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An analysis of multiple captures in *Permoyscus* with a critique on methodology

BRADLEY J. BERGSTROM

Museum of Natural History and Department of Systematics and Ecology, The University of Kansas, Lawrence, KS, U.S.A. 66045 Received October 12, 1985

BERGSTROM, B. J. 1986. An analysis of multiple captures in *Peromyscus* with a critique on methodology. Can. J. Zool. 64: 1407-1411.

Multiple captures obtained in Sherman traps are reported for Peromyscus maniculatus (66 intraspecific, 6 interspecific) and P. difficilis (12 intraspecific, 4 interspecific) in Colorado. Multiple capture frequency in P. maniculatus. (3.53%) was higher than in P. difficilis (1.94%), which probably resulted from the greater weights of P. difficilis. Only one case of injury or death was noted in 84 multiple captures. Multiple captures occurred in traps in which the treadles were significantly less sensitive to tripping than traps that captured single mice, which suggested that pairs of mice did not enter the traps simultaneoulsy. Adult mice were disproportionatley sampled in single captures because of the insensitivity of the tripping mechanism. For the same reason, immature mice were disproportionately sampled in multiple captures. These trap-related biases can create spurious age and sex associations within multiple captures. Trap bias should be tested explicitly before attempting to analyze multiple-capture data from single-capture traps. A "socially null" model of random encounter of traps by captured pairs fits many of the data presented here and is suggested as the appropriate null hypothesis for these analyses. If live-trapping data must be used to address questions of social behavior, the use of actual multiple-capture traps, preferably to study long-term associations

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Des captures multiples de *Peromyscus maniculatus* (66 ir spécifiques et 4 interspécifiques) ont été enregistrées dans de multiples était plus élevée chez *P. maniculatus* (3,53%) que ci grande de *P. difficilis*. Un seul cas de blessure ou mort a été enr sont produites dans les pièges où les mécanismes déclencheurs n'ont capturé qu'une souris, ce qui semble indiquer que les so souris adultes étaient capturées de façon disproportionnée dar grande du mécanisme déclencheur. Pour la même raison, les so les pièges à captures multiples. Ces artéfacts d'échantillonna concernant les associations quant à l'âge ou au sexe dans les ca éprouvées explicitement avant l'analyse de données de captures modèle "socialement nul" de la rencontre aléatoire du même pie et il semble que ce soit là la meilleure hypothèse nulle à utiliser a animaux vivants doivent être utilisés dans les études sur les o captures multiples, préférablement du genre qui permet d'étude **Introduction**The study of social organization in small, nocturnal mammals animaux vivants doivent être utilisés dans les études sur les o captures multiples, préférablement du genre qui permet d'étude **Sausses of animals trapped together in multiple-capture traps** Syas suggested by Davis (1955). Later, Getz (1961, 1972). Des captures multiples de Peromyscus maniculatus (66 intraspécifiques, 6 interspécifiques) et de P. difficilis (12 intraspécifiques et 4 interspécifiques) ont été enregistrées dans des pièges Sherman dans le Colorado. La fréquence des captures multiples était plus élevée chez P. maniculatus (3,53%) que chez P. difficilis (1,94%), probablement à cause de la masse plus grande de P. difficilis. Un seul cas de blessure ou mort a été enregistré parmi les 84 captures multiples. Les captures multiples se sont produites dans les pièges où les mécanismes déclencheurs étaient significativement moins sensibles que ceux des pièges qui n'ont capturé qu'une souris, ce qui semble indiquer que les souris capturées n'entraient pas dans le piège en même temps. Les souris adultes étaient capturées de façon disproportionnée dans les pièges à captures uniques, à cause de la sensibilité moins grande du mécanisme déclencheur. Pour la même raison, les souris immatures étaient capturées de façon disproportionnée dans les pièges à captures multiples. Ces artéfacts d'échantillonnage peuvent amener le chercheur à tirer des conclusions fausses concernant les associations quant à l'âge ou au sexe dans les captures multiples. Les erreurs dues aux pièges devraient donc être éprouvées explicitement avant l'analyse de données de captures multiples dans des pièges destinés à capturer un seul animal. Un modèle "socialement nul" de la rencontre aléatoire du même piège par deux souris s'ajuste à plusieurs des données présentées ici et il semble que ce soit là la meilleure hypothèse nulle à utiliser au cours de ces analyses. Lorsque des pièges propres à capturer les animaux vivants doivent être utilisés dans les études sur les comportements sociaux, il est préférable d'utiliser des pièges à captures multiples, préférablement du genre qui permet d'étudier les associations à long terme entre des individus.

