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Interspecific Territoriality in Two Sympatric Species of *Peromyscus* (Rodentia: Cricetidae)

Jerry O. Wolff[1], Mark H. Freeberg[2], and Raymond D. Dueser[3]

[1] Department of Biology, University of Virginia, Charlottesville, Virginia 22901, USA
[2] Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824, USA
[3] Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22901, USA

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Summary. Aggressive behavior of two morphologically and ecologically similar sympatric congeners, *Peromyscus leucopus noveboracensis* and *P. maniculatus nubiterrae*, was studied in the field to determine whether coexistence between these two species could be mediated by interspecific territoriality.

In intra- and interspecific paired behavioral trials conducted in the home range of one of the animals, resident animals won between 53 and 93% of paired encounters against opponents of either species. Thus, dominance was site-specific and not species-specific.

Strong defense in centers of home ranges and lower levels of aggression on the periphery suggest that both species have defended core areas (territories) with peripheral areas of home range overlapping with neighbors of either species. Social organization of these two species is apparently based on mutual recognition of neighbors and intolerance and aggression toward strangers.

Introduction

Interspecific territoriality has been proposed as a mechanism by which two similar animal species distribute themselves in a heterogeneous habitat (Murray 1971; Wilson 1975). Interspecific territoriality has been reported for birds (e.g. Orians and Willson 1964; Cody 1969, 1973; Cody and Brown 1970; Murray 1971, 1976; Gochfeld 1979), salamanders (Thurow 1976; Jaeger 1981), and has been hypothesized (Wilson 1975), but not adequately shown for mammals.

Field studies on aggressive behavior of partially sympatric or parapatric small mammals have revealed that one species typically dominates another (Miller 1964; Grant 1969, 1971; Colvin 1973; Montgomery 1978; Randall 1978; Glass and Slade 1980). These and other studies have related aggressive behavior to spacing (Grant 1972; Randall 1978; Rowley and Christian 1976) and competitive exclusion (Miller 1964; Grant 1971, 1972; Montgomery 1978; Randall 1978). In most behavioral investigations, aggressive behavioral trials have been conducted under laboratory conditions in a neutral arena, where both animals were in unfamiliar surroundings. These studies concluded that interspecific aggression leads to competitive exclusion of the subordinate species from a portion of its range into a restricted microhabitat. The studies have been conducted on pairs of species in which each species has a microhabitat preference but can expand into other habitats if more specialized competitors are absent. However, interspecific dominance relations between two similar species which coexist in a common habitat without habitat segregation have not been examined. Under these conditions, interspecific aggression should lead to interspecific territoriality if each species exhibits comparable levels of aggression and dominance. Also as we will demonstrate in the following discussion, interspecific dominance trials in a neutral arena and/or under laboratory conditions may be misleading and not representative of events in nature.

We studied dominance relations between two similar congeneric species of small mammals in the field. If the two species are similar enough, and if they persist in a homogeneous environment with limited but defensible resources, they should exhibit interspecific territoriality. Dominance should be site-specific and not species-specific. This hypothesis was tested by observing aggressive behavioral interactions in an arena under field conditions in the home range of one of the tested animals.

In this paper, we accept Gochfeld's (1979) criteria for defining interspecific territoriality: (a) Where they occur in local sympatry, two species must occupy nonoverlapping territories; (b) such nonoverlap must be maintained to a large extent by interspecific aggression generally involving the same types of behavior manifest in intraspecific territoriality; and (c) the nonoverlap should not be primarily determined by differential habitat selection on a habitat mosaic.

The two species used in our study were the white-footed mouse (*Peromyscus leucopus noveboracensis*) and the cloudland deermouse (*P. maniculatus nubiterrae*) which coexist over the entire range of *P. maniculatus* in the Appalachian Mountains of the eastern United States. They are similar in body size and weight, morphology, and general ecology (Hall and Kelson 1959; Hamilton and Whitaker 1979; J. Wolff and R. Dueser, in preparation). Externally they are almost identical except *maniculatus* has a slightly longer and tufted tail. At low densities, the two species show slight microhabitat differences (C. Handley-personal communication) but Wolff and Dueser (in preparation) have shown that at moderate and high densities, these species exhibit extensive habitat overlap; individuals of both species occupy partially overlapping home ranges; and each species will colonize an area vacated by the other. Both species use similar nest sites (Wolff and Hurlbutt 1982). Live-trapping indicated that in years of abundance all suitable habitat was occupied by individuals of one species or the other.

