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REPRODUCTIVE PATTERNS IN THE PINE VOLE

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ABSTRACT: Reproductive potential in the pine vole is low compared with other small rodents including other species of voles. Age of maturity is late. Males do not reach puberty before 51 days and females before 77 days. Estrus and ovulation are not spontaneous but tend to be induced by mature males. Gestation is long (24 days). Litter sizes are small (2.8 young weaned per female). Litters are produced less frequently because, although females mate and conceive within 3 days of parturition, prolonged gestation insures a minimum of 24-27 days between litters. Only dominant females in a group carry litters to term regardless of the age of other females in the group. Life span is short and crowding delays reproductive maturity thereby reducing potential for large population increases.

INTRODUCTION: Highlights of the first Eastern Pine and Meadow Vole Symposium noted that a serious pine vole problem exists and that much research will be required to find the real solution to the problem. Control is now exercised through the use of toxicants. However, in New York State environmentalists and wild life groups who were opposed to the use of pesticides succeeded in prohibiting Endrin in 1971. Without Endrin the pine vole problem worsened and last fall as a "stop-gap measure" the Commissioner of the Department of Environmental Conservation lifted the ban temporarily. The lifting of the ban brought many protests but the Commissioner clearly had no choice. The apple crop was in danger and at that point in our understanding of the pine vole, poisoning offered the only consistently reliable means of control. But there may be other ways of limiting pine vole populations. I hereby present my findings on reproductive patterns in the pine vole in the hope that thorough understanding of the life cycle of this animal may suggest other safer means for restricting its growth.

Problems faced by the apple growers notwithstanding, the pine vole has a low reproductive potential compared with other voles. Age of maturity is late. Estrus is sporadic and occurs infrequently in the absence of mature males. Gestation is long effectively increasing the length of time between successive litters and thereby limiting the number of litters during a reproductive season. Litter sizes are small. Only dominant females reproduce which limits numbers of fecund females. Crowding has a deleterious effect upon reproduction. Life span is short and population numbers are self restricting.

REPRODUCTIVE PATTERNS: Age of Reproductive Maturity. Both male and female pine voles matured at a later age than other voles. The earliest age for males was 7 weeks 3 days (51 days) and for females 11 weeks (77 days).

To test age of puberty, twelve young males were paired with females of known maturity. The age at which they were able to sire a litter was noted. All males were successful in siring litters between the ages of 51 and 77 days (Figure 1). As a further check of sexual maturity, histological sections of testes from developing males were examined microscopically. They showed that production of mature sperm did not

begin until the age of 6-7 weeks. By 8 weeks all testes examined showed mature sperm. Table 1 compares age of maturity of pine vole males with 2 other common vole species.

Female puberty was determined in a similar fashion. Twenty three experimental females were placed with fertile males for a period of 24 weeks. The age at which each was able to conceive and carry a litter to term was noted. Twenty one of the 23 were successful in conceiving a litter between the ages of 11 weeks and 24 weeks (Figure 1). By 15 weeks more than half (13 of 21) had matured. An examination of histological sections from ovaries of 8-10 week old animals revealed they were submature. Some contained tertiary ovarian follicles but none had preovulatory follicles or corpora lutea. On the other hand, 89% of 12 week old females had ovaries with preovulatory follicles and corpora lutea indicating

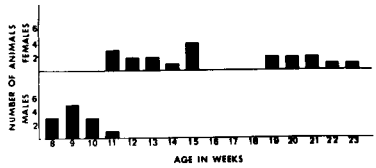

Figure 1. Age at which males successfully sired a litter and females conceived and carried a litter to term.

Table 1. Age at which males of three species of vole sired a first litter

Animal	Age of Maturity in Days	Investigator
M. ochrogaster	35+	Richmond and Stehn (1976)
M. pennsylvanicus	35	Hamilton (1941)
M. pinetorum	51+	Schadler (1977)

+ Laboratory Populations

they had mated and ovulated or were in readiness to ovulate. Table 2. compares age of maturity of pine vole females with other species of voles.