[Traduit par la revue]

-glasses of animals trapped together in multiple-capture traps Was suggested by Davis (1955). Later, Getz (1961, 1972), Kalinowska (1971), Mihok (1979), and Reich and Tamarin (1984) expanded on the technique. A similar, but more indirect, method involved analysis of associations among animals within pairs of single-capture traps placed at the same station (Spencer et al. 1982). The degree of spatial association inferred from these studies may be overestimated, since animals are "baited" to a trap (see Van Horne 1982). In case of a double capture, there is no way to determine whether the two animals traveled to the trap together or at what proximity they would otherwise occur. In such cases, animals may occur together in a trap (or at a station) simply because they foraged in the same area (on a coarse-grained level) and detected the trap at some distance. Some investigators have gone a step further and posited that multiple captures occurring (usually at low frequencies) in single-capture traps could provide data on both the spatial and temporal components of these associations. Blaustein and Rothstein (1978), Spencer et al. (1982), and Verhagen and

Verheyen (1982) assumed that the capture of a pair of animals in a single-capture trap was an instantaneous event and therefore most or all pairs captured together (regardless of whether they were ever recaptured together) not only tolerated each other in the trap, but actually traveled to the trap in tandem. Contrary to these studies, Bergstrom and Sauer (1986) found that weight bias in single-capture traps precluded the inference of a temporal component to multiple captures (i.e., simultaneous capture, implying "social traveling"). Furthermore, out of 10 studies, only 1 (Petersen 1975) reported any incidents of specific pairs being recaptured in single-capture traps. This and the fact that several studies (Evans and Holdenried 1943; Dunaway 1968; Petersen 1975; this study) report substantial numbers of interspecific multiple captures argue against the utility of these data for resolving the specific question of social traveling or pair formation.

The present study illustrates how single-capture trap bias may produce spurious age and sex associations within multiple captures, given that simultaneous capture of the pair cannot be assumed. Data on 84 multiple captures involving Peromyscus maniculatus and P. difficilis, along with the results of several other published studies, are at least in part consistent with a "socially null" random encounter model of multiple captures. Conclusions about sex and age associations made in some of these studies are suspect because no trap bias was assumed.

Methods

Multiple captures of cricetid rodents were recorded during the summers (June through September) of 1982 through 1984 at several study areas within the Roosevelt National Forest, Larimer and Boulder counties, Colorado. Elevations of the sites ranged from 1800 to 2300 m. Vegetation was predominantly mixed ponderosa pine (*Pinus ponderosa*) – Douglas-fir (*Pseudotsuga menziesii*) forest, with open woodland – dry scrub habitat on south-facing slopes. *Peromyscus maniculataus* was widespread in this area and was more euryecious than *P. difficilis*. The two species were sympatric but largely allotopic in most study sites, with *P. difficilis* being more common on south-facing slopes and generally at lower elevations where the canopy was more open and the substrate rockier (B. J. Bergstrom, unpublished data). The trapping periods encompassed the active breeding seasons for both species of *Peromyscus* in this area as determined by this study, Halfpenny (1980), and Cinq-Mars and Brown (1969).

