Luangwa Game Reserve, Zambia, during the period 25 September to 10 October, 1964. Daily records were obtained on males considered resident in a circumscribed area (*2*).

Four male pukus, drugged with succinylcholine chloride, were individually marked and then released. One of these was observed 46 times in an area of 7.5 ha and another, 23 times in an area of 21.0 ha. Data obtained on three other males that could be recognized by natural characteristics indicated that they occupied areas varying in size from 5.0 to 12.5 ha. In addition, at least four other males occupied rather circumscribed areas during parts of several days. In all, nine areas could be recognized (Fig. 1). The sizes of ranges occupied by individual males were determined on the basis of daily records, as well as data obtained from driving these males around intentionally or unintentionally. When a disturbed male deserted his territory he would usually return within 10 to 20 minutes.

I consider the ranges described to be territories, since they were (i) occupied intermittently or continuously by the same males and (ii) defended against intruding males who also occupied territories. This concept does not imply that territories were occupied for a much longer time than the study period. Several territories overlapped because males invaded neighbors' territories which were temporarily vacated. That part of the study area which was regularly occupied by territorial males was considered "territorial ground" (*1*). This ground was the most open part of the study area.

Most interactions among males, and matings with females, took place in the center of the territorial ground. Boundaries were defended more by ritualized display than by fighting. No serious fights were observed. Displays included the animals' facing each other and rapidly wagging their tails, but erection of the phallus and laying back of ears as described by Buechner for the kob (*3*) were not observed. On several occasions an intruder was evicted in a chase by a residential male. On one occasion an intruder was pursued by a territorial male to the opposite boundary of his territory. Most interactions by territorial males were stimulated by outside disturbances, such as human beings or lions walking through the study area. A "bachelor" band of young adult males occupied a range

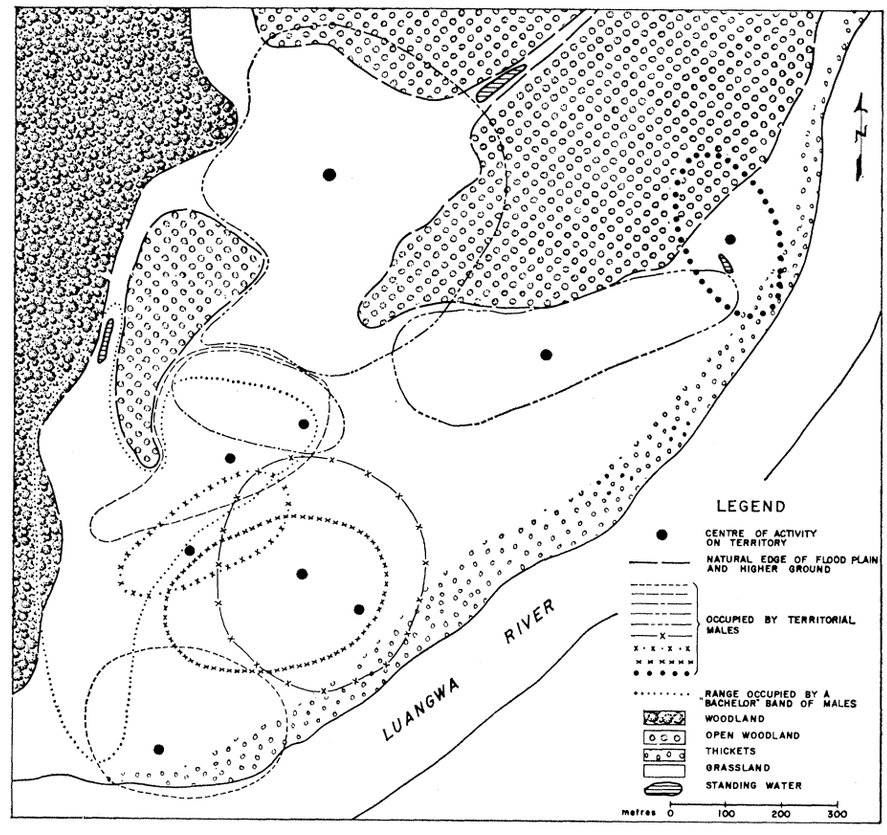

Fig. 1. Territories of puku in the Luangwa Game Reserve, Zambia.

west of the "territorial ground." Occasionally some of these males were seen on territories, and sometimes they were chased off by occupants of the territories (Fig. 1).

