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George A. Feldhamer
Southern Illinois University Carbondale

Leslie B. Rodman
Southern Illinois University Carbondale

Timothy C. Carter
Southern Illinois University Carbondale

Eric M. Schauber
Southern Illinois University Carbondale, schauber@siu.edu

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Multiple Captures of White-footed Mice (Peromyscus leucopus): Evidence for Social Structure?

GEORGE A. FELDHAMER,[1] LESLIE B. RODMAN,
TIMOTHY C. CARTER[2] AND ERIC M. SCHAUBER
Department of Zoology, Southern Illinois University, Carbondale 62901
Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale 62901

ABSTRACT.—Multiple captures (34 double, 6 triple) in standard Sherman live traps accounted for 6.3% of 1355 captures of *Peromyscus leucopus* (white-footed mice) in forested habitat in southern Illinois, from Oct. 2004 through Oct. 2005. There was a significant positive relationship between both the number and the proportion of multiple captures and estimated monthly population size. Multiple captures were all intraspecific and occurred significantly more often from Nov. through Mar. when animals were not reproductively active, but this was confounded by seasonal changes in abundance. Age/gender distribution of animals in double captures did not differ from that expected from random pairing. We suggest that sociality and synchronous entry of two white-footed mice into traps were the primary determinants of double captures; sensitivity of traps may have been the primary factor in triple captures.

INTRODUCTION

Multiple captures of small mammals ($\geq$ 2 individuals caught in a single-capture live trap at the same time) are relatively rare events that have been used to infer aspects of the social and reproductive behavior of several species of small, cryptic, nocturnal rodents. Whether multiple captures are random events (Bergstrom, 1986) or result from synchronous trap entry by socially affiliated pairs or groups remains a contentious issue, with potential implications not only for small mammal population dynamics, but for disease transmission (Calisher *et al.*, 2000). Bergstrom and Sauer (1986) felt double captures resulted from ''random nonsynchronous encounters'' at traps with increased springing tension, and suggested the following criteria needed to be met in double captures to infer social traveling: (1) no interspecific captures; (2) equal springing weight in traps with single and double captures; (3) nonrandom age-sex ratios; (4) recaptures of the same pairs; (5) no adult-juvenile pairs; and (6) proportion of double captures is independent of population density. Taulman *et al.* (1994) rejected several of these criteria. They argued that bias for double captures caused by unequal trap spring tension (criterion #2) was ''intractable'' because of various environmental factors and that single captures of small light individuals often occur in the same traps as double captures. They also rejected criterion #5 because direct observations of several species of small mammals show that adults may lead juveniles while traveling (*cf.*, Kaufman and Kaufman, 1987). Criterion #6 also is highly problematic in differentiating between the contrasting hypotheses of social traveling or random encounters given that ''the double capture rate would be expected to increase with population density whether the animals traveled in pairs or met randomly at the trap'' (Taulman *et al.*, 1994:359).

Several investigators have concluded that double captures are indicative of social interaction. Petersen (1975) concluded that 98 double captures (2 triple) of Mexican desert rodents, primarily *Baiomys taylori* (northern pygmy mice) and *Reithrodontomys megalotis* (western harvest mice) occurred because of social bonding and high densities. Likewise,

[1] Corresponding author: e-mail: feldhamer@zoology.siu.edu
[2] Present address: Department of Biology, Ball State University, Muncie, IN 47306, USA

Blaustein and Rothstein (1978) suggested 81 doube captures (2 triple) of western harvest mice in California resulted from social traveling and synchronous trap entry. Spencer *et al.* (1982) also attributed 24 multiple captures of *R. fulvescens* (fulvous harvest mice) in Texas to males and females traveling in pairs. Taulman *et al.* (1994) attributed 15 double captures of fulvous harvest mice and 16 double captures of *R. humulis* (eastern harvest mice) to social traveling. For 172 double captures of enclosed *Mus musculus* (house mice), Drickamer *et al.* (2003) found juveniles occurred more frequently than expected, as did adult females and related individuals. Feldhamer (1977) attributed 16 double captures of *Microtus montanus* (montane voles) to sociality, whereas 16 double captures of *Peromyscus maniculatus* (deer mice) may have resulted from trap insensitivity. Likewise, Jenkins and Llewellyn (1981) could not attribute 21 double captures of deer mice to social interactions. Previous reports of multiple captures in *P. leucopus* (white-footed mice) are limited. Novak (1983) discussed 14 double captures from a site in central Illinois and Christopher and Barrett (2007) documented 79 double captures of white-footed mice in Georgia.