Trapping involved the use of Sherman live traps $(7.5 \times 7.5 \times 23.0 \text{ cm})$ baited with a mixture of rolled oats, scratch grain, and sunflower seeds, and provided with cotton nesting material. Animals were sexed, aged, and weighed. Following procedures explained in Bergstrom and Sauer (1986), during a portion of the last two field seasons, springing weights were measured for all traps involved in single or multiple captures as well as traps that had been disturbed (bait consumed) but remained open. Trapping grids covered a very large area and were operated on a rotating basis, so the effective population sampled was large, and as a result recaptures were not likely. Individual mice were not marked.

The distributions of trap springing weights were compared for four groups of traps, those that captured immature mice singly, adult mice singly, or two mice simultaneously, and disturbed but open (DBO) traps, using one-way ANOVA with Student-Newman-Keuls (SNK) multiple comparisons tests (Sokal and Rohlf 1981). DBO traps were open traps in which the bait had obviously been eaten, the cotton trampled, and (or) the treadle area covered with fresh droppings (traps were always cleaned and rebaited, and the cotton fluffed before setting). In other words, a mouse had completely entered the trap and remained in it for some time, yet managed to leave without springing the trap. Random association among sex and age classes in double captures (hypothesis 3: Slade 1976) as well as sex-age interactions were tested with G^2 log-likelihood ratio statistics using binomial probabilities to calculate expected values, since the population sampled was large (see Slade 1976). Both intrinsic (to the multiple captures) and extrinsic (from the single captures) estimates of sex- and age-ratio binomial parameters were used and their effects compared.

Results

Total captures of *Peromyscus maniculatus* equalled 1869, with 66 intraspecific double captures (3.53%), two intraspecific triple captures (each involving an adult female with two immatures), and six interspecific multiple captures, four of these with *P. difficilis. Peromyscus difficilis* was captured 618 times with 12 intraspecific double captures (1.94%).

To analyze whether variation in treadle sensitivity among traps affected the probability of single captures of animals of different weights (hypothesis 1: Slade 1976), I regressed the weights of *P. maniculatus* from 102 single captures on trap springing weight (see Bergstrom and Sauer 1986) (Fig. 1). The slope of the regression line is significantly greater than 0 (P <0.01), while an even stronger effect (P < 0.001) is shown by regressing minimum animal weights within groups of the predictor variable. This is because mice of all weights were able to be captured by the most sensitive traps, whereas only heavier



FIG. 1. Animal weight versus minimum springing weight of trap for a sample of 102 single captures of *Peromyscus maniculatus*. Because of inconstant error variances, regression line displayed is only for the minimum animal weight in each of nine categories of springing weight (i.e., only for the solid circles). For that regression: Y = 7.83 + 0.284X, $R^2 = 92.1\%$. See text for further explanations.

mice were captured in less sensitive traps; hence error variances were not constant. Since lighter animals are mostly immatures, this bias means that immature mice will be underrepresented in the live-trapping sample. A comparison of springing weights for different capture classes (Table 1) further shows this to be the case, and also demonstrates that double captures in this study occurred in traps that were significantly less sensitive than traps that captured single mice. As expected, the DBO traps had springing weights that were much greater than the weight of an average deer mouse (18.1 g). Mean springing weights of all categories (Fig. 1) were significantly different (F = 50.30, P < 0.001; SNK tests, all P < 0.05).

Age categories of *P. maniculatus* were defined by body weight: immature mice weighed 16 g or less (only two actual adults were misclassified by this technique). Among single captures, the proportion of adults was 0.520, whereas the proportion of adults was only 0.468 among double captures. Indeed, the lighter immature mice were more prone to be involved in multiple captures. The proportion of males did not vary between single captures (0.429) and double captures (0.440).

The data for those double captures of *P. maniculatus* that could be cross-classified by both sex and age are presented in Table 2. A test of quasi-independence was performed after expected values were generated by iterative proportional fitting (IPF) (Fienberg 1977). Although the overall association among age and sex classes is nonsignificant ($G^2 = 6.65$, df = 3, P = 0.084), this obscures (because of the marginal constraints imposed by cells 1,1 and 4,4) an interesting relationship in the upper 2 × 2 subtable ($G^2 = 4.63$, df = 1, P < 0.05). Immatures of different sexes occurred together more often than expected, as did adults of different sexes, whereas adult female – immature male (the most prevalent combination in Getz's (1972) study) and adult male – immature female combinations occurred less often than expected.