Contrary to Buechner's statements (*1*), the centers of territories were not closely cropped or heavily trampled; the territories defended by male pukus were much larger than those he described for the Uganda kob. This may be because the population density was lower or because of different environmental factors.

Individual females did not associate with a particular male. Rather, groups of females wandered continuously and associated for relatively brief periods with territorial males.

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18 March 1965

Mus musculus: Experimental Induction of Territory Formation

Abstract. *In groups of house mice* (Mus musculus) *an experimentally imposed sequence of experience led to the establishment of male territories in suitably designed observation pens. This sequence consisted of familiarization with the area followed by combat with and social dominance over another male who was then removed, and a final step in which defeat on the home ground of a similarly experienced male was coupled with victory over the latter on familiar ground.*

Territoriality, as used here, is any behavioral phenomenon which effects the exclusion of some category of conspecific organisms from space inhabited by the territorial individual or group. For *Mus musculus*, the general consensus has been that territorial behavior is absent, or at most weakly

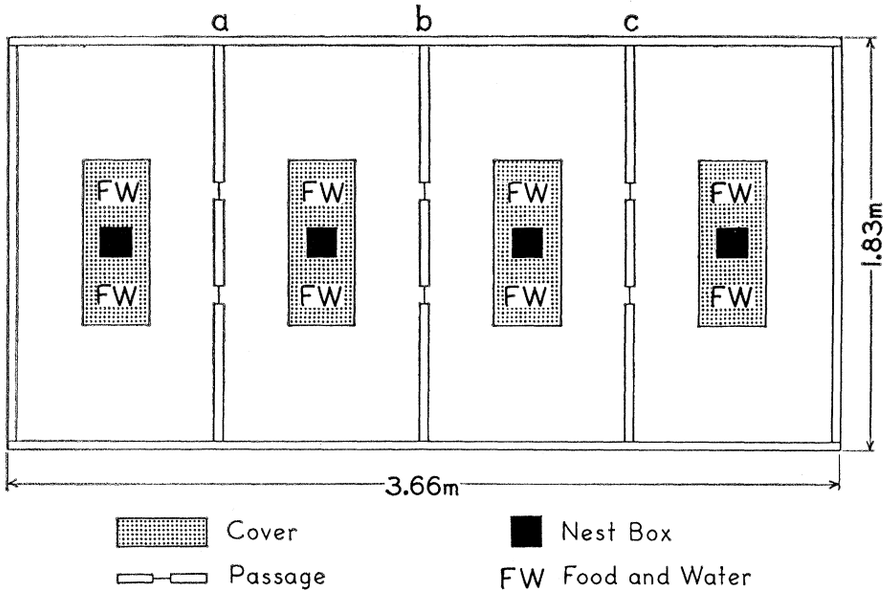

Fig. 1. Floor plan of experimental cage, showing locations of covers with nest boxes, food, and water, and of passageways between compartments.

developed in both wild and laboratory strains (*1*). This view has been supported by experiments with individual mice in the laboratory (*2*, *3*) and by observation of both free-living and confined populations (*4*). One of us has, however, reinterpreted these reports and proposed that territorial behavior is a well-developed part of the social repertory of this species (*5*). This view is supported by the report of Crowcroft (*6*), although his conclusions and operational definition have been challenged by Davis (*7*) and by Eibl-Eibesfeldt (*8*) in his account of the defense of family territories by all adult members of the group ("Grossfamilie"). Circumstantial evidence of a genetic nature is also available, in that patterns of gene distribution indicate a high degreee of genetic isolation between family groups (*9*).

