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SOCIAL ORGANIZATIONS AND REPRODUCTION IN FREELY REPRODUCING COLONIES OF PINE VOLES IN THE LABORATORY

Margaret H. Schadler
Union College, Schenectady, New York

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Union College
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Freely reproducing colonies of pine voles reared in confined laboratory enclosures have a definite social organization and a predictable pattern of reproduction which results in limitation of population size. Colonies that were established in the laboratory with a single breeding pair showed that: 1) populations were self-limiting, 2) rank order existed with the founding female occupying a dominant position in the hierarchy, 3) reproduction was generally confined to the founding female and 4) the non-reproducing members of the colony showed that they did become reproductive when they were paired with normal mates. This paper is a preliminary report of the above events as they were recorded in a study of six colonies in my laboratory.

Six freely growing populations were established in metal enclosures one meter square in size. Enclosures were equipped with covers consisting of two metal trays, 22x36 cm in size, that were raised 5 cm from the floor of the enclosure. Animals were maintained on a photoperiod of 12L:12D at a temperature of 16-18 C. Wood shavings were provided for litter and nesting material and animals were fed Wayne Rat Lab Blox, Wayne Guinea Pig Pellets, apple and water.

Each colony was started with a founding pair in which the female was pregnant with her first or second litter. Populations were permitted to reproduce without disturbance except for cage cleaning and necessary handling until they ceased growing. The end point for cessation of growth was set at 60-90 days after the birth of the last surviving litter except in the case of Pen E. In this pen all the animals died over a weekend because they ran out of water. Colonies were observed 3-5 times a week to record births and deaths and to note behavior.

The six populations showed different growth curves and they varied considerably in their final population size (see Figure 1). In Pens A, B, C, and F the populations ceased growing because as density increased, newborn litters did not survive. Births continued but infant mortality was 100%. In Pen D, births of new litters ceased and the population leveled off. Adult mortality was not a factor except in Pens E and F in which animals died of thirst.

A breakdown by enclosure shows the following:

Pen A leveled off at 11 adults. The largest number was 16 including infants that did not survive to weaning age.

Pen B had 16 adults with a maximum of 20 including infants that died.

Pen C had 28 adults with a maximum of 31 including infants.

Pen D had 8 adults. Growth in size in this cage ceased because the reproductive female stopped having litters.

Pen E lost all its animals at 150 days because the water bottles were emptied over a weekend. At that time there were 16 adults and 5 juveniles that were 36 days of age. Four days before the disaster, two infants were born that survived only two

days. Thus Pen E had 21 adults and juveniles with a maximum of 23 individuals including infants.

Pen F lost animals over the same weekend in which Pen E animals died and again the water bottles were empty. Before the disaster, the colony numbered 23 animals ten of which survived. Afterward, numbers leveled off at 17 animals with a maximum of 21 including litters that did not survive to weaning age.

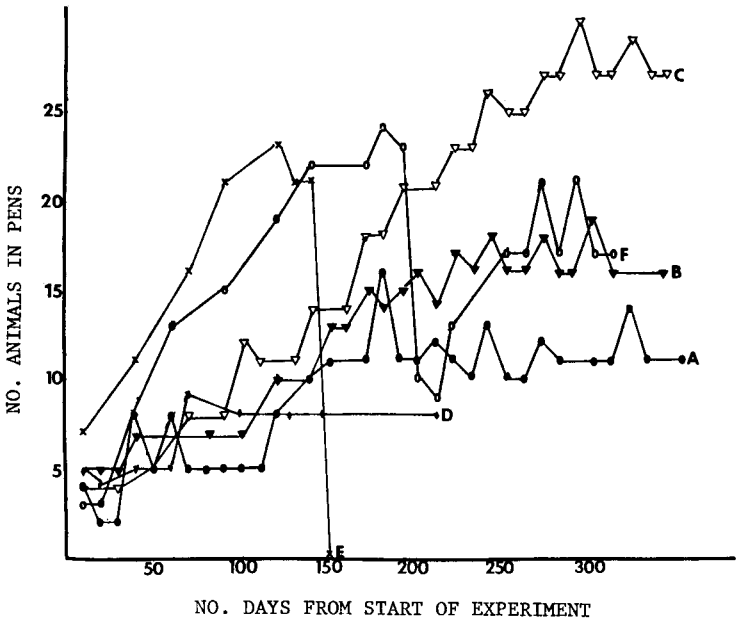

Figure 1. Growth of populations in six experimental pens.