Getz (1972) suggested that traps designed for multiple captures, such as the Ketch-All trap used by Reich and Tamarin (1984) are necessary to address questions of social behavior related to double (or multiple) captures. We agree with Taulman *et al.* (1994) that single capture traps may be better for inferences of social traveling because animals must enter nearly simultaneously to be captured together. Traps designed for multiple captures certainly give information on social tolerance but not on proximity of individuals prior to being trapped because they place ''no temporal restriction on the subsequent entry of animals into an already occupied trap'' (Taulman *et al.*, 1994:357). Here we discuss possible social implications of 40 multiple captures (34 double; 6 triple) of white-footed mice that occurred during a study of the rodent community in forested habitat of southern Illinois impacted by a tornado. We differentiate between double captures (a pair of animals in a single-capture live trap) and multiple captures (≥ 3 animals in a single-capture live trap).

METHODS

The study was conducted on Mermet Lake Conservation Area (MLCA), Massac County, Illinois, which is managed primarily for waterfowl and upland game hunting. The area encompasses about 785 ha dominated by *Quercus palustris* (pin oak), *Q. alba* (white oak) and *Q. phellos* (willow oak) forest, old fields and about 280 ha of permanent water. On 6 May 2003 a large tornado reduced 166 ha of forest at MLCA to a tangled landscape of broken snags and shattered woody debris. No small mammal live trapping had been conducted on the area prior to our study.

We established live trap transects to investigate small mammal diversity, abundance, survival and reproduction at two forest sites with tornado damage and at two undisturbed forest sites. One transect in the damaged area was in a salvaged timber area and one was in an unsalvaged area with extensive downed woody debris. Each transect had 50 stations at approximately 10-m intervals. We placed one large Sherman live trap (7.6 × 7.6 × 25.4 cm) at each station and a small Sherman trap (5.1 × 6.4 × 16.5 cm) at every other station for a total of 75 traps per transect. Traps were baited with cracked corn and sunflower seeds and placed in cover within 2 m of each station point. Each transect was operated monthly for a 3-d period from Oct. 2004 through Oct. 2005. We recorded species, gender, body weight and breeding condition (scrotal, pregnant, lactating) for all captured individuals. They were individually marked by toe clipping/ear punching and released at the point of capture. Traps were not cleaned following a capture. For all procedures on live animals we followed humane guidelines approved by the ASM Animal Care and Use Committee (1998).

We considered individuals in breeding condition or with body weight >16 g as adults. Monthly population estimates were calculated using the Jolly-Seber Model with heterogeneous survival, POPAN5 program (Arnason and Schwartz, 1999). We used logistic regression in SAS (SAS Institute, Cary, North Carolina) to test whether the proportion of multiple captures differed with population size, transect or breeding season (Apr.–Oct.) vs. nonbreeding season. Transect and breeding season were included as categorical variables, whereas estimated population size was a continuous variable. We used a backward stepwise procedure with these three variables to determine the most important explanatory variable or variables. To test whether double captures were nonrandomly distributed with respect to the age and gender of the mice involved, we took the observed age/gender structure of the animals involved in double captures and randomly selected pairs of animals from this pool without replacement. We then calculated two test statistics based on the age/gender contingency table of randomized pairings: the χ^2-statistic and the maximum cell value. We repeated this random selection 1000 times using the PopTools add-in in Microsoft® Excel, and took the proportion of randomizations that produced test statistics exceeding observed values as the *P*-value.

Results

During 8454 trap nights, we caught 547 individual white-footed mice 1355 times. They made up 77.9% of the 702 individual small mammals captured. We also captured 123 *Blarina carolinensis* (southern short-tailed shrews), 12 house mice, 10 *Microtus pinetorum* (pine voles), 5 *Oryzomys palustris* (rice rats), 4 *Microtus ochrogaster* (prairie voles) and 1 *Zapus hudsonius* (meadow jumping mouse). Only white-footed mice were involved in multiple captures; 34 double captures and 6 triple captures. The 40 multiple captures involved 73 different individuals. Six individuals were part of multiple captures twice, and two individuals were involved three times, all but once with different partners. Multiple capture frequency of *Peromyscus leucopus* accounted for 6.3% of total captures and occurred only in the larger Sherman traps.

Multiple captures included 31 double and 5 triple captures on the two tornado-damaged sites; only four multiple captures occurred on the undisturbed sites. Throughout the year, monthly estimates of *Peromyscus leucopus* population size on the damaged sites were 2–10× higher than on the undamaged sites. Based on logistic regression, there was a significant (Wald χ^2 = 8.5, d.f. = 1, P = 0.0036) positive relationship between the proportion of multiple captures and population size (Fig. 1). Reproductively active individuals were captured on all transects from Apr. through Oct. During this 7 mo period there were only six multiple captures, whereas during the 5 mo without reproductive activity 34 multiple captures occurred. However, population sizes were generally greater during the nonbreeding months. Transect and breeding season were not statistically significant predictors of the proportion of multiple captures after accounting for population size in logistic regression (both P > 0.3) and both were deleted from the model during stepwise selection.

