that had held shrews \( (\chi^2 = 0.31, \text{d.f.} = 1, P = 0.56) \). Captures of juvenile or subadult mice could not be related to captures of shrews because of small sample sizes.
DISCUSSION

Heterosexual bias in consecutive captures of white-footed mice occurred in our study as it has in previous studies. However, we know of no previous analysis that shows the persistence of heterosexual bias for more than 2 consecutive trappings. Particularly striking was the fact that the 3rd captures showed the same bias in relation to the 1st capture as did the 2nd captures (Table 2). The only effect of sex of a 2nd-captured mouse appeared to be an increase in the relative number of opposite sex in the 3rd captures (continued heterosexual bias).

Biases in recaptures of breeding versus nonbreeding animals did not occur as expected. We expected increased avoidance of traps that had contained the same sex when the 2nd mouse was in breeding condition, as reported for the house mouse (Drickamer 1995). Rather, we found that breeding females occurred more than expected in traps previously occupied by females (contrary to the general pattern for females) and that breeding males had a higher than expected frequency in traps previously occupied by breeding males (Table 3). Reduced preference of breeding females for traps with male odor may be related to the avoidance of males by pregnant females (Korytko and Vessey 1991). The preference of breeding males for traps that previously held breeding males may be a sign of aggressiveness toward other breeding males, even though female white-footed mice appear more territorial than males (Korytko and Vessey 1991; Metzger 1971). Of course, alternative hypotheses could also explain our results, and experiments designed to test the effects of male odors on the capture of pregnant females and breeding males are needed.

Although we did not expect it, juveniles were captured more than expected after the capture of a juvenile. We suspect that this pattern reflected the small home ranges of juveniles. Juveniles generally stay near their nest and disperse as subadults (Stickel 1968), so more juveniles than adults would occur in the immediate vicinity of a trap near a successful nest, thereby increasing the likelihood of consecutive captures of juveniles. In other traps, juvenile captures were rare relative to adult captures, which reduced the likelihood of consecutive capture of an adult and a juvenile.

Previous studies reported neither avoidance of predator odors in general by white-footed mice (Mazdzer et al. 1976) nor specific avoidance of the odor of shrews by meadow voles (Boonstra et al. 1981). Mazdzer et al. (1976) attributed the lack of response by white-footed mice to the fact that they used odors of rare predators, but short-tailed shrews were relatively common in our study. White-footed mice may react more to the odor of shrews than do meadow voles because adult mice and short-tailed shrews have comparable weights, whereas adult voles are often twice the size of the shrews. Female mice may not have responded differently from males in our study because they did not perceive shrews in a trap as a danger to their young, which were likely hidden some distance from the trap. Again, experiments explicitly designed to test our hypotheses are required.

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LITERATURE CITED

Boonstra, R., and C. J. Krebs. 1976. The effect of odour on trap response in Microtus townsendii. Journal of Zoology (London) 180:467–476.

Boonstra, R., F. H. Rodd, and D. J. Carleton. 1981. Effect of Blarina brevicauda on trap response of Microtus pennsylvanicus. Canadian Journal of Zoology 60:438–442.

Daly, M., and P. Behrends. 1984. Effect of moving traps between trapping stations upon rodent retrapping data. American Midland Naturalist 112:205–207.

Daly, M., M. I. Wilson, and P. Behrends. 1980. Factors affecting rodents’ response to odors of strangers encountered in the field: experiments with odor baited traps. Behavioral Ecology and Sociobiology 6: 323–329.
DRICKAMER, L. C. 1984. Captures of two species of Peromyscus at live traps baited with male and female odors. Journal of Mammalogy 65:699–702.

DRICKAMER, L. C. 1995. Odors in traps: does most recent occupant influence capture rate for house mice? Journal of Chemical Ecology 21:541–555.

FENNEBERG, S. E. 1980. The analysis of cross-classified categorical data. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.

GETZ, L. L., C. M. LARSON, AND K. A. LINDSTROM. 1992. Blarina brevicauda as a predator on nestling voles. Journal of Mammalogy 73:591–596.

GURNELL, J., AND J. LITTLE. 1992. The influence of trap residual odor on catching woodland rodents. Animal Behaviour 43:623–632.

HESKE, E. J. 1987. Responses of a population of California voles, Microtus californicus, to odor-baited traps. Journal of Mammalogy 68:64–72.

KORYTKO, A. I., AND S. H. VESSEY. 1991. Agonistic spacing behaviour in white-footed mice, Peromyscus leucopus. Animal Behaviour 42:913–919.

MAZZIOTTO, E., M. R. CAPONE, AND L. C. DRICKAMER. 1976. Conspecific odors and trappability of deer mice (Peromyscus leucopus noveboracensis). Journal of Mammalogy 57:607–609.

METZGER, L. H. 1971. Behavioral population regulation in the wood mouse Peromyscus leucopus. American Midland Naturalist 86:434–448.

STICKEL, L. F. 1968. Home range and travels. Pp. 373–411 in Biology of Peromyscus (Rodentia) (J. A. King, ed.). Special Publication. American Society of Mammalogists 2:1–593.

STOODART, D. M., AND P. A. SMITH. 1986. Recognition of odour-induced bias in the live-trapping of Apodemus sylvaticus. Oikos 46:194–199.

TEW, T. 1987. A comparison of small mammal responses to clean and dirty traps. Journal of Zoology 212:361–364.

WOLF, M., AND G. O. BATZLI. 2002. Effects of forest edge on populations of white-footed mice Peromyscus leucopus. Ecography 25:193–199.

ZAR, J. H. 1999. Biostatistical analysis. 4th ed. Prentice and Hall, Upper Saddle River, New Jersey.

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