AGONISTIC BEHAVIOR OF THE NORTHERN GRASSHOPPER MOUSE  
(ONYCHOMYS LEUCOGASTER BREVIauritus) 

DAVID G. RUFFER

ABSTRACT.—A study of agonistic behavior of captive northern grasshopper mice was made in enclosures measuring not less than 15 x 15 feet. Observations demonstrated the pattern of aggression in both inter- and intraspecific encounters. Data showed that dominant-subordinate relationships were maintained by nonviolent agonistic encounters. A line of small burrows effectively marked the edge of the well defended territory.

Previous papers (Ruffer, 1965a, 1965b, 1965c, 1966), have been concerned with burrowing, juvenile molt, sexual behavior, and calls of the northern grasshopper mouse (Onychomys leucogaster breviauritus). The present paper covers some aspects of agonistic behavior in this species.

Verplanck (1957) defined agonistic behavior as a broad class of behavior types that includes attack, threat, appeasement, and flight. Scott (1958b) similarly regarded agonistic behavior as any sort of adaptation associated with a contest or conflict between two animals. Aggressive behavior is that part of agonistic behavior limited to fighting (Scott, 1958a), and territoriality is a part of agonistic behavior since, among other things, it reinforces dominance relationships and reduces sexual fighting (Carpenter, 1958).

METHODS

Methods of study and capture locations of the mice used have been previously described (Ruffer, 1965a, 1965c). Briefly, they involved the use of direct, tape-recorded observations, 16 mm infrared motion pictures, 35 mm still photographs, and event-recorded data acquired from wild-captured mice held in cages not less than 6 x 6 x 12 inches. Mice were obtained from several areas in western Oklahoma. Observations were made by placing various size groups of mice of all combinations of sexes, all in breeding condition, in large enclosures measuring not less than 15 x 15 ft sq. Data used in this paper represent 162 pairings involving a total of 112 individual mice and including 47 male-male, 43 female-female, and 72 male-female encounters. Of these 162 pairings, 6 (3.7%) represent single replicas of pairs. An attempt was made to simulate in the enclosures the habitat from which the animals were taken. The enclosures were lighted by 100 watt red bulbs which did not noticeably affect the behavior of the mice. The observer was located behind a canvas blind. A total of 63 adult mice were used in the study. In so far as possible, laboratory-acquired data were confirmed by field observations.

RESULTS

The pattern of aggression in O. leucogaster was similar in intra- and interspecific encounters and consisted of the aggressor rapidly pursuing the victim, with repeated pounces at it, until the aggressor obtained a hold with the forefeet. Should the victim assume a defensive posture, in which it stood on its hind legs, tail stiff, ears perked up, back straight, and forefeet raised against the thorax, paws down, the aggressor nipped at its tail and legs until the
victim was forced to expose its back to attack. Using the forefeet, the aggressor then seized the victim from the rear and bit through the parietal region of the skull. The victim was killed within 10 sec after seizure. The claws were never used as weapons.

A grasshopper mouse that was being defeated in a fight was not killed during the first three or four encounters if it assumed a submissive posture lying on its side with the forefeet against the thorax, tail stiff, ears back, and eyes closed. When this posture was assumed, the attack stopped for from 4 to 12 min before the subordinate was again attacked. Subsequent attacks would occur whether or not the subordinate maintained the submissive posture.

**Interspecific Encounters**

Twenty-three interspecific encounters were staged between *O. leucogaster* and *Dipodomys ordii*, *Perognathus hispidus*, *Reithrodontomyss megalotis*, *Peromyscus maniculatus*, *P. leucopus*, *Sigmodon hispidus*, and *Mus musculus*. These inevitably resulted in death of the subordinate within 3 hr of the initial contact. *Onychomys leucogaster* was never killed, even when in encounters with male *Sigmodon hispidus* that were three times as heavy as the *O. leucogaster*. Although both male and female grasshopper mice would kill other mice, if a male-female pair encountered another animal, the male was the aggressor and the female remained in or near the next burrow during the encounter.

**Intraspecific Encounters**

Observations indicated that within the 162 intraspecific pairs, and in 14 groups of 3 to 5 animals, a dominant–subordinate relationship was established with the first three agonistic encounters, and lasted for the duration of the contact between the animals. In like-sex encounters, the subordinate was killed within 3 days of initial contact, with 70% being killed within 24 hr. Frequency records of agonistic encounters between members of groups of mice indicated that there was one dominant and a group of subordinates which lacked a hierarchy.

Intraspecific encounters were initiated by, and interspersed with circling. Of 132 recorded like-sex encounters, the diameter of the circle was more than 36 cm, and in 174 recorded unlike-sex encounters it was 10 to 15 cm in diameter (about the body length of the participating individuals). This circling was immediate and always of the aforementioned type, indicating immediate and accurate sex recognition.

