

Social dynamics and multiple capture trap associations of Meadow voles (*Microtus pennsylvanicus*)

By L. M. REICH and R. H. TAMARIN

Boston University, Department of Biology, Boston, Mass. USA

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Abstract

Presented is an inferential method for studying social behavioral relationships based on the examination of short-term variations in multiple-capture live-trap association patterns. This method is applied to a population of meadow voles (*Microtus pennsylvanicus*) in Massachusetts, and entails assigning variables which describe tendencies towards positive or negative and stable or unstable social associations. A higher level of social stability was shown by females as compared to males and by adults and subadults as compared to juveniles. Of all groups, reproductive females exhibited the highest level of social stability, and reproductive males the lowest. Reproductive females also exhibited the greatest tendency towards negative associations. Months of increasing population density were characterized by a tendency towards positive associations, while months of declining population density did not show these tendencies. These observations provide support for models of female territoriality, and are consistent with behavioral models of population regulation in voles.

Introduction

Studies of the social behavior of free-ranging rodents have frequently employed information gleaned from multiple-capture live-trapping. Implications of multiple capture trapping for various aspects of social structure have been made by GETZ (1972) and REICH and TAMARIN (1984) for *Microtus pennsylvanicus*, BLAUSTEIN and ROTHSTEIN (1978) for *Reithrodontomys megalotis*, VERHAGEN and VERHEYEN (1982) for *Apodemus sylvaticus* and *Clethrionomys glareolus*, and JENKINS and LLEWELLYN (1981) for *Peromyscus maniculatus* and *P. truei*, to cite just a few examples. DAVIS (1955), and others following him, used multiple capture trapping as an inferential method of describing social behavior on an individual level, the assumption being made that an animal which tends to be captured singly is exhibiting a relative tendency towards avoidance of others, as compared to one which tends to be captured in groups of two or more individuals, which is thereby exhibiting a relative tendency towards attraction to others. In the present paper, we extend this paradigm to the population level and examine it dynamically. We look at population-wide trends in single-capture versus multiple-capture trapping, with reference to short-term changes in these patterns as indicators of social dynamics. This analysis was applied to a population of meadow voles (*Microtus pennsylvanicus*) which was undergoing fluctuations in population density over a period of two and a half years.

The entry of an individual vole into a trap is an event which is influenced by diverse factors, many of which relate to behavioral characteristics of that individual. The effect of conspecific odor on trap-entry is well known (for example, STODDART 1982), and other means of communication between animals inside and outside a trap can also influence trap-entry. The present analysis looks at patterns of trap-entry on the population level, and offers an interpretation which attributes these patterns to social factors.

Materials and methods

The study area was a 2.4 hectare field located at the Broadmoor/Little Pond Wildlife Sanctuary in South Natick, Massachusetts, USA. The field, a grass meadow bordering on mixed woodland, was divided into four trapping grids by a corrugated galvanized steel vole-proof fence (TAMARIN et al., in press). Each grid consisted of 100 trap stations, with a distance between trap stations along a line and the distance between lines of 7.6 meters.

A Ketch-All multiple capture live trap (Kness Manufacturing Co., Albia, Iowa, USA) was placed at each trap station. These traps were very effective in capturing meadow voles in multiple capture groups. The traps are constructed in such a way as to permit some degree of olfactory, auditory, tactile, and visual contact between individuals inside the trap and individuals outside the trap. All traps were set once each month (one trapping period), baited with oats and provided with cotton for nest material, and checked over a two-day period. All voles captured were individually marked with numbered ear tags and released at their point of capture after data on sex, reproductive condition, and weight were collected. Reproductive condition was assessed by testes position in males, and vaginal patency and amount of lactation tissue around the nipples in females (TAMARIN et al., in press). Age classes (adult, subadult, or juvenile) were determined by weight according to the criteria of KREBS et al. (1969).

During the 30 months of this study (September 1979 to March 1982), the vole population, as is typical for this species, was undergoing dramatic fluctuations in population density, exhibiting two spring declines (1980 and 1981) to troughs of approximately 10–15 voles per 0.6 hectare grid, followed by increases to peaks of approximately 150 voles per grid. No demographic "crash" (KREBS and MYERS 1974) occurred during the study period, but a "crash" was recorded subsequent to the study, in the spring of 1982. A full description of the demography of the population may be found in TAMARIN et al. (in press).

