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MULTIPLE CAPTURES OF *PEROMYSCUS LEUCOPUS:* SOCIAL BEHAVIOR IN A SMALL RODENT

The capture of more than one individual in a live trap can often provide information on the social behavior of small mammals, but the conclusions drawn from these data will depend on the type of live trap used. Davis (1955) and Getz (1972) used multiple capture traps and analyzed their data with respect to attraction and repulsion of individuals both within and between different age and sex classes. Petersen (1975), Feldhamer (1977), Blaustein and Rothstein (1978), Jenkins and Llewellyn (1981) and Spencer et al. (1982) gained information on the formation of associations during foraging and dispersal from multiple captures made in single capture traps. Other studies have included anecdotal information on multiple captures but have not analyzed the data rigorously enough to shed light on the social organization of the species involved.

This paper reports multiple captures of *Peromyscus leucopus*, a species for which multiple capture data have not previously been analyzed in the literature. The results are then related to previous studies on multiple captures of cricetines.

METHODS

Livetrapping took place in Robert Allerton Park, 7 km SW Monticello, Piatt Co., Illinois. The habitat consisted of virgin upland and floodplain deciduous forest dominated by red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) in the upland and green ash (*Fraxinus pennsylvanicus*) and silver maple (*A. saccharinum*) in the floodplain.

Two 3.1-ha trapping grids were established, one in each habitat, each consisting of 77 Longworth live traps located at 20 m intervals. Traps were baited with cracked corn, supplied with cotton, and placed in protective cages (Getz and Batzli, 1974). Traps were prebaited 1 day and trapped the following 3 days every 3 weeks from December 1980 through June 1981. Animals captured were marked with a numbered monel fish fingerling tag, and the trap location, sex, weight, and reproductive condition were recorded for all captures. Age was estimated from weight as described by Novak (1981).

Multiple capture frequency and the type of pairing (homosexual or heterosexual) were analyzed using log-linear three-dimensional contingency table analysis incorporating age and sex as the other two variables. The advantages of this approach have been listed by Jenkins and Llewellyn (1981). One need not assume independence of the variables age and sex, and one can then examine the dependence of any variable on age and sex, singly or together, after removing any association between age and sex in the population. Two separate three-dimensional analyses were performed since a four-dimensional analysis would have resulted in an excessive number of empty cells.

RESULTS

Individuals involved in 14 multiple captures (20 individual mice, eight recaptures) are arranged according to age, sex, and pairing type in Table 1. Overall there were 1833 captures on both grids, with an overall multiple capture frequency of 0.015 for *P. leucopus*.

To make valid statements about the tendency of mice to travel in pairs it must be shown that the mice entered the traps at approximately the same time. For a multiple capture to occur in a single capture trap, one of two things could have happened. Either the mice entered the trap at the same time or one mouse entered the trap without springing it, a second mouse entered later, and then the trap was activated. If the mice first entering the traps were too light to spring the trap, then (assuming all traps are equally sensitive) the average weight of the lighter member of each pair should differ from the average weight of adult and subadult mice caught in single captures, which was not the case ($t = 1.49$, $P > 0.10$).

Multiple capture frequency depended on both age and sex as shown by significant two-way interactions ($G = 13.58$, $P < 0.001$ and $G = 9.30$, $P < 0.005$, respectively). A complex interrelationship among all three variables was shown by the significant three-way interaction ($G = 15.84$, $P < 0.001$). Since the sex ratio during all trapping periods did not differ from parity (Novak, 1981), male and female adults were about equally prone to multiple capture but male subadults were much more likely to be involved in multiple captures than female subadults. Age-sex interaction was not significant ($G = 2.00$, $P > 0.10$). None of the hierarchical models fit the data adequately except the one incorporating all two-way interactions and the three-way interaction between all variables.

TABLE 1.—*Number and frequency of multiple captures of* Peromyscus leucopus *in age, sex, and pair type.*

Sex	Age	Pair[1] type	N individuals	Multiple capture frequency[2]
Male	Adult	Ho	3	0.014
Male	Adult	He	9	
Male	Subadult	Ho	5	0.042
Male	Subadult	He	1	
Female	Adult	Ho	0	0.015
Female	Adult	He	9	
Female	Subadult	Ho	0	0.004
Female	Subadult	He	1	

[1] Ho-homosexual, He-heterosexual.

[2] [2 × (# double captures)]/[# single captures + 2 × (# double captures)].