In the experiment reported here, field and laboratory observations were utilized in designing a cage and a sequence of experiences incorporating the elements which appeared to be involved in territory formation in nature. The experimental cages shown in floor plan in Fig. 1 consisted of plywood walls 75 cm high resting on a concrete floor. In each of the four compartments a complex two-story cover was placed, containing a nest box at its center and food and water stations at each end (Fig. 2). This cover provided a focal area where mice spent approximately 85 percent of the time in which they were active outside the nest box, and within which individuals could be identified and interactions observed. In combination with the compartment in which it was placed, each cover provided a complexly structured area with which the animals could become familiar and within which needs for food, shelter, hiding places, and escape routes could be met. The area of the cover was in turn set off by the surrounding open space, beyond which walls of the compartment formed outer points of reference. These geometric relationships were intended to reproduce elements of natural environments which were believed to be significant in the formation of territories. Passage between the compartments was provided by holes (2.5 cm in diameter) which could be closed with metal slides. Illumination for observation purposes was provided by 25-watt red bulbs, or white bulbs screened with red cellophane.

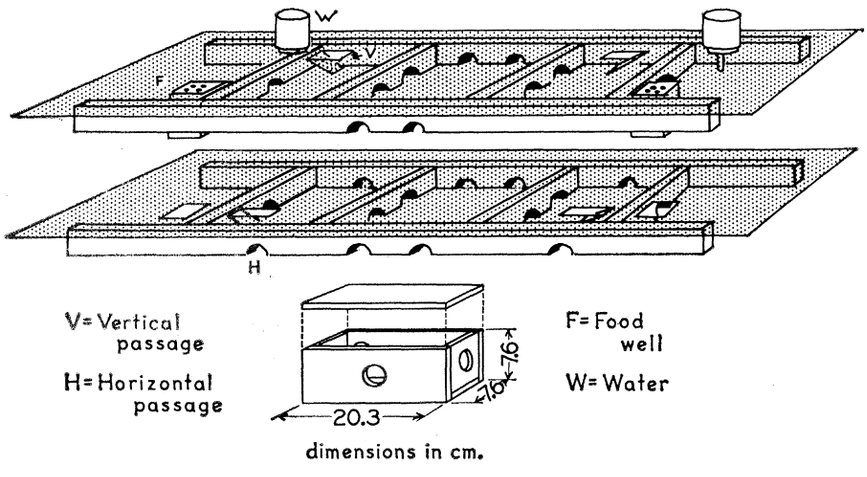

Fig. 2. Elements of a cover in expanded view. Stipple indicates sheets of galvanized wire screening.

Procedure and results reported here apply to ten replicate experiments in which F_1 progeny of crosses between wild mice and a partially inbred laboratory stock were used. In pilot experiments, wild-caught mice, and mice of a partially inbred laboratory stock were also used (*10*).

At the start of each experiment the metal slides were closed and a male and female mouse were placed in each of the four compartments for an adjustment period of at least 48 hours. At the end of this interval, passageways in partitions *a* and *c* (Fig. 1) were opened, and the resulting contacts were observed from a vantage point above the cages. The first interaction between the two males encountering each other in each half of the cage consisted of one or more violent fights in which the combatants locked together and rolled about, biting and squeaking. Timed fights lasted from 10 to 30 seconds. When one male broke off the contest and fled, the issue had usually been resolved with the fleeing male taking up a subordinate role.