Voies were classified according to the size of their capture group, defined as the total number of conspecific individuals captured in the trap in that trap-check. Trap co-occurrences of voles with other rodent species were rare, and were excluded from the present analyses. Since each trapping period consisted of two trap-checks, a vole captured on the two successive trapnights would be classified with two capture group size values for that trapping period.

We analyzed short-term population variations in capture group size displayed by individuals captured on both nights of a trapping period. All instances of an individual being captured on both nights of a trapping period were isolated, and the size of the capture groups on those two nights were compared. Three variables, designated A, B, and C, were defined to describe the relationship of capture group sizes on these two nights (Table 1).

Variable A was used to describe whether a vole was captured in groups of the same size or of different sizes on the two successive trapnights. A vole was assigned a value of $A = 1$ if it was captured in groups of different sizes on the two trapnights, and a value of $A = 2$ if it was captured in groups of the same size on the two trapnights. If a vole was captured in groups of different sizes on the two trapnights ($A = 1$), then it was assigned a value of Variable B which differentiated between those voles captured in a smaller group ($B = 1$) and those captured in a larger group ($B = 2$) on the second of the two trapnights. If a vole was captured in groups of the same size on two successive trapnights ($A = 2$),

Table 1

Definitions of variables used to describe the relationship of capture group sizes displayed by a vole caught on successive trapnights

Variable	Value	Meaning
A	1	Vole is captured in groups of different sizes
	2	Vole is captured in groups of the same size
B (A = 1)	1	Vole is captured in smaller groups on second night
	2	Vole is captured in larger groups on second night
C (A = 2)	1	Vole is captured individually on both nights
	2	Vole is captured in pair groups on both nights
	3	Vole is captured in groups of three or larger on both nights

then it was assigned a value of Variable C, which described the level at which the capture group size was remaining constant. A value of $C = 1$ was assigned to a vole if it was captured individually on two successive trapnights, $C = 2$ if it was captured in a group of two individuals on the two trapnights, and $C = 3$ if it was captured in a group of three or more individuals on the two trapnights. For voles classified as $C = 2$ or $C = 3$, the individual identity of the other vole or voles was not considered.

Analyses involved comparing the distribution of voles based on sex, reproductive condition, and age class in categories described by these three variables by X^2 contingency table analysis. In addition, data were compared between months of population increase and months of population decline.

Results

In the two and a half years of this study, 6,513 meadow vole captures were recorded.

Variable A differentiates between voles captured in same-size groups and those captured in different-size groups on two successive trapnights. Overall, 68.2 % of the voles captured on both nights of a trapping period were captured in a different size group on the second night (Table 2). This tendency was significantly greater in males than it was in females, but reproductives and non-reproductives did not differ from each other. Juveniles were much less likely than adults or subadults to be captured in the same size capture group on two successive trapnights. Of the four groups (reproductive and non-reproductive males and females), reproductive females had the highest tendency to be captured in a group of the

Table 2

Occurrence of variable A in different classes of voles and the results of contingency table analysis
Percentages are given in parentheses

Group	A = 1	A = 2	X^2
Overall			
Males	621 (70.6)	259 (29.4)	4.34*
Females	590 (65.8)	306 (34.2)	
Reproductives	657 (67.4)	318 (32.6)	0.53
Non-reproductives	555 (69.1)	248 (30.9)	
Adults	620 (65.3)	330 (34.7)	18.9***
Subadults	431 (68.5)	198 (31.5)	
Juveniles	145 (81.5)	33 (18.5)	
Months of increase			
Males	300 (73.0)	111 (27.0)	4.05*
Females	328 (66.8)	163 (33.2)	
Reproductives	386 (66.8)	192 (33.2)	6.28*
Non-reproductives	243 (74.8)	82 (25.2)	
Adults	322 (64.7)	176 (35.3)	16.67***
Subadults	180 (72.2)	69 (27.7)	
Juveniles	117 (81.8)	26 (18.2)	
Months of decline			
Males	187 (64.0)	105 (36.0)	0.24
Females	160 (62.0)	98 (38.0)	
Reproductives	142 (64.8)	77 (35.2)	0.54
Non-reproductives	205 (61.7)	127 (38.3)	
Adults	185 (64.0)	104 (36.0)	0.62
Subadults	151 (61.4)	95 (36.6)	
Juveniles	9 (69.2)	4 (30.8)	

* $p < 0.05$; ** $p < 0.001$.

same size on two successive trapnights. Thirty-seven percent of reproductive females were so captured, compared to about 30 % for the other three groups, and this difference was significant ($X^2 = 10.91$, $p < 0.05$).