The type of pairing in multiple captures depended on both the age and sex of the animals as shown by the significant two-way interactions ($G = 5.81$, $P < 0.025$ and $G = 8.82$, $P < 0.025$, respectively). More females and adults were involved in heterosexual pairings whereas more males and subadults were involved in homosexual pairings than expected based on the population sex-age structure. The age-sex interaction was not significant ($G = 2.00$, $P > 0.10$). A three-way interaction model could not be fitted since one of the marginal totals was zero and therefore a degree of freedom is lost (Fienberg, 1970). None of the models fit the data adequately except the one incorporating the three two-way interactions.

No correlation was found between either the number of multiple captures or percent multiple captures and population density, using the pooled data from both grids ($r = 0.47$, $P > 0.20$ and $r = 0.16$, $P > 0.50$, respectively). However, population densities on the grids do not share a common temporal pattern (Novak, 1981), and therefore data from each grid were analyzed separately. No significant correlation was found for the floodplain grid between either the number of multiple captures ($r = 0.46$, $P > 0.20$) or the percent multiple captures ($r = 0.34$, $P > 0.20$) and population density. On the upland grid a significant negative correlation was found for the number and percent of multiple captures and population density ($r = -0.73$, $P < 0.05$ and $r = -0.86$, $P < 0.005$, respectively). However, the fact that no multiple captures were recorded for seven of the nine sampling periods tends to weight the correlation more heavily toward the two outlying values and casts doubt upon the biological significance of the correlation (Draper and Smith, 1966: 94).

There were significantly fewer multiple captures during the breeding as compared to the nonbreeding season (normal approximation of the binomial test, $z = 2.95$, $P < 0.005$). The pattern of pairing that emerges is as follows (numbers in parentheses represent the number of described pairs compared to all pairs caught during the time period): at the beginning of the nonbreeding season all multiple captures consisted of male-adult/male-subadult pairs (2:2). As the nonbreeding season progressed, the frequency of multiple captures increased and consisted largely of adult heterosexual pairs (7:9, 1 pair MS-MS, 1 pair MS-MA). At the inception of the breeding season, only adult heterosexual pairs were captured (3:3). As the breeding season progressed and juveniles appeared in the population, the number of multiple captures fell to zero.

DISCUSSION

Although the results suggested that mice involved in multiple captures entered the traps at approximately the same time, this does not necessarily mean that they were travelling together. Because multiple captures are low frequency events, it is possible that the multiple captures were due to random encounters. If the encounters were random, then the age-sex distribution of animals involved in multiple captures should not differ from the age-sex distribution of all adult and subadult animals involved in single captures at the time the multiple captures occurred, which was not the case ($G = 11.96$, $P < 0.01$).

Jenkins and Llewellyn (1981) warned that differences in weight between mice in different age-sex groups can lead to erroneous conclusions. Because males and females of equal age did not differ significantly in weight ($t = 0.70$, $P > 0.20$ for subadults and $t = 1.63$, $P > 0.05$ for adults), differences in multiple capture frequency and pairing type between sexes were not affected by weight. However, age differences were confounded with weight, since an individual's age was determined by its weight. If weight were responsible for the differences between mice of different ages then the proportion of subadults to adults involved in multiple captures should be significantly greater than the proportion of subadults to adults involved in single captures, which was not the case ($G = 0.002$, $P > 0.95$). Therefore, the age-sex differences in multiple capture frequency and pairing type are real and are not artifacts of weight differences between mice in different groups.

If it is postulated that like-sex adult-adult and adult-subadult pairs display more agonistic behavior than like-sex subadult-subadult and heterosexual (outside the breeding season) pairs (Burt, 1940), then the temporal pattern of pairing and the results of the contingency table analyses are readily understood. The proportion of adults in the population increased from 57% at the beginning of the non-breeding season to 100% during the early stages of the breeding season (Novak, 1981). Therefore, a trend of increasing frequency of heterosexual pairing is expected as time progresses from the inception of the non-breeding season. Furthermore, female *P. leucopus* with litters are known to be aggressive toward males (Burt, 1940; Nicholson, 1941), and therefore proportionately fewer multiple captures are expected during the breeding season. More *Reithrodontomys megalotis* were involved in multiple captures during the non-breeding season in California (Blaustein and Rothstein, 1978) but not in Mexico where the reverse was true (Petersen, 1975). More multiple captures also occurred during the breeding season for *Baiomys taylori* (Petersen, 1975) and *R. humulis* (Dunaway, 1968), whereas no significant difference in the proportions of multiple captures between the breeding and non-breeding seasons could be detected in *Peromyscus maniculatus* (Jenkins and Llewellyn, 1981). The differences between species and within species in different habitats could reflect different degrees of sociality, differences in sampling, or stochastic differences.