Despite the fact that colonies showed different growth patterns, many generalizations are possible. They are discussed below.

REPRODUCTION

In all pens the surviving animals were post pubertal at the time the experiments were terminated. Only a few, however, participated in reproduction. The following observations were made on the reproducing animals.

Males - mating was not observed. Thus, in the absence of genetic markers it was not possible to tell which males were reproducing.

Females - observations of pregnancy and nursing showed that in all pens except Pen B, only the founding female gave birth. In Pen B, one female from the first generation of offspring had four litters but only

two animals survived from these litters. Thus in the laboratory the reproductive patterns are structured with most births being limited to the oldest female.

After the experiments were completed, non-reproducing animals from four pens were checked to determine their state of sexual maturity. Voles from Pens A,B, and C were sacrificed and their gonads examined histologically. Animals from Pen D were paired with normal, mature mates to check for fertility.

Data show that all of the females born into experimental colonies A, B, and C had tertiary (mature) ovarian follicles (Type 7). Six had preovulatory follicles (Graafian follicles) and two had corpora lutea indicating they had ovulated. Despite the obvious maturity of the gonads, these animals did not reproduce. Testes, on the other hand were not all mature. Most of the males had depressed testicular weights and lowered numbers of mature sperm. All pens contained some males with mature testes. In Pens A and B the founding male had mature testes but in Pen C the testes of the founder had regressed. Pen D voles (four males and four females) were paired with normal mates to check fertility. Three of the females and one of the males had successful copulations within two to four days of pairing and the fourth female conceived fourteen days afterward. Young were delivered after a nomal gestation period. Clearly in Pen D the suppression of reproduction was behavioral rather than maturational.

BEHAVIOR

Pine voles are social and when they are at rest, they cluster in large groups in a preferred spot under cover. Enclosures were equipped with two covers in order to determine if all animals would group under one shelter or if they would disperse and occupy both covers. Colonies had a preferred cover and about 65% of the time all colony members rested under the same cover. If the second cover was used, a minimum of one or two animals used it. The second cover appeared to have more value as a temporary shelter for foraging animals than as a colony resting spot.

Rank order was examined in Pens A, B, and C. Pen A had one dominant female, the founding female and two dominant males, one of which was the founder. Pen B had two dominant females, the founder and one female from the first generation of offspring. This female was the one offspring that became reproductive. Pen B also had two dominant males. Pen C had a single dominant animal, the founding females. The founding male in this cage occupied a very subordinate position. In all cases founding females were dominant. Observations on reproduction showed that all of the dominant females had litters.

The subordinate females showed mature gonads but they did not give birth to litters. The dominant males and in some cases the subdominant males had mature testes but the lowest ranking males had small testes and depressed sperm production.

Activity levels changed as populations grew more crowded. When numbers were low, pens were quiet and activity was restricted to feeding and cacheing. As numbers increased, animals were observed in apparent aimless running outside of the shelters. Threatening sounds and boxing, but not actual fighting and wounding, were common. Food and water were consumed in large quantities and containers were emptied rapidly. In the case of Pens E and F the animals died of

thirst, because extra water bottles were not added to compensate for the increase in activity with the result that existing bottles were emptied over a weekend.

When populations were low, young were well cared for. Nursing mothers clustered with other members of the group but this did not appear to disrupt parental care. Infants were firmly attached to the mother's nipples and they had a high rate of survival. If infants were detached from the mother and removed from the cover, they were retrieved by the mother or by other members of the colony.

As population densities grew, parental care was disrupted. Infants were often observed detached from the mother. If they wandered from the shelter or were removed from it, they were not retrieved or if they were retrieved, members of the colony carried them around the exposed areas of the enclosure and occasionally pulled them from each other's mouths. Adults did not wound or kill infants, but when parental care was disrupted, infants did not survive.

In summary, pine vole colonies are self-limiting because: 1) infants die before they reach weaning age or 2) the reproducing female ceases to deliver young. Establishment of rank order limits the number of reproductive females. Social organization that dictates that animals crowd together regardless of the available space keeps the reproductive female in constant contact with all colony members. As crowding increases and normal activity is disrupted, reproduction and parental care is affected and population growth ceases.