The pattern obtained in the months of increase is similar to the overall pattern, except that in months of increase non-reproductive voles showed a greater tendency than reproductive voles to be captured in a different size group on two successive trapnights. However, a sharp contrast to the overall pattern was seen for voles in months of population decline, where no significant differences in the distribution of Variable A based on sex, reproductive condition, or age class, were found.

It should be noted that the total number of individuals captured during months of population increase exceeds the number of individuals captured during months of decline. This is due to the fact that the months of increase include a few months of peak density, and the months of decline a few months of low density. Because of this, it is not possible to directly compare trends in these variables between these demographic periods, since the variables are related to population size (the chance of catching larger groups increases with higher population density, since the density of traps was constant). Rather than making a direct comparison, the two demographic periods are compared by looking at the differential distribution of the variables among the sex, reproductive and age groups within months of increase and months of decline.

Variable B differentiates between voles captured in a larger or smaller group on the

Table 3

Occurrence of variable B in different classes of voles and the results of contingency table analysis
Percentages are given in parentheses

Group	B = 1	B = 2	X^2
Overall			
Males	363 (58.5)	258 (41.5)	3.37
Females	313 (53.1)	277 (46.9)	
Reproductives	379 (57.7)	278 (42.3)	1.79
Non-reproductives	298 (53.7)	257 (46.3)	
Adults	364 (58.7)	256 (41.3)	14.63***
Subadults	246 (57.1)	185 (42.9)	
Juveniles	60 (41.4)	85 (58.6)	
Months of increase			
Males	169 (56.3)	131 (43.7)	1.46
Females	169 (51.5)	159 (48.5)	
Reproductives	211 (54.7)	175 (45.3)	0.24
Non-reproductives	128 (52.7)	115 (47.3)	
Adults	186 (57.8)	136 (42.2)	7.89*
Subadults	99 (55.0)	81 (45.0)	
Juveniles	50 (42.7)	67 (57.3)	
Months of decline			
Males	109 (58.3)	78 (41.7)	0.25
Females	89 (55.6)	71 (44.4)	
Reproductives	87 (61.3)	55 (38.7)	1.74
Non-reproductives	111 (54.1)	94 (45.9)	
Adults	113 (61.1)	72 (38.9)	2.94
Subadults	79 (52.3)	72 (47.7)	
Juveniles	6 (66.7)	3 (33.3)	

* $p < 0.05$; *** $p < 0.001$.

second of two successive trapnights. Overall, 55.8 % of voles captured on both nights of a trapping period were captured in a group of smaller size on the second of the two nights (Table 3). There were no significant differences based on sex or reproductive condition, but juveniles were more likely than adults or subadults to be captured in a larger group on the second trapnight. The same pattern was obtained when only voles from months of population increase were considered but the tendency of juveniles to be captured in a larger group on the second of two nights was less pronounced during these months. During months of population decline there were no differences based on sex, reproductive condition, or age class.

Variable C differentiates among voles captured in a stable group size of one, two, or three or more individuals on two successive trapnights. Most voles, with the exception of juveniles, were found most often in a group of $C = 1$ (Table 4), while juveniles were found most often in a group of $C = 3$. In comparison with males, females showed a greater tendency to be captured in a group of $C = 1$. In other words, a given female who was captured in equal size groups on two successive trapnights was significantly more likely to be captured by herself on both of those trapnights, while a male was more likely to be captured in a group of two or larger. Reproductive voles had a greater tendency to be captured in a group of $C = 1$, while non reproductive voles had a greater tendency to be captured in a group of $C = 3$. There was a strong tendency for adults to be captured in a