Materials and Methods

Approximately 300 *Peromyscus leucopus* and *P. maniculatus* males and females were live-trapped on six 1-ha grids in a mature oak-maple (*Quercus-Acer*) forest within 0.5 km of the Mountain Lake Biological Station in Giles County, Virginia. Grids consisted of 64 trap stations set 12.5 m apart in an 8 × 8 array. Two Sherman live-traps were set at each station, one on the ground and one at a height of between 1 and 2 m in a tree. Traps were set between 1900 and 2030 h and checked the following morning. Grids were run for 3 or 4 days each week from 18 June through 8 August, 1981. All animals were ear-tagged for identification, and species, sex, weight, and trap location recorded. Adult males ($\geqq 17$ g) and anoestrous but sexually mature females ($\geqq 17$ g) were used in dyadic encounters.

One-hundred and fifty eight intrasexual pairings, both between and within the two species, were conducted. Paired animals had comparable body weights (± 2 g) and in most cases were taken from noncontiguous home ranges. For each pairing one of the animals was randomly chosen to be the home animal, and the contest was conducted at the trap station where it was caught.

Dyadic encounters were conducted between 0800 and 1000 h in a clear, open-bottom, plastic cylinder, 32 cm in diameter and 48 cm high. The animals were on natural substrate and could see their surroundings. A removable cardboard partition was used to divide the arena in half and to keep the mice temporarily separated. Approximately 20 s after the mice were introduced to different sides of the arena, the partition was removed. Initially, the trials were conducted for 10 min. It soon became apparent that decisions were made in the first few minutes. Consequently, trials were reduced to 5 min each. The results of the initial encounter between the mice, which usually occurred within seconds after they were introduced, were indicative of the final outcome.

Two observers were used, one to record the behavior of each animal. The description of behaviors were modified from Colvin (1973):

Offensive Approach: Orientation and movement of one animal towards its opponent which elicit an offensive or defensive response in the latter.

Attack: A sudden lunge toward an opponent, resulting in contact.

Chase: Following rapidly behind a retreating animal.

Retreat: Rapid escape resulting from an attack or offensive approach by the opponent.

Determining the Outcome. The criteria for determining the outcome of an interaction were as follows:

(1) Winner: The animal with the highest total number of attacks, offensive approaches, and chases was declared the winner.

(2) Draws: Both animals had the same number of retreats and/or aggressive behaviors. (Aggression included offensive approaches, attacks, and chases in which one animal attempted to displace an opponent).

(3) No aggression: If neither animal exhibited any aggression towards the other, the interaction was declared nonaggressive.

Results

The results of 131 pairings in which a win/loss decision was made are shown in Table 1. The individual behaviors are described in frequency/minute of the 5- and 10-min trials. χ^2-tests revealed no significant differences in number of dominant and submissive behaviors exhibited between species or sexes. The number of wins by home animals of both species was significantly greater than expected by chance in all eight pairing combinations, except when *maniculatus* females visited at *leucopus* females (Binomial statistic; Table 1). Even in this case, the home animal lost only 27% of the encounters (Fig. 1).

In intraspecific pairings, *leucopus* males and females won at home in 57 and 60% of the encounters, respectively (Fig. 1). *P. maniculatus* males and females won at home in 62 and 73% of the encounters, respectively. The percentage of home wins did not differ significantly between males and females ($\chi^2 = 2.0$, *d.f.* 1, $P > 0.10$) or between species ($\chi^2 = 1.0$, *d.f.* 1, $P > 0.10$).

In interspecific pairings, *leucopus* males and females won at home in 75 and 53% of the en-

Table 1. Number of dominant and submissive behaviors exhibited by *P. leucopus* and *P. maniculatus* in 131 of the 158 paired trials in which a win/loss decision was made. The first animal of each pair is the home animal, the second animal is the visitor. Behaviors are shown as frequency/min (S.D.). Significance level for probability of home animal winning was determined by binomial statistic