Three types of intraspecific encounters were recognized: fights, chases, and approaches. Any agonistic contact between two individuals, except for nips at the tail, was considered a fight. In a fight the two animals faced each other, raised to their hind legs, back straight, tails stiff, ears perked, with the forefeet raised against the chin, and sparred. They then met and often assumed a "lock posture" with their ventral surfaces together at near right angle, or they merely jumped at each other. While in the lock posture they rolled...
TABLE 1.—Frequency of agonistic encounters during the first and third half hour of contact for O. leucogaster.

<table>
<thead>
<tr>
<th></th>
<th>First half-hour</th>
<th>Third half-hour</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fights</td>
<td>obs = 28</td>
<td>obs = 3</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>ex. = 27.65</td>
<td>ex. = 3.35</td>
<td></td>
</tr>
<tr>
<td>Chases</td>
<td>obs = 3</td>
<td>obs = 33</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>ex. = 3.35</td>
<td>ex. = 32.65</td>
<td></td>
</tr>
<tr>
<td>Violent Encounters Total</td>
<td>31</td>
<td>302</td>
<td>333</td>
</tr>
</tbody>
</table>

All Encounters

<table>
<thead>
<tr>
<th></th>
<th>First half-hour</th>
<th>Third half-hour</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Violent</td>
<td>obs = 297</td>
<td>obs = 36</td>
<td>333</td>
</tr>
<tr>
<td></td>
<td>ex. = 251.9759</td>
<td>ex. = 81.0200</td>
<td>448</td>
</tr>
<tr>
<td>Nonviolent</td>
<td>obs = 42</td>
<td>obs = 73</td>
<td>115</td>
</tr>
<tr>
<td></td>
<td>ex. = 87.0200</td>
<td>ex. = 27.9799</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>339</td>
<td>115</td>
<td>448</td>
</tr>
</tbody>
</table>

around and attempted to bite the back of the other's head. In the chase, the aggressor pursued the victim for distances of 3 to 15 ft. Chases were frequently interspersed with fights.

In the approach, the subordinate animal moved away at the approach of the dominant. An approach by the dominant to within a distance of 12 ft could cause retreat.

Since one function of a dominant-subordinate relationship is to reduce the amount of fighting between the individuals involved, it would seem that once dominance had been established, the frequency of these three types of agonistic encounters would change. In an attempt to measure the effect of this relationship on the frequency of agonistic types, 16 groups of three animals involving four groups each of the four sex combinations were established. This involved a total of 48 individuals (24 males and 24 females) with no individual being involved in more than one group. These groups of three were placed together in an enclosure, and the frequency of each agonistic type was recorded during the first and third half hour after release. Since dominance was always established within the first half hour, frequencies recorded during this time indicated encounters during establishment, and those during the third half hour indicated encounters after establishment of dominance relationship. Of the three types of encounters, chasing and fightings were termed violent, whereas approaches were termed nonviolent. Table 1 demonstrates that it is permissible to group fighting and chasing together in the single category "violent encounters," because the proportion of these two types is nearly identical in the first and third half hours. It is obvious from
inspection of the table that the frequency of both kinds of encounters is much
greater in the first than the third half hour, but the relative frequencies of
ights and chases are not changed. From inspection it is further obvious that
the observed values are almost in perfect agreement with expectation. Be­
cause of the low expected frequency of fights in the third half hour, Chi­
square analysis of this table is untrustworthy, but the Fisher Exact Test in­
dicated a probability of 0.5621 for the observed and all more extreme tables.

Violent and nonviolent encounters are compared in Table 1. Contingency
analysis, corrected for nonindependent observations (Edwards, 1958), gives
a deviation from expected values of ± 45.02 with a resulting Chi-square of
141.275 which indicates a probability of much less than 0.0001. Thus the null
hypothesis, that violent and nonviolent encounters occur in the same propor­
tion during the first and third half hours, is rejected; there being a much
larger proportion of nonviolent encounters during the third half hour.

Under these conditions, although an animal was more likely to engage
in a nonviolent agonistic encounter after establishment of the dominant­
subordinate relationship, the relative proportions of fights and chases (violent
encounters) remained the same. In addition, the total number of all encoun­
ters was significantly lowered during the third half hour (P = < 0.0001).

**Territoriality**

Burt (1940) defined a territory as the defended portion of the home range
when the latter is defined as, "... that area about its established home which
is traversed by the animal in its normal activities of food-gathering, mating,
and caring for young." Observations indicated that *O. leucogaster* had a
strongly defended territory, larger than the enclosure, but of undetermined
size. When more individuals than one male-female pair (or when more than
one individual of the same sex) were placed in the enclosure, the subordinates
were forced, by the dominant, to limit their activity to one small corner of
the enclosure. This corner contained no burrows of the dominant, and the
border of the area was marked with a series of holes 3 cm deep where it took
a sandbath. Subordinates did not cross this "line" when the dominant was
out of the burrow, and often rolled in the holes when one was encountered.
The "line" did not restrict movements of the dominant. Twice the lines were
relocated carefully where they were respected as a territorial boundary in
the same way they had been in the previous location.