As Getz (1972) and later investigators have done, it is of interest to collapse on the sex and age variables to analyze

 TABLE 1. Distributions of minimum springing weights of traps involved in a variety of capture situations in a study of *Peromyscus* maniculatus

	N	$\bar{X}(g)$	SD
Immature mice, single captures	40	16.62	7.88
Adult mice, single captures	49	21.63	10.87
All double captures	32	26.39	15.54
Disturbed but open (DBO)	28	53.75	16.81

 TABLE 2. Double captures of Peromyscus maniculatus cross-classified by sex and age

	Female		Male	
	Adult	Immature	Adult	Immature
Female				
Adult	6	11	7	5
Immature		5	2	10
Male				
Adult			1	4
Immature				5

NOTE: Total captures = 56.

 TABLE 3. Double captures of Peromyscus maniculatus presented in a complete contingency table designed to analyze the associative structure of the sex and age variables

	A–A	I–I	A –]
F-F	6	5	11
M–M	1	5	4
M-F	7	10	7

NOTE: Cell 3,3 combines cells 1,4 and 2,3 from Table 2. M, male; F, female; A, adult; I, immature. Total double captures = 56.

associations within each of these variables among the double captures. These single classification tests are valid when sex and age are independent in the data. Unfortunately, because of the uncertainty in assigning the off-diagonal cells, a 2×2 test of independence (Sokal and Rohlf 1981) between sex and age has zero degrees of freedom. A complete table can be constructed, however, to test for independence between three pairing types of sex and three pairing types of age (Table 3). Overall, there was no significant associative structure ($G^2 = 4.58$, P = 0.33, expected values via IPF), which means that sex and age were independent and single classification tests are meaningful. The observed values for these tests are equivalent to the row and column marginals, respectively, of Table 3. There was no significant departure of any sex pairing category from that expected by random encounter of animals (Table 4A). A significant deficit of adult-immature pairs was observed (Table 4B); the biological significance of this negative association is clouded by the inherent confounding of age with weight and the demonstrated effect of weight bias on the occurrence of multiple captures. When age-ratio estimates were obtained from single captures, a significant excess of immature pairs was observed (Table 4B). Recall that the age-ratio parameter estimate varied substantially depending on whether single or double captures

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(A) Single-classification test of sex association within double captures of *Peromyscus maniculatus* in Sherman traps

			$(Obs Exp.)^2$
	Obs.	Exp.	Exp.
F–F	22	19.4	0.35
M-F	25	30.6	1.01
M-M	15	12.0	0.75
Total	62	62.0	
	$\chi^2 = 2.1$	1, P > 0.1	

(B) Single-classification tests of age association within double capture
pairs of P. maniculatus, using expected values generated from single
captures (extrinsic) and double captures (intrinsic)

	Intrinsic			Extrinsic	
	Obs.	Exp.	$\frac{(\text{Obs.} - \text{Exp.})^2}{\text{Exp.}}$	Exp.	$\frac{(\text{Obs.} - \text{Exp.})^2}{\text{Exp.}}$
 A–A	19	13.8	1.96	17.0	0.24
A–I	21	31.4	3.44	31.4	3.44
I–I	23	17.8	1.52	14.5	4.98
Total	63 X	63.0 $x^2 = 6.92$	2, $P < 0.01$	$ \begin{array}{l} 62.9\\ \chi^2 = 8 \end{array} $	8.66, P < 0.005

NOTE: F, female; M, male; A, adult; I, immature.

were used as the sample; this probably resulted from the weight bias and variable sensitivity of the traps. However, the presumed reason why immature (lighter) animals might be disproportionately sampled in double captures pertains only to the first animal to enter the trap uncaptured (following the scenario of random, sequential encounter discussed by Bergstrom and Sauer (1986)). The second animal into the trap (which hypothetically causes its closure) is not as likely to be an immature as was the first but should conform in probability to the true age proportion in the population. Thus, the most accurate binomial age-ratio estimate for generating expected values lies somewhere between the intrinsic and extrinsic estimates.