Species	Sex	Total no. of trials	No. of wins	Offensive approach	Attack	Chase	Retreat	*P*
P. leucopus	F	20	12	0.09 (0.17)	0.11 (0.17)	0.01 (0.04)	0.10 (0.32)	0.002
P. leucopus	F		1	0.07 (0.19)	0.03 (0.13)	0.01 (0.04)	0.19 (0.34)	
P. leucopus	F	15	8	0.10 (0.16)	0.11 (0.16)	0.03 (0.10)	0.19 (0.38)	0.194
P. maniculatus	F		4	0.03 (0.07)	0.07 (0.12)	0 (0)	0.14 (0.28)	
P. maniculatus	F	15	14	0.18 (0.23)	0.10 (0.15)	0.03 (0.07)	0 (0)	0.0001
P. leucopus	F		1	0.07 (0.21)	0.07 (0.21)	0.03 (0.07)	0.66 (0.69)	
P. maniculatus	F	15	11	0.12 (0.25)	0.19 (0.28)	0	0.04 (0.11)	0.011
P. maniculatus	F		2	0.03 (0.07)	0.03 (0.07)	0	0.39 (0.46)	
P. leucopus	M	35	20	0.09 (0.16)	0.13 (0.27)	0.01 (0.04)	0.10 (0.23)	0.010
P. leucopus	M		7	0.08 (0.22)	0.05 (0.14)	0	0.21 (0.28)	
P. leucopus	M	20	15	0.27 (0.37)	0.18 (0.24)	0	0.07 (0.12)	0.004
P. maniculatus	M		3	0.06 (0.14)	0.04 (0.12)	0	0.21 (0.34)	
P. maniculatus	M	16	10	0.26 (0.37)	0.11 (0.24)	0.03 (0.09)	0.04 (0.08)	0.046
P. maniculatus	M		3	0.01 (0.05)	0.06 (0.14)	0	0.34 (0.70)	
P. maniculatus	M	22	18	0.23 (0.33)	0.10 (0.22)	0	0.06 (0.11)	0.0002
P. leucopus	M		2	0.06 (0.10)	0.04 (0.08)	0	0.30 (0.26)	

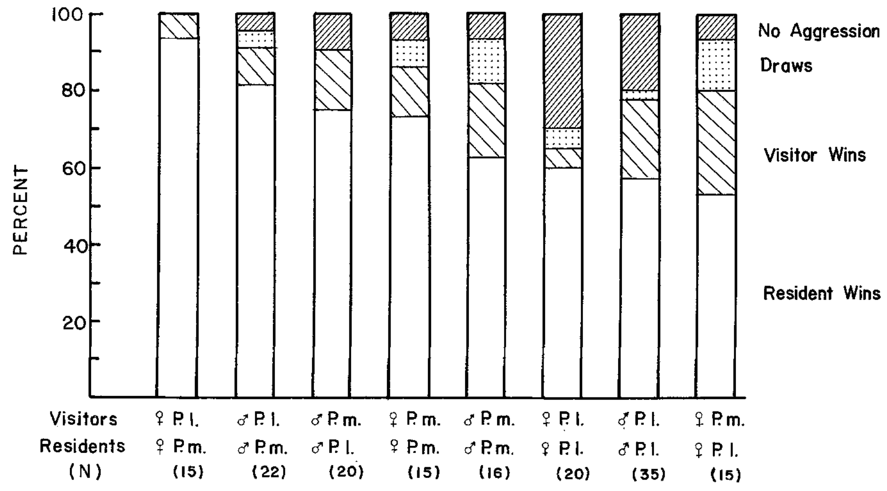

Fig. 1. Percentage of home wins, visitor wins, draws, and no aggression outcomes in 158 intra- and interspecific pairs of *P. leucopus* (*P.l.*) and *P. maniculatus* (*P.m.*). *N* number of pairings

counters, respectively. *P. maniculatus* males and females won 82 and 93% of their home encounters, respectively. In both situations, *maniculatus* males and females won more home encounters than their *leucopus* counterparts. However, the only significant difference was *maniculatus* females winning at home more often than *leucopus* females winning at home ($\chi^2 = 10.96$, *d.f.* 1, $P \leq 0.001$). *P. maniculatus* females won more home encounters than *maniculatus* males, but *leucopus* females did not win more home encounters then *leucopus* males. The number of wins by home animals did not differ significantly in inter- versus intraspecific pairings ($\chi^2 = 1.0$, *d.f.* 1, $P > 0.10$).