Table 4

Occurrence of variable C in different classes of voles and the results of contingency table analysis
Percentages are given in parentheses

Group	C = 1	C = 2	C = 3	χ^2
Overall				
Males	142 (42.0)	92 (27.2)	104 (30.8)	15.14***
Females	208 (56.4)	69 (18.7)	92 (24.9)	
Reproductives	216 (57.8)	83 (22.2)	75 (20.1)	27.47***
Non-reproductives	135 (40.4)	78 (23.4)	121 (36.2)	
Adults	221 (58.6)	88 (23.3)	68 (18.0)	49.25***
Subadults	109 (41.3)	62 (23.5)	93 (35.2)	
Juveniles	17 (28.8)	10 (16.9)	32 (54.2)	
Months of increase				
Males	56 (37.1)	43 (28.5)	52 (34.4)	12.07**
Females	110 (55.3)	35 (17.6)	54 (27.1)	
Reproductives	129 (58.6)	49 (22.3)	42 (19.1)	40.20***
Non-reproductives	37 (28.5)	29 (22.3)	64 (49.2)	
Adults	118 (60.2)	47 (24.0)	31 (15.8)	49.13***
Subadults	34 (34.0)	21 (21.0)	45 (45.0)	
Juveniles	12 (24.5)	9 (18.4)	28 (57.1)	
Months of decline				
Males	66 (55.0)	32 (26.7)	22 (18.3)	3.44
Females	73 (67.0)	21 (19.3)	15 (13.8)	
Reproductives	58 (70.0)	18 (21.7)	7 (8.4)	6.56*
Non-reproductives	82 (55.8)	35 (23.8)	30 (20.4)	
Adults	75 (64.1)	25 (21.4)	17 (14.5)	3.05
Subadults	60 (56.1)	28 (26.2)	19 (17.8)	
Juveniles	4 (80.0)	0 (0)	1 (20.0)	
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$				

group of $C = 1$, and a strong tendency for juveniles to be captured in a group of $C = 3$. Reproductive females had the strongest tendency to be captured in groups of $C = 1$ (66 %, compared to 36–48 % for the other three groups). Non-reproductive males had the strongest tendency to be captured in groups of $C = 2$ or $C = 3$ (64 %, compared to 34–55 % for the other three groups). The distribution of this variable among the four sex and reproductive condition classes was highly significant ($X^2 = 47.25$, $p < 0.001$).

As with the previous two variables, the patterns exhibited during the months of increase were similar to the overall pattern. During months of decline, the distribution of variable C showed less of a relationship to the various classes of voles. The only difference during months of decline was a greater tendency of non-reproductive voles to be captured in a group of $C = 3$, and a greater tendency for reproductive voles to be captured in a group of $C = 1$.

Discussion

This paper is an attempt to expand the paradigm of DAVIS (1955) and more recent workers, who used multiple capture trapping as a static, indirect assessment of social behavior. The three variables which characterize the dynamics of individual multiple capture patterns were used to generate, by an extension of this paradigm, population-wide measures of sociality. Several conjectures had to be made. Clearly, these conjectures are meaningless on the individual level, since when one considers a single vole in a trap, that vole, presumably, has very little control over the number and characteristics of other voles who decide to enter that trap. But the present analyses attempt to look at group and population trends in these capture group tendencies. We believe that there is usefulness in comparing these aspects of the behavior of the vole population between the sexes, reproductive condition classes, and age classes, and during different demographic periods.

Variable A , which classified individuals as either remaining constant or changing in their capture group size, was interpreted as a relative measure of the stability of social groups. A population characterized by individuals showing more likelihood to be captured in groups of the same number of individuals from night to night was assumed to be exhibiting a higher degree of social stability than was a population characterized by individuals which were more likely to be captured in groups of different sizes on successive trapnights. In other words, the alterations in social relationships which would characterize a population in a state of social instability would be manifested in changes in night-to-night capture group affinities. However, it should be pointed out that the probability of a voles being captured in the same size group from night to night, logically depends on the group size, since it would tend to be more likely that a small group would maintain its composition than would a larger group. Accordingly, voles with a higher tendency to be captured singly (such as reproductive females) should be more likely to be classified as $A = 1$, which is exactly what is seen. However, the higher tendencies towards single captures cannot entirely explain the distribution of Variable A . In a previous study (REICH and TAMARIN 1984), it was shown that females are captured singly in about 32 % of their captures, yet they are classified as $A = 1$ in the present study, 66 % of the time (Table 2). Similarly, males are captured singly in about 28 % of their captures (REICH and TAMARIN 1984), yet they are classified as $A = 1$ in the present study, 71 % of the time (Table 2). Thus, while it is true that much of the variation in Variable A might be explained on the basis of single-capture tendency, a large part of this variation cannot be attributed to this factor.