Subordinates would enter the dominant's territory while the dominant was
in a burrow, but ran to the corner when the dominant appeared. Thus, non­
vioent encounters were most important in maintaining a dominant–subordinate
ratio (see Table 1). Although females neither established nor helped defend
territories, if two or more females were placed in an enclosure, a dominance
relationship was established and the subordinate was eventually killed. Mice
in addition to one male–female pair could not remain in an enclosure more
than two nights without being killed.
The pattern of aggression described here, which included pursuit by the aggressor, following by pouncing on the victim, seizing the victim from the rear, and piercing of the rear of the skull, has been reported by Clark (1962b), although he did not comment on the defensive posture. The submissive posture with the animal lying on his side in the sand differed from that described by Eisenberg (1962) for the closely related species *Peromyscus maniculatus* in which the mouse sat with his eyes closed and for *P. californicus* in which the posture was accompanied by the victim turning away from the aggressor. However, Eisenberg did describe a posture that he labeled "defeat," which is similar to what is termed submissive for *O. leucogaster*. The defeat posture is described as the result of superior attack whereas submission is the avoidance of contact. Thus, the posture of *O. leucogaster* is probably submissive as described, and differs from the defeat with respect to Eisenberg's distinction. In the same report Eisenberg described a lock posture in both species that was identical to that described for *O. leucogaster*.

It is generally known that grasshopper mice are not abundant except in localized instances. My trapping records for several areas in western Oklahoma and southwestern Arizona supported this assumption. For a wide variety of reasons, published reports on home range size cannot be directly compared. However, Burt (1940), Hediger (1950), and McNab (1963), have stated that predatory animals must have a larger home range than herbivorous species. Burt (1940) studied several herbivorous species and found the home range of *Peromyscus leucopus* to be less than 0.5 acres in breeding females and 1.5 acres for old males, 0.2 acres for *Synaptomys cooperi*, 0.2 acres for *Microtus pennsylvanicus*, and 0.25 acres for *Microtus (Pitymys) pinetorum*. Ruffer (1961) found that both male and female *Peromyscus leucopus* had a home range of approximately 0.2 acres. Williams (1955) found mature male *P. maniculatus* to range over 0.81 acres whereas mature females ranged over 0.63 acres.

On the other hand, Blair (1953) found the mean home range of four male *Onychomys torridus* to be 7.8 acres; five females ranged over 5.9 acres. Four male *O. leucogaster* had an average range of 5.8 acres. These few data, coupled with my trapping experience, indicate that grasshopper mice, being predatory rodents, have a larger home range than closely related, nonpredatory genera, and would account in part for their sparse distribution.

Territory is related to home range in being the defended portion of the home range. Although home ranges may overlap, territories seldom do (Burt, 1940; Ruffer, 1961), and the size of territory and size of home range are not necessarily related. Noble (1939) found that territories offered a clear advantage to subordinate animals in that a subordinate, in his own territory, could win a fight with an otherwise dominant animal; likewise, as my data show, a subordinate was reluctant to fight in the territory of another mouse. Carpenter (1958) included the following functions of territoriality in a list
of 32: territoriality disperses a population, ensures adequate space, prevents over-population, reinforces dominance, and reduces sexual fighting and killing. These are clearly advantageous to any mammal, and have been demonstrated to be functions in grasshopper mice.

McNab (1963) demonstrated that the type of food of a species appears to be one important determining factor for the size of home range and hence territory. His distinction between hunters and nonhunters shows that hunters need a larger home range because of the spatially diverse nature of the food supply. A nonhunter has much more food available per unit space than does a hunter. The spatial aspects of home range and territoriality are augmented in grasshopper mice by a system of burrow types arranged throughout the territory to provide places of retreat (Ruffer, 1965a).

My data indicated that *O. leucogaster* has a large, well defined territory that is respected by other mice and is defended by nonviolent encounters. This is opposed to Clark's (1962a, b) observations. He found that laboratory-reared grasshopper mice could be kept indefinitely in groups of five or more. This would indicate that either the mice were not territorial, or that the territoriality was broken down. If pairs of grasshopper mice are kept in cages smaller than the size of a five-gallon aquarium territoriality will break down and several generations could live together. If these same individuals are ever released into a larger cage or into an enclosure, territoriality was reinforced and the litters had to be separated. This seems to indicate that Clark's observations were affected by the small cage he used.

Observations indicated that smell played an important role in establishing and maintaining a territory. The scent for marking apparently came from a concentration of sebaceous-like glands in the anal region. The sandbath that accompanied sign-posting included rubbing the anal region in the hole dug at the edge of the territory. Eisenberg (1963) suggested that sandbathing evolved as a means of chemical communication involving ventral rubbing, and has secondarily become involved in grooming. This seems to be supported by the data on the grasshopper mouse, which indicate that because of the need for a larger territory, the aspects of sandbathing relating to chemical communication were retained throughout the evolution of grasshopper mice and have become almost ritualized.

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LITERATURE CITED

RUFFER—AGONISTIC BEHAVIOR IN ONYCHOMYS


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