In eight pairings where a home animal was a definite winner, we conducted a second trial a week later with the same animals at the home site of the losing visitor animal. In six of these cases, the animal that lost when it was a visiting animal, reversed the decision and won when it was at home. In the other two cases, a win decision was changed to no aggression in one case, and a *maniculatus*

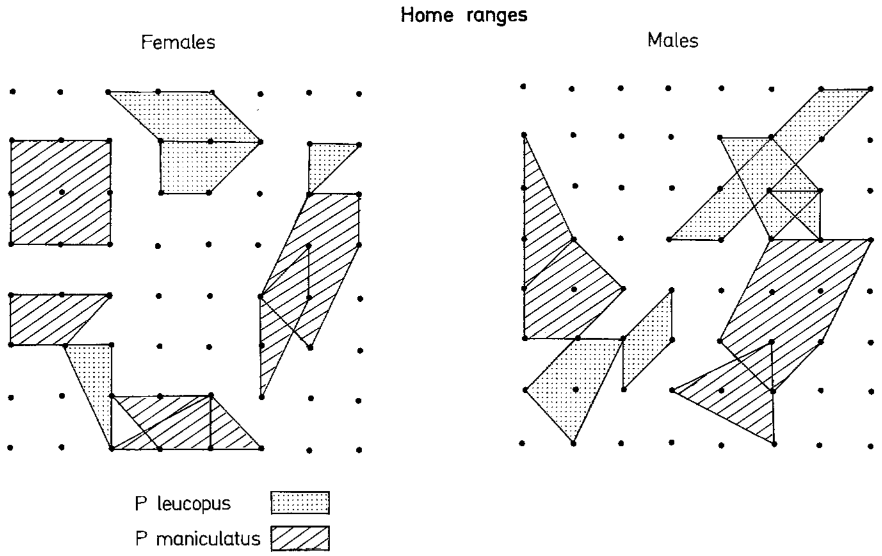

Fig. 2. Minimum boundary home ranges of 4 *P. leucopus* and 6 *P. maniculatus* females and 5 *leucopus* and 4 *maniculates* males on grid 3. Ranges are based on live-trapping data gathered from 12 April – 5 July, 1981. Minimum home range estimates on the 5 remaining grids showed a similar pattern

female visitor defeated a *leucopus* resident in the second. Thus, home animals won in 14 of the 16 trials. The probability of an animal winning at home was significant ($\chi^2 = 9.0$, *d.f.* 1, $P \leqq 0.005$).

We had estimates of the minimum home ranges of home animals in 133 of the 158 paired encounters. Of these 133 trials, 75 were conducted on the periphery of the resident animal's home range and 58 were conducted in the center of the home range. Home animals won 41 or 55% of the 75 trials conducted on the periphery of their home ranges and 34 resulted in losses, draws, or no aggression. Of the 34 trials which resulted in draws, no aggression, or losses to the home animal, 11 were conducted with neighbors which had contiguous or partially overlapping home ranges. Of the 58 trials conducted in the center of the home ranges, 50 or 86% were won by the home animal and 8 resulted in draws, no aggression, or losses. The probability of an animal winning in the center of its range was significantly greater than the probability of winning on the periphery ($G = 15.2$, *d.f.* 1, $P < 0.001$).

The minimum home ranges of 10 female and 9 male resident *Peromyscus* which were captured 141 times on one of the live-trapping grids are shown in Fig. 2. Resident animals were those individuals weighing $\geqq 14$ g caught at 3 or more trap stations over at least a 3-week period from 12 April – 5 July, 1981. An additional 7 females and 5 males were caught less than 3 weeks or on the periphery of the grid. The home range maps show essentially exclusive areas for most animals with only partial overlap occurring between some individuals. Under the assumption that interspecific territorial behavior acts to disperse animals on the grid, one would expect to observe relatively little interspecific overlap between home ranges if there were behaviorally-mediated spacing.

The percent of range overlap was determined by measuring the proportion of the total range of one species and sex that spatially overlaps that of another species and sex. Four *leucopus* females occupied 766 m^2 (10%) of the grid, none of which overlapped the range of *maniculatus* females. Home ranges of *leucopus* females abutted one another, but there was no measurable overlap between individuals. Six *maniculatus* females occupied 1,991 m^2 (26%) of the grid. Fourteen percent of female *maniculatus* home ranges overlapped each other. Five *leucopus* males occupied 1,225 m^2 (16%) of the grid, 9% of which overlapped the range of other *leucopus* males. None of the 4 male *leucopus* home ranges overlapped those of any male *maniculatus*. Four *maniculatus* males occupied 1,684 m^2 (22%) of the grid, and only 1 of the 4 residents exhibited range overlap with another *maniculatus* male. Range overlap was similar in males and females of both species.