Estrus. Female pine voles did not show estrous cycles comparable to those of laboratory rats and mice. Vaginal smears indicated that all stages of estrus (proestrus, estrus, metestrus and diestrus) occurred in voles but periods were sporadic and often did not occur in the absence of mature males.

Estrus was studied for 28 consecutive days in 10 mature females housed adjacent to mature males in the same cage but separated by a wire barrier to prevent mating. No patterns of cyclicity occurred. Periods of estrus varied from 1 day to 22 days and were separated by periods of diestrus lasting for a minimum of 1 day and a maximum of 9 days.

Males had a profound effect upon estrus. In my experiment 29

diestrus females housed in isolation were placed with mature males.

Table 2. Age at which females of five species of vole conceived a first litter

Animal	Age of Maturity in Days	Investigator
M. ochrogaster	40 40+	Fitch (1957) Richmond & Stehn (1976)
M. pennsylvanicus	25-28	Hamilton (1941)
M. agrestis	21+	Chitty (1966)
Clethrionomys glareolus	32+	Peters & Clarke (1974)
M. pinetorum	77+	Schadler (1977)

+ Laboratory Populations

Twenty four of the 29 reacted by entering estrus by the 5th day (Table 3). Vaginal smears showed the presence of sperm in all estrous animals indicating all females had mated.

Table 3. Number of females in diestrus (N=29) on day zero which showed estrous smears within five days

	Day Number				
	1	2	3	4	5
Number Females	0	0	14	8	2

Mating. Pine vole females were promiscuous and mated during estrus with any available male. The above evidence indicated that the presence of mature males induced females to go into estrus and mate. For this reason a large number of litters can be sired by a single male.

Ovulation. Ovulation was also male induced. In my colony no ovulation occurred without mating. Histological examination of ovaries and Fallopian tubes revealed that ovulation was completed and the ovum in the duct within 24 hours after coitus. This finding concurs with that reported by Kirkpatrick and Valentine.

Gestation. Gestation was 24 days which is long compared with other voles. In my laboratory only one litter out of several hundred was recorded as having been delivered in less than 24 days. These animals were born in 23 days. However, all infants died immediately suggesting they may have been born prematurely. Kirkpatrick and Valentine also noted

a 24 day gestation. Table 4 compares gestation in pine voles with that in other voles.

Intervals Between Litters. The majority of healthy pine vole females produced a new litter every 24-25 days (Figure 2). Females showed immediate post partum estrus and all but a few conceived within 4 days. Those not conceiving immediately usually did not become pregnant for many days or weeks.

Litter Size. Litters were small. The average number of animals born in 150 litters and the number that survived to weaning are presented in Table 5. In the laboratory, females averaged 3.11 young born per litter. However, not all survived and the number reduced to 2.75 at weaning.

Table 4.* Length of gestation and litter size in the genus *Microtus* as determined in the laboratory

Species	Gestation (days)	Litter (range)	Size (mean)	References
arvalis	19-21	N.D.	N.D.	Reichstein, 1964
agrestis	19.7	2-8	4.7	Bread, 1969
californicus	N.D.	1-9	4.7	Colvin and Colvin, 1970
longicaudis	N.D.	N.D.	4.0	Colvin and Colvin, 1970
montanus	N.D.	3-9	6.0	Colvin and Colvin, 1970
"	21	N.D.	4.7	Pinter and Negus, 1965
ochrogaster	21-23	1-8	3.8	Richmond and Conaway, 1969
"	N.D.	1-7	3.9	Colvin and Colvin, 1970
oeconomus	20-21	N.D.	N.D.	Asdell, 1964
oregoni	N.D.	1-6	3.8	Colvin and Colvin, 1970
pennsylvanicus	21	N.D.	N.D.	Lee et al., 1970
"	N.D.	2-8	5.5	Colvin and Colvin, 1970
pinetorum	24-25	N.D.	1.8	Kirkpatrick and Valentine, 1970
"	24	1-6	2.8	Schadler, 1977

* All data except Schadler (1977) excerpted from a review article by Hasler (1975).

