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Pine voles {Pitymys pinetorum (Audubon and Bachman), or Microtus pinetorum (LeConte)} are pests of significant economic importance to orchardists in several eastern and northeastern states. The purpose of this report is to selectively review the status of pine vole research from the control, biological, ecological, and behavioral aspects, and to recommend the research needed to develop effective, economical, and safe programs for controlling this problem.

THE PINE VOLE PROBLEM

Pine voles are causing an estimated annual $50 million loss in apple production in eastern and northeastern U.S. These animals are considered by many orchardists to be the most serious animal pest in orchards. No other pest-caused agricultural problem is driving orchardists out of business. On several farms in New York State, more than 75 percent of the trees have been killed by pine voles.

Direct loss in New York alone is estimated at $12 million annually. McCue (1977) estimated the reduction in apple production in Virginia for the period 1973-75 at $11 million annually. These estimates probably are conservative. Apple growers, extension specialists, researchers, and industry organizations have described significant losses of apple trees and reduced vigor in damaged trees throughout the range of the pine vole (Pearson 1977, Smith 1977, Kolbe 1977, McCue 1977, Clark 1977, Butler 1977, Showalter 1977, Lowe 1977, Barber 1977, Ferguson 1977).

Damage to food crops by pine voles was noted over 100 years ago by Kennicott (1857). Hamilton (1935) estimated that orchard mice (Microtus spp.) caused a $500,000 annual loss to fruit trees in New York, and he reported a similar figure for Connecticut. Garlough (1944) described an orchard near Charleston, West Virginia, in which one thousand 18-year-old trees were killed by pine voles.

Pine vole damage to apple trees is usually confined to subsurface root destruction in contrast to surface trunk girdling by meadow voles (Microtus pennsylvanicus). Larger roots are frequently completely stripped of bark and cambium while smaller roots are entirely cut away.

HISTORICAL REVIEW

Taxonomy and Distribution. One member of the genus Microtus, subgenus Pitymys, occurs in the United States. The subgenus contains two species and six subspecies. Only two of these subspecies, M. p. pinetorum and M. p. scalopsoides are considered within the scope of this report. The former occurs from Virginia south to Georgia and Alabama and west to Illinois. The latter occurs from Virginia north into New England, west into Iowa, and thence south to Kentucky (Hall and Kelson 1959).

Reproduction. The literature clearly defines a relatively low reproductive potential for pine voles. Embryo counts from numerous studies indicate a mean litter size of approximately two with a maximum of four (Hamilton 1935, Richmond and Roslund 1949, Gifford and Whitehead 1951, Roberts and Early 1952, Horsfall 1963, Miller and Getz 1969, Paul 1970). The breeding season appears continuous from about February to October-November throughout the range of the pine vole (Hamilton 1935, Benton 1955, Miller and Getz 1969, Paul 1970). The annual peak in breeding activity occurs in September-October. Recent evidence provided by Horsfall (1963) and Richmond et al. (1977) indicates females were pregnant each month of the year. Thus, it appears that the duration of the breeding season may be controlled by geographic and physiographic influences and other environmental factors. Paul (1970) reported a potential of up to 12.5 litters female/year. The gestation period for captive females is approximately 24 days (Kirkpatrick and Valentine 1970).

Population Structure. Pine vole sex ratios have been reported as 1:1, and during the summer months 45 percent of the population consists of subadults and young (Miller and Getz 1969, Paul 1970). Extreme variations in both ratios were noted depending on population density, reproductive activity, and time of year.

Longevity. The low survival time for pine voles is described by Richmond and Roslund (1949), Gifford and Whitehead (1951), Roberts and Early (1952), Conner (1960), 1966), and Gentry (1968). Miller and Getz (1969) show that only about 19 percent of males and females were recaptured 2 months after their first capture. Hayne (1977), in his projection of survival rates over time, suggests that a population of pine voles would be eliminated (reduced to 1 percent of its original size) in about 330 days--assuming no recruitment. The average and maximum survival times shown by Miller and Getz (1969) was 2-6 months and 12 months, respectively, similar to those described by Burt (1940) and Stickel and Warbach (1960).

Population Cycles and Fluctuations. Pine vole populations have been described as cyclic, but there have been few long-term studies specifically designed to study this phenomenon and the published data are somewhat contradictory. Hamilton (1935, 1938) cites three instances where pine vole populations drastically decreased or increased during periods of 2-5 years. He attributed these fluctuations to cyclic behavior. Benton (1955), however, found no evidence of cyclic tendencies during his study. Annual fluctuations in population density are described by Benton (1955), Gentry (1968), Miller and Getz (1969), Paul (1970) and Gettle (1975). Population density varied widely within and between specific locales and appeared to be related to interactions between environmental conditions and intrinsic factors. For example, Gettle (1975) found that pine vole populations in Pennsylvania were highest but less mobile in the fall and lowest and more mobile in the spring.

Population Density. Accurate estimates of pine voles per unit area in orchards are difficult to project because habitat factors (topography, soil type, soil moisture) can have a significant impact on distribution. Horsfall (1951, 1964) estimated vole density at close to 80 per acre (approximately 2 per tree) in a heavily infested orchard in Virginia. Hamilton (1938) estimated populations as high as 200-300 per acre in an apple orchard in New York. Population densities in non-orchard or natural habitats (mixed woodlands) are normally significantly less than that found in-orchard (Stickel and Warbach 1960). Thus, it appears that the orchard environment provides pine voles an optimum habitat with maximum carrying capacity. A single burrow system normally provides space for one to three pine voles, although Byers (1977) found extremes of up to 22 voles per tree in Virginia. Byers also observed that under serious damage situations it was not uncommon to find up to 10 percent of the trees harboring eight or more pine voles.

Habitat (orchard only). Pine voles are basically fossorial. Burrows, 1 to 2 inches in diameter, are generally very shallow, usually no more than 3 or 4 inches deep but occasionally may attain a depth of a foot or more. The deeper zones of the burrow system are usually confined to the tree trunk area. Nests and food caches are usually found in these deep systems (Byers 1977). Surface and subsurface runways are usually confined within the dripline of individual trees. On the surface, the presence of pine voles is indicated by trails, partial tunnels, mounds of soil at the terminals of active burrows, vertical and near horizontal burrow openings, and, all too frequently, dead or dying apple trees.

Movement and Activity Patterns. Studies of pine vole movements have centered around home range and daily movement patterns. Horsfall (1956) noted 1/4 acre as a maximum home range in Virginia apple orchards, but considered the average much smaller. Fitch (1958) reported that 70 percent of the pine vole recaptures occurred within 10 yards of previous captures. Stickel and Warbach (1960), in a woodland habitat, recorded movements of less than 40 yards for 14 of 16 pine voles captured four or more times. Miller and Getz (1969) noted the average maximum diameter of home ranges (greatest distance between captures corrected for trap spacing) as 32.7 to 33.7 meters for females and males, respectively. Paul (1970) observed that the home range and movement of pine voles was related to tree spacing with colonies of mice