For 32 double captures in which gender and age were determined for both individuals, the age/gender distribution of animals involved did not differ significantly from expectation under random pairing (Table 1; χ^2 = 20.1, randomization P = 0.95; maximum cell value = 15 adult male - adult female pairs, randomization P = 0.90).

Discussion

Multiple captures reported in most studies are generally rare relative to single captures, although percentages are highly variable. Part of this variability may reflect different
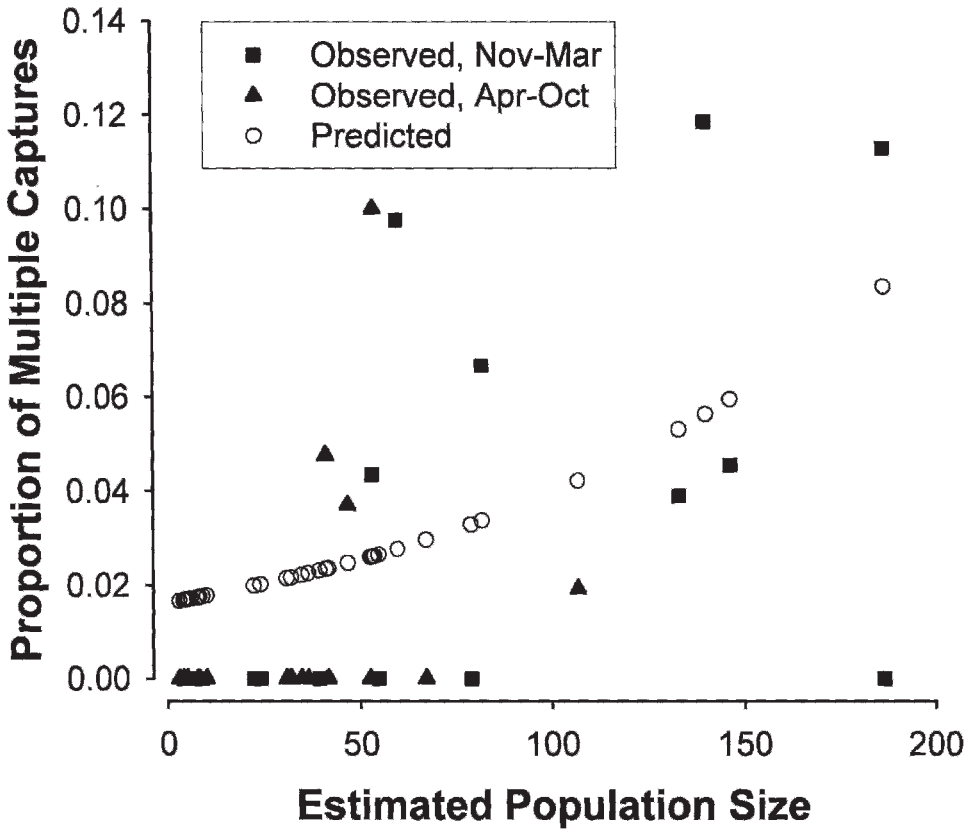
FIG. 1.—Proportion of multiple captures of white-footed mice (*Peromyscus leucopus*) relative to estimated population size from disturbed and undisturbed forest habitat, Mermet Lake Conservation Area, Massac County, Illinois, from Oct. 2004 through Oct. 2005. Predicted values were determined from logistic regression

analytical approaches of investigators (*see* Drickamer *et al.*, 2003). Multiple captures in our study accounted for 6.3% of the total captures of *Peromyscus leucopus,* which was about four times higher than the rate reported for white-footed mice by Novak (1983). Jenkins and Llewellyn (1981) reported a multiple capture rate of 8.9% for deer mice. Conversely, Spencer *et al.* (1982) found only 0.47% multiple captures for fulvous harvest mice. They

TABLE 1.—Age (adult or juvenile/subadult) and gender frequency distribution of 32 double captures of *Peromyscus leucopus* on Mermet Lake Conservation Area, Massac County, Illinois, from Oct. 2004 through Oct. 2005