Individuals involved in multiple captures more than once usually were caught with two different individuals which suggests that any pairing is temporary and would not lead to the establishment of monogamy as in *R. megalotis* (Blaustein and Rothstein, 1978) or *Peromyscus polionotus* (Blair, 1951; Foltz, 1980). As pairing was proportionately more common in the non-breeding season, the most likely possible benefits would be increased foraging efficiency, increased predator detection or escape probability, increased thermoregulatory efficiency by huddling (Vogt, 1981), or a combination of the three. The pair switching indicated by the recapture results is consistent with Vogt's (1981) studies on the use of torpor and huddling by *P. leucopus* during cold weather to prevent heat loss. Animals in huddling groups showed a staggered pattern of arousal from torpor which could account for the pair switching shown by the recapture results. All of the above benefits are not sex-specific and thus the actual sexual composition of pairs would be determined by the temporal changes in the agonistic behavior of individuals within and between age-sex classes.

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INGESTION OF MOLDY SEEDS BY HETEROMYID RODENTS

Heteromyid rodents are primarily granivorous (Reichman, 1975) and some species store large quantities of seeds in their burrows or in surface caches (Vorhies and Taylor, 1922; Shaw, 1934; Hawbreker, 1940). Seeds gathered have usually been inoculated with an array of soil fungi (primarily of the group Fungi Imperfecti), the spores of which are in soil, and the rodents' cheek pouches and burrows. Nineteen species of fungi of the genera *Aspergillus*, *Penicillium*, and *Rhizopus* have been isolated from the cheek pouches of *Dipodomys merriami* (D. T. Wicklow, pers. comm.). If the seeds are subsequently placed in the rodents' burrows for storage, the fungi are exposed to conditions ideal for growth and mycotoxin production (approximately 27° C and 100% relative humidity; Kay and Whitford, 1978). The molds found in association with the rodents and their seeds produce both beneficial and detrimental products. Some of the potential benefits (e.g., increased nutrition) of the fungal products accrue only after the fungi have grown on the seeds for some time and altered their chemical make-up. Conversely, other chemicals produced by the fungi are advantageous in low concentrations, but become toxic in high doses (see Ciegler and Bennett, 1980).

Because we have found moldy seeds and their toxic products in heteromyid burrows, we designed an experiment to determine if a heteromyid rodent, *Perognathus intermedius*, would ingest moldy seeds. We hypothesized that these rodents should prefer slightly moldy seeds over unmoldy controls and over very moldy seeds because intermediate stages of fungal infection are most likely to produce some beneficial products without having developed harmful mycotoxins.

Sixteen *P. intermedius* (average weight = 16.5 g), trapped on the Jornada Experimental Range near Las Cruces, New Mexico, were used to test seed preferences. The mice were housed in 20-l glass terraria and maintained under a 12L:12D cycle. *Panicum virgatum* seeds, which are known to be eaten by heteromyids (Reichman, 1978) were used in the feeding experiment. The seeds, donated by the Manhattan, Kansas Soil Conservation Service Plant Materials Center, were dusted with desert soil from Portal, Arizona, to inoculate them with fungal spores associated with typical heteromyid habitat. Burrow conditions were simulated by incubating packets of seeds (1.25 g) in a growth chamber at 30°C, and 100% RH. Stages of mold colonization were achieved by staggering incubations so that at the time of feeding each rodent was offered seeds incubated for 0 (control), 8, 11, and 15 days. Preliminary studies indicated these time periods reflected important developmental stages of fungal activity. Generally, 0 day seeds were dry while 8 day seeds were imbibed and sticky with the onset of fungal growth. Eleven day seeds exhibited substantial hyphal growth and the start of conidia development, and 15 day seeds attained maximal hyphal growth and conidia development. Seeds were stained four colors with vital dyes (red, brown, yellow, and green) to distinguish incubation times. A 4 by 4 Latin Square (colors = rows, columns = animals) with incubation times as treatments was repeated over the four shelves on which the rodents' terraria were placed. This yielded an experimental design in which color was rotated among incubation times to control for effects of different dyes. To control for shelf position the Latin Square design was repeated on each of the four vertically displaced shelves on which the animals were kept.

For 3 days preceding the feeding trial, the mice were fed 1.25 g each of 0, 8, 11, and 15 day seeds placed in a single, mixed pile to familiarize them with the different seed conditions. After the 3 days of prefeeding, the rodents were starved for 24 h and offered 1.25 g (dry weight) of each of the four groups of seeds. Each group was placed in a separate pile. *P. intermedius* require 1.75 g/d of *P. virgatum*, as determined by a weight based metabolic formula in Morton et al., (1980) and the average cal/g of the grass seed. By offering less than the minimum daily requirement of seed for each incubation time, each rodent was forced to make