Female pine voles have only 4 mammae which precluded large litters.

As might be expected, the survival of litters in the wild is less than that in the laboratory. Field researchers reported 2.0-2.2 young per female. For comparison of litter sizes in the pine voles with that of other voles see Table 4.

SOCIAL FACTORS AND REPRODUCTION: Effects of Crowding. Pine vole reproductive potential was significantly reduced when animals were crowded. Placement of more than 10 newly weaned voles in an enclosure

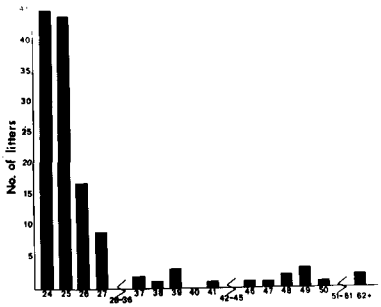

Figure 2. Intervals in days between 132 litters born to permanently paired breeding stock.

(in this case 20 gallon aquaria) resulted in lack of of sexual maturation and no reproduction. Microscopic examination of histological sections of gonads from 12 week old crowded animals (normal ovaries and testes are typically mature at that time) showed incomplete gametogenesis and abnormal appearing gonads.

Table 5. Litter size at birth and at weaning

Number in litter	1	2	3	4	5	6
Number of litters	8	33	62	33	10	4
Total number of animals in each litter size category*	8	66	186	132	50	24
Number surviving to weaning+	8	62	158	110	31	20

*Mean 3.11 ± 0.09
+Mean 2.75 ± 0.09

Effect of Dominant Female on Reproduction. Only dominant females reproduced. In compatible groups of animals with several females reproduction was limited to the dominant animals.

This was demonstrated in one of my experiments which called for freely growing colonies. A freely growing colony is originated by a single reproductive pair. Any young that are produced are not removed at weaning but are allowed to remain in the parent pen. The colonies were maintained for 11 months until they ceased growing at which time all females were 14 weeks of age or older. Only the dominant females reproduced. These females were the founding mothers and in one cage one member of the first litter born to the colony. None of the other females was fertile.

DISCUSSION AND CONCLUSION: Conclusions drawn from laboratory studies about reproduction in the wild may be risky. However, it is probably safe to assume that late age of maturation, induced estrus and ovulation, 24 day gestation and 24-27 day intervals between litters are comparable. We know litter sizes do not differ much. Three different researchers reported litters of 2-2.2 animals per female in the wild compared with 2.75 young raised in the safety of our laboratory.

Evaluation of effects of pine vole social organization upon fertility is probably a bit riskier. However, let us assume that in wild populations crowding does repress fertility. Let us also suppose that reproduction is restricted to the dominant female in any social group. Both conditions have been widely reported for other small rodents and they probably occur in the wild in pine voles also.

Field researchers tell us that pine voles live in social groups or colonies that may number as many as 16 animals. If social factors do indeed affect reproduction, an orchard population may possess only a limited number of fecund females. Because a single male can mate with any number of females, population size depends upon the number of fertile females.

Clearly we are not talking about a large number of reproducing animals in a highly fertile species. Pine voles do not evidence dramatic population explosions and declines as do many other voles. In addition they are short lived. Hayne calculated survival rate for 3 months (when large numbers of females should be coming into sexual maturity) to be 29%. By 5 months the rate decreased to 13% and only 1% lived 1 year. The life cycle of an animal with a low reproductive potential and a short life span has vulnerable points. Perhaps the next stage in the control effort on the pine vole should concentrate on those vulnerable points.