Discussion

Resident animals regardless of species won a disproportionate number of paired dyadic encounters, and intruders usually lost. This supports our hypothesis that dominance is site-specific and not species-specific. It appears as though the animal that arrives first on a piece of ground is able to hold it against intruders. This finding is similar to the 'residence effect' or 'beachhead' phenomenon described for interspecies dominance (Corbet 1961; Morris 1969; Grant 1972). When animals that had won at home were paired as intruders with the same animal in subsequent trials, they usually lost. Animals which were tested in the center of their home ranges won significantly more encounters than those tested on the periphery of their ranges, out of their home ranges, or with immediate neighbors. These results suggest that both species have a defended core area with aggression decreasing away from the center of their range. *P. leucopus* and *maniculatus* apparently exhibit site-specific dominance with residents defending home territories both intra- and interspecifically. However, both species have peripheral areas of their home ranges which are not defended or are defended to a lesser degree. Brenner et al. (1978) reported a similar condition for the eastern chipmunk (*Tamias striatus*). They found that resident animals had core areas in their home ranges where the animal was dominant to all intruders. Such core areas center around key features of the animal's habitat, typically nest sites and foraging areas (Brenner et al. 1978). Although we did not experimentally test for core and peripheral areas, the separation of the two peromyscines in our study fit the pattern of defended core areas or territories with nondefended portions of the home range overlapping slightly those of neighbors. These core areas are probably near the nest and/or foraging areas (Wolff and Hurlbutt 1982).

In our study, 11 trials which were conducted between known neighbors resulted in no aggression. Recognition and tolerance of neighbors and aggression and intolerance of strangers has been termed the 'dear enemy' phenomenon (Fisher 1954), and has been reported for *Peromyscus leucopus* (Vestal and Hellack 1978) and for salamanders (*Plethodon*) (Jaeger 1981). Both studies found that neighbors appeared to recognize each other and showed low levels of aggression whereas strangers were intolerant and aggressive toward each other. They concluded that social organization was based on mutual recognition of neighbors with some type of dominance relationship between them and aggression toward strangers. *P. leucopus* and *maniculatus* in our study appear to exhibit a similar social organization.

Numerous studies have produced supporting evidence for territoriality or mutually exclusive ranges for *leucopus* (e.g. Burt 1940; Nicholson 1941; Redman and Sealander 1958; Myton 1974; Metzgar 1973; Madison 1977). Female *leucopus* seem to show less range overlap than males (Metzgar 1973; Madison 1977). However, these differences were not apparent in our study. Rowley and Christian (1976) found that *leucopus* females were also aggressive toward *Microtus pennsylvanicus*. In our study, *leucopus* home ranges abutted one another, but showed minimal overlap intrasexually.

No systematic studies have been conducted on the social organization of *P. maniculatus nubiterrae*, and studies on other subspecies of *P. maniculatus* have been inconclusive. Storrer et al. (1944) and Terman (1961) have found that *P. m. bairdii* exhibit a territorial or mutual avoidance spacing system, but Blair (1940) found considerable overlap of ranges in the same subspecies. Manville (1949) found little or no overlap in ranges of adult *P. m. gracilis*, but Blair (1942) found considerable overlap in their ranges. In our study, *P. m. nubiterrae* exhibited only partial overlap in home ranges. From the aggressive behavior we observed in resident individuals, we concluded that both species defended a portion of their range and therefore it could be considered a territory.

Pairing of individuals in a neutral arena showed that *maniculatus* dominated *leucopus* in the majority of the behavioral encounters (J. Cranford, personal communication; S. Gardner, unpublished; J. Wolff, unpublished). Using these unpublished results, one could wrongly conclude that *maniculatus* can competitively exclude *leucopus* from preferred habitat. Our field studies, however, indicate that each animal exhibits the residence effect and can effectively exclude intruders of either species from its territory. Thus, dominance is determined in part by the context in which the trial is conducted. In this case, dominance is characteristic of an animal in its home territory.

The interspecific aggression exhibited between these two species of mice is probably a consequence of their morphological and ecological similarity. Our findings support predictions by Murray (1971) and Wilson (1975) that competitive coexistence between closely related, physically similar species may be mediated through interspecific territoriality. The two species are ecologically behaving as one. The potential implications of this territoriality for competitive coexistence are most likely to be realized at high population densities, such as those observed here. This, however, does not preclude other mechanisms for coexistence under different situations.

In contradiction to Murray, we found dominance is not species-specific, but rather site-specific. Individuals of either species can defend their core area against members of either species. Although each species may have different microhabitat tolerances, they do maintain themselves in the same habitat and apparently achieve comparable reproductive success (J. Wolff and R. Dueser, in preparation). Consequently we conclude that interspecific territoriality can be adaptive in the same way that intraspecific territoriality is adaptive.

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