Variable B , which classified individuals as being captured in a larger or smaller group on the second trapnight was interpreted as a relative population-wide measure of "social motivation" reflecting a state of change in social structure. A population characterized by individuals tending to be captured in a larger group on the second night were thought of as exhibiting a tendency towards more positive (attraction) associations, while a population

characterized by voles which tended to be captured in a smaller group on the second night was thought of as exhibiting a tendency towards more negative (avoidance) associations. This assumption is the dynamic representation of Davis' paradigm. If an individual captured in a larger group is showing more sociality than one captured in a smaller group, then population-wide changes in either direction from night-to-night can be assumed to reflect population changes in motivations towards increased or decreased sociality. Variable B is not influenced by voles having a greater tendency towards larger or smaller capture groups. Variable C, which classified individuals according to the capture group size at which they were remaining constant from night to night, was, like Variable B, also assumed to be a population-wide measure of "social motivation", the difference being that Variable C reflects the stable aspects of social structure rather than its flux. A population characterized by voles which were captured individually on both nights ($C = 1$) was assumed to be exhibiting a tendency towards stable negative associations, while populations characterized by voles which were captured in pair groups on both nights ($C = 2$) or in groups of three or more individuals on both nights ($C = 3$) were assumed to be exhibiting a tendency towards stable positive associations. As for Variable B, the assumptions underlying this variable reflect the dynamics of Davis' paradigm. Because Variable C, like Variable A, could be expected to be directly related to population density, direct comparisons between the two demographic periods could not be made.

Within the framework of these assumptions, differences were discovered between groups based on sex, reproductive condition, and age class, in their respective social interaction tendencies. Different patterns in the distribution of these variables when the population was undergoing increases and declines in density were also seen.

A higher level of social stability was shown by females as compared to males and by adults and subadults as compared to juveniles, as indicated by the greater tendency or males and juveniles to be captured in different size groups on successive trapnights (Variable A). Of the four sex and reproductive condition classes, reproductive females exhibited the highest level of social stability, and reproductive males the lowest. Although stable, reproductive females also exhibited the highest tendency towards negative associations (Variable C). This tendency was likewise seen in reproductives and adults of both sexes, while males and non-reproductives of both sexes exhibited tendencies towards positive associations.

These observations are consistent with the model of female territoriality in voles presented by MADISON (1980), which describes reproductive females as defending exclusive territories, and reproductive males as ranging over several female territories. Territorial exclusiveness of reproductive females is reflected in the present study by their tendency towards stable, negative associations with other reproductive females. The tendency of reproductive males to exhibit unstable, positive associations, as observed in the present study, is also consistent with this model.

Behavioral models of population regulation in voles (KREBS 1978; TAMARIN 1983) postulate that differences in social interactions exist between populations undergoing increases in density and those undergoing declines in density. Such differences were noted in the present study. Tendencies towards higher levels of social stability (Variable A) were seen in months of increase, and this was strongest in the subadult age class and in non-reproductives of both sexes. Months of increasing population density were also characterized by a greater tendency towards positive associations (Variable C), and again, this effect was strongest in subadults and in non-reproductives, especially females. Months of declining population density did not show these trends.

Differences between months of population increase and decline were most evident in the subadult age class. This is consistent with models attributing demographically-significant differential dispersal to these voles (GAINES and McCLENAGHAN 1980). Unfortunately, sample sizes were too small to permit further subdivision of groups to be able to

look at sexes and reproductive condition classes within separate age classes in months of population increase and decline.