	Juv/Sub Male	Adult Male	Juv/Sub Female	Adult Female
Juv/Sub Male	3	2	2	1
Adult Male	X	2	1	15
Juv/Sub Female	X	X	1	0
Adult Female	X	X	X	5

removed individuals from the site, however, which probably lowered the frequency of multiple captures because it reduced population density. Nonetheless, the rate reported by Spencer *et al.* (1982) was much lower than the multiple capture frequency rate of 6.5% (Petersen, 1975) and 25.0% (Blaustein and Rothstein, 1978) for western harvest mice, but similar to the 0.2% rate reported for house mice by Drickamer *et al.* (2003). The 69 double captures of *Apodemus sylvaticus* (wood mice) reported by Verhagen and Verheyen (1982) were only about 0.6% of total captures. Likewise, their 33 double captures of *Myodes* [*Clethrionomys*] *glareolus* (bank voles) were only 0.39% of total captures.

We found a positive relationship between both the frequency and the proportion of multiple captures and population size (criterion #6 of Bergstrom and Sauer, 1986), as have most other investigators (Blaustein and Rothstein, 1978; Jenkins and Llewellyn, 1981; Petersen, 1975). Although the rate of multiple capture may be expected to increase with population density (Taulman *et al.*, 1994), this is not always the case (Novak, 1983).

Variability in the age-gender ratios and seasonality of multiple captures was another criterion (#3) of Bergstrom and Sauer (1986). Adult male-female captures accounted for about 47% of our double captures in which age and gender of both animals were determined, which was similar to their frequency in the population. Likewise, Jenkins and Llewellyn (1981) found no combination of age-gender categories of double captures exceeded that expected by chance. Neither did Granjon and Duplantier (1993) for 78 double captures of *Mastomys natalensis* (Natal mastomys) in single capture traps. Often, however, a greater number of adult male-female double captures is the norm (Blaustein and Rothstein, 1978; Christopher and Barrett, 2007; Petersen, 1975) and generally is attributed to reproductive activity and mating.

Even though we found more multiple captures occurred during the nonbreeding season–as did Blaustein and Rothstein (1978), Verhagen and Verheyen (1982) and Novak (1983)–pairing of adult males and females may be a beneficial prelude to the breeding season and possible mating. It is difficult, however, to differentiate between the potential benefits of social traveling vs. increased population size as the primary determinant of increased multiple captures outside the breeding season. Regardless, additional benefits of social traveling may accrue from ''increased foraging efficiency, increased predator detection or escape probability, increased thermoregulatory efficiency by huddling or a combination of the three'' (Novak, 1983:712). As breeding progresses and females are pregnant or lactating, they become increasingly aggressive and asocial (Wolff, 1989) and juvenile males disperse. Rates of multiple captures throughout much of the reproductive season might be expected to be minimal, as we found.

We set trap triggers as sensitive as possible so that body weight of individuals involved in multiple captures should have been a minimal factor. We attempted to determine trap sensitivity based on the number of traps in which multiple captures of *Peromyscus leucopus* occurred that also took a much lighter short-tailed shrew during the same trapping period. Only four traps met this criterion: one of them had three double captures and another had a triple capture. So few traps met the criterion perhaps because white-footed mice avoided traps previously occupied by shrews (Wolf and Batzli, 2002). If trap insensitivity were the primary cause of double captures, we would expect to see them make up a constant proportion of such captures irrespective of population abundance. The increased proportion of double captures we observed at high population sizes provides support for the hypothesis that synchronous entry of socially affiliated animals into traps was the prime determinant of double captures. Social interaction as the prime determinant in double captures also is strongly suggested by the lack of any interspecific multiple captures (criterion #1 of Bergstrom and Sauer, 1986), lack of any injuries suggesting agonistic

behavior between conspecific *P. leucopus* captured together and the number of individuals taken in more than one multiple capture event (criterion #4 of Bergstrom and Sauer, 1986). Only one pair was taken together twice, however, suggesting that pairs may not remain together for prolonged periods, as noted by Novak (1983).

The fact that we had multiple captures only in large Sherman traps also could indicate social interaction. For pairs of mice traveling together, small traps may preclude simultaneous or sequential entry simply because of trap size. Small Sherman traps do not preclude capture of single animals, however (Dalby and Straney, 1976; Maly and Cranford, 1985; Whittaker *et al.*, 1998). Alternatively, double captures only in large Sherman traps might suggest that the smaller traps had more sensitive treadle mechanisms.

Like many previous studies, ours is somewhat of a ''mixed bag'' in terms of double captures as support for the alternative hypotheses of social traveling or random events. However, the preponderance of evidence supports sociality and synchronous entry as explanations for double captures of white-footed mice in this study, whereas the most conservative explanation for the triple captures we observed was lack of trap sensitivity.

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