Discussion

Conclusions about social structure in rodents from multiple capture studies employing single-capture traps are suspect because of the biases introduced by the variably insensitive tripping mechanism (Bergstrom and Sauer 1986; this study). A disproportionate occurrence of immature mice in multiple captures may appear to be a significant result in a test of social causes of multiple trappability (hypothesis 2: Slade 1976), yet this result can be explained merely by a bias in the mechanism (Table 1). Few studies have analyzed animal age or weight as a variable. Novak (1983) and Jenkins and Llewellyn (1981) found no difference in the age distributions between single and double captures; however, this result did not demonstrate "social traveling," because multiple captures may have occurred in traps with greater springing weights than traps that captured single mice, both groups of mice having the same weight distributions. Feldhamer (1977) did find that disproportionately lighter P. maniculatus occurred in multiple captures, yet he wrongly concluded that multiply captured *Microtus montanus*

must have entered simultaneously because there was no weight difference. Blaustein and Rothstein (1978) performed a laboratory test of the trappability of a small sample of their traps and concluded that trap bias was not important; actually 16% of these traps failed to spring after one animal entered, whereas 20% of their captures in the field were multiple. Notwithstanding the similarity of these two proportions, even if none of the traps failed to spring in the lab, the experiment was inconclusive, since it was not done blind and it was possible for the investigators to have inadvertently adjusted the treadles more delicately than under less amenable field conditions. Furthermore, exposure to the weather can decrease the treadle's sensitivity even if the trap has been carefully set to begin with (personal observation).

For those studies that only examined association by sex (e.g., Spencer et al. 1982; Petersen 1975), age (or weight) may have confounded the interpretation if there were significant interactions between age and sex. This interaction effect may appear to yield significant sex associations which actually have only "hitchhiked" along with the age-weight variable. When age and sex are found to be independent in the data set, sex associations in multiple captures are meaningful (e.g. Jenkins and Llewellyn 1981); however, they should only be interpreted as implying social tolerance or repulsion (sensu Davis 1955), since simultaneous entry can only reasonably be inferred after analysis of weight distributions of animals and traps (as Table 1) proves nonsignificant.

To approach the problem of age-sex dependency, two studies have employed log-linear analysis of three-way contingency tables. Jenkins and Llewellyn's (1981) analysis tested only tendencies for classes to be involved in multiple captures, and not associations between classes. Novak's (1983) use of the technique was invalid because he counted individuals (28), when the basic units appropriate for analysis were multiple captures themselves (14). For example, as long as we have no way of distinguishing adult male – immature female from immature female - adult male (by knowing which animal entered the trap first), this particular double capture is only one event. By adding an artificial "pairing type" variable, the event is arbitrarily split and the sample size artificially doubled without any increase in information. The same questions can be addressed validly by an analysis of the associative structure of Table 3, and if the variables are independent, by singleclassification goodness of fit tests for each variable separately.

In this study, significant effects between certain sex-age categories were found within the subtables of Table 1. Several other studies have reported positive association between the sexes in multiple captures of various cricetids (Dunaway 1968; Petersen 1975; Blaustein and Rothstein 1978; Spencer et al. 1982). Mihok (1979), Getz (1961, 1972), Getz et al. (1981), and Reich and Tamarin (1984) reported more complex associations involving sex and reproductive status. Both Sheppe's (1967) and Feldhamer's (1977) reported associations had insufficient sample sizes for valid chi-square analysis (see Cochran 1954), while Montgomery's (1979) chi-square test was improperly performed (for sex association in *Apodemus sylvaticus*, he reports $\chi^2 = 6.99$, but actually $\chi^2 = 0.22$).