It may be argued that the measurement of these variables does not really describe details about social relationships, because different kinds of associations are being considered together. Surely, there are many and varied reasons for two or more voles to "associate" with each other, yet these three variables do not distinguish, for example, a reproductive female captured with a reproductive male from one which is captured with a single juvenile. Knowing the exact composition of capture groups based on sex, reproductive condition and age would clearly provide us with more information about possible motivations for group associations. However, it was the intention of the present study to see if there is value in simply describing the population and segments of the population based solely on the night-to-night changes in capture group association patterns. The fact that consistent differences in these patterns were evident indicates that there is indeed value in such an approach. We believe that this paper demonstrates a potential usefulness of multiple-capture live-trapping data for analyses of social behavior which extend beyond simply describing the distribution of individuals in single or multiple capture groups. Furthermore, it underscores the necessity of considering social factors as contributing to trap bias in multiple-capture demographic studies.

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Zusammenfassung

*Die Dynamik sozialer Beziehungen bei Wiesenmäusen (*Microtus pennsylvanicus*) aufgrund von Assoziationen in mehrfach fangenden Lebendfallen*

Vorgeführt wird eine Methode zur indirekten Beobachtung sozialer Beziehungen bei Wühlmäusen, die auf kurzfristigen Änderungen der Assoziationen in mehrfach fangenden Lebendfallen beruht. Bei Wiesenmäusen (*Microtus pennsylvanicus*) in Massachusetts konnten mit diesem Verfahren verschiedene Variable zur Neigung zu Gruppenbildungen und zur Stabilität dieser Gruppen erfasst werden.

Höhere soziale Stabilität konnte bei Weibchen gegenüber Männchen und bei älteren gegenüber jungen Tieren ermittelt werden.

Die höchste soziale Stabilität wurde bei fortpflanzungsfähigen Weibchen, die geringste bei fortpflanzungsfähigen Männchen festgestellt. Fortpflanzungsfähige Weibchen zeigten auch die geringste Tendenz zu Assoziationen. Bei wachsender Bevölkerungsdichte neigen die Mäuse eher zu Assoziationen als bei sinkender. Diese Beobachtungen sprechen für Territorialität der adulten Weibchen. Sie stehen in Einklang mit Vorstellungen über die Dichteregulation bei Wühlmäusen durch Änderungen im Verhalten.

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Authors' addresses: LAWRENCE M. REICH, Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv, 69978, Israel; ROBERT H. TAMARIN, Department of Biology, Boston University, Boston, Massachusetts, 02215, USA

Migration and speciation of the South American Iniidae (Cetacea, Mammalia)

By H. GRABERT

Geologisches Landesamt Nordrhein-Westfalen, Krefeld

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Abstract

The South American Iniidae immigrated from the Pacific coastal regions to the lake system of the sub-Anden molasse¹ troughs in the Miocene some 15 million years ago. Here, following the disappearance of the link with the Pacific sea as a consequence of the Anden orogenesis in the Pliocene (5 to 1.8 million years ago), they had to adapt to the sub-Anden lakes of the freshwater molasse. These lakes were very turbid owing to the huge load of sediment delivered from the geologically rapidly rising cordilleras. The Iniidae reacted to this with a reduction of their visual capacity. The prototype *Inia boliviensis* ensued in the Bolivian sub-Anden troughs. They migrated via the Iquitos gate to the larger Amazon – Orinoco river system during the Pleistocene (1.8 million to 10 000 years ago). Here they developed into the “modern” *Inia geoffrensis* (larger brain, reduced dental count). At the beginning of the Holocene some 10 000 years ago the surrounding landscape changed from the previous semiarid savanna to the rainforest with its black water. This water separated the, upto that time, united turbid water regions of the Amazon – Orinoco and formed, in the region of the present Rio Negro, and acid black water barrier, avoided by the *Inia geoffrensis* and thus causing the development of subspecies, the *Inia geoffrensis geoffrensis* and the *Inia geoffrensis humboldtiana*. The former of these subspecies is bound to the Amazon and the latter to the Orinoco river system (TREBBAU and VAN BREE 1974).

¹ Molasse (trough) is a term of the French-Swiss Alpine geology and means sinking troughs neighboured to young orogens (e. g. the Alpes or the Anden), filled up by coarse rubble caused by the uplifting mountains.