Behavioral criteria for establishment of a dominant–subordinate relationship between two males at this point were as follows. The subordinate male fled the initial fight and the dominant male pursued until the subordinate escaped. Thereafter the subordinate male displayed behavior patterns which tend-

ed to minimize the frequency and severity of contacts with the dominant. Frequently, these included an initial outburst of exploratory activity in which the subordinate male looked and stretched upwards along the walls and in the corners of the cage as though searching for a route of egress. While this apparent search for an exit did not always occur and was brief, being terminated by a voluntary shift to other activity or by the approach of the dominant male, it is tempting to speculate that emigration might occur at this time in a non-confining environment. Subsequent to, or in the absence of, this exploratory phase, the subordinate male spent its active time on exposed vantage points on top of the covers, or away from the covers in "neutral corners" of the compartments. On the approach of the dominant male, the subordinate male either fled with the dominant in pursuit, or assumed a "submissive posture" (*8*) in the neutral corner, whereupon the dominant male sniffed or groomed the subordinate and went elsewhere. Characteristic behavior of the dominant male also included periodic tours of the two compartments in apparent search for the subordinate. Again, speculation might suggest that persistent or recurring persecution would tend to cause emigration of the subordinate mouse.

Observations were continued for 1 hour after the deciding encounter, and the cage was observed again 12 to 24 hours later to ascertain that the relationship had persisted.

It was expected that at this point in the experiment the cage would contain two males which had experienced victory and dominated a pair of compartments. In the 10 runs of the Calgary series, 19 of the expected 20 males became subordinate, and on the subsequent check 14 still behaved as subordinates and 5 were dead. In the remaining instance the first encounter led directly to establishment of exclusive territories by the two males, rather than dominance by either.

To begin the next part of the experiment, subordinate males were removed to simulate emigration. The passageways in partition *b* were then opened. The encounter between the two remaining (dominant) males consisted of a fight or series of fights as previously described. In this case the specific outcome was predictable, with victory going to whichever mouse was fighting on home ground. The defeated male then returned to the half of the cage where it had been dominant. There a second fight eventually took place and the previously defeated individual was victorious in turn on its home terrain. This experience of a single victory and a single defeat was in most cases sufficient to train the two, each avoiding the area occupied by the other thereafter.

Criteria for establishment of territory at this point were as follows. Fighting ceased. Each mouse avoided the terrain held by the other. The passageways connecting the areas occupied by the two males became foci of activity and were frequently visited by both males in what Crowcroft (*6*) has referred to as patrolling. A patrolling male watched the openings from beneath the neighboring cover, then visited each opening briefly, peering through. It either did not venture through the opening at all, or penetrated only 10 to 15 cm before turning back. No contact with the other mouse was required to cause retreat. If both males checked the passageways simultaneously, interaction was limited to a few seconds sparring through the opening. Persistence of this behavior was checked 24 hours after its initiation had beeen observed, and if the mice were continuing this pattern at that time, territory was considered to have been established and the individuals were removed and the cage cleaned in preparation for replication of the experiment with a new group of mice.

Six of the ten runs followed the sequence described. In two runs the second phase resulted in dominant-subordinate relationships; in a third, one contestant was killed. In the remaining run, territorial behavior developed at the end of the first encounter between two of the males, as previously mentioned. One of these territorial individuals was allowed to encounter the dominant male in the other half of the cage and the formation of a third territory resulted. Thus 15 of 21 males completing the sequence established territories as here defined.

It appears probable that a male mouse dispersing from a natural population will undergo an experience sequence similar to that imposed here. When suitable and unclaimed habitat is found such an individual will establish a home range with which it becomes familiar. At some point in the process a mate may be acquired. Thereafter, any challenge is likely to come from a wandering male unfamiliar with the area. Laboratory studies of fighting in mice (*3, 7, 12*) have shown that victory in combat is favored by familiarity with the area, presence of familiar mice, and previous experience of victory. Displacement of an individual already established on a home range would therefore be unlikely, and would become progressively less likely with succeeding victories. Boundaries to territories could be established through encounters similar to those occurring in the second part of our experimental sequence.

The role of females in these experiments was usually passive and their involvement in combats occurred only through mistaken identity, occurring in the midst of contests between males. A minority of females did display aggressive behavior towards strange mice of both sexes, a behavior suggestive of the development of group defense of a territory as described by Eibl-Eibesfeldt (*8*).

We hope that the experimental approach described here will open a path for the systematic exploration of the various aspects of territorial behavior and its role in dispersion, dispersal, population dynamics, and evolution in "the mouse."

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