Multiple captures in Sherman and Longworth traps are generally low frequency events, ranging from 0.47 (Spencer et al. 1982) to 20% (Blaustein and Rothstein 1978). The frequencies generally are lower for Longworth traps, which are designed to be more sensitive than Shermans (see Chitty and Kempson 1949). Multiple capture frequencies for Young's traps, which are much larger and relatively insensitive, range from 13 to 43% among nine species (Evans and Holdenried 1943).

The confounding effect of trap bias on the analysis of associations in multiple captures suggests that a null hypothesis of the causes of multiple captures in single-capture traps needs to be developed. There is considerable evidence, reviewed below, that animal size and population density affect the probability and composition of such multiple captures.

Animal size—In this study and Feldhamer's (1977), lightweight P. maniculatus were disproportionately sampled in double captures. This may explain the preponderance of I-I (immature-immature) pairs found by Sheppe (1967), Montgomery (1979), and Verhagen and Verheyen (1982), and implicated in this study. Jenkins and Llewewllyn (1981) concluded that the lower frequency of multiple captures for P. truei (compared with P. maniculatus) could most easily be explained by its larger size. Similarly, in this study, P. maniculatus (avg. wt. 18.1 ± 4.0 g) was involved in multiple captures 1.8 times as frequently as P. difficilis (avg. wt. 25.9 ± 7.3 g). In Petersen's (1975) study, of the 17 species trapped, 6 of the 7 lightest were involved in multiple captures, and by far the most multiple captures occurred in the lightest species (Baiomys taylori). The second lightest, Perognathus flavus, was not involved in multiple captures but occurred at very low densities. From Evans and Holdenried's (1943) data on nine species, there is a significant negative rank correlation (P < 0.05) between size rank and multiple capture frequency.

Population density—Petersen (1975), Blaustein and Rothstein (1978), and Jenkins and Llewellyn (1981) all reported significant positive correlations between population density and multiple capture frequency. Although density changes often correspond with certain transitions in the population's breeding cycle which may account for changes in pair formation and social tolerance, this result is consistent with the "socially null" model of random encounter.

Finally, the case of interspecific multiple captures supports the null model. In this study, one-third of P. difficilis' multiple captures were interspecific with P. maniculatus. Evans and Holdenreid (1943) reported that 41 of their 88 multiple captures among nine species were interspecific. Dunaway (1968) and Petersen (1975) also reported substantial numbers of interspecific captures, involving four and three species, respectively. If animals trapped together are not socially bonded, evidence for huddling groups cited by Novak (1983) seems a plausible explanation for the amicability displayed between partners in multiple captures. This study found only one case of death (one P. maniculatus was partially consumed by another, but cause of death was unknown) and no other injuries out of 84 multiple captures, including interspecific captures. Four other studies have reported a low incidence of fighting and deaths within multiple captures (Duanway 1968; Feldhamer 1977; Spencer et al. 1982; Verhagen and Verheyen 1982). Evans and Holdenried (1943) reported roughly half of their double captures of a variety of species resulted in one of both animals dying. Though unstated, it is possible that these deaths resulted from exposure.

Only in the unlikely event that animal size and population density can be controlled for, that trap bias can explicitly be ruled out, and that age and sex are found to be independent, can comparisons be made between species, or between studies using the same procedures, concerning relative sociality of individuals in the population cross-classified by age and sex. This perhaps applies to Petersen's (1975) and Blaustein and Rothstein's (1978) results on frequency of multiple captures of Reithrodontomys megalotis. The present study and Bergstrom and Sauer (1986) have shown that the factors potentially biasing this type of analysis cannot be assumed away. Beyond this, it seems that the repeated recapture of specific pairs of animals (as Getz, 1972 suggested) is necessary for the presentation of a strong case for multiple-capture associations resulting from social behavior. The use of actual multiple-capture traps can better address this question, and in general is preferred when asking questions about social tolerance or avoidance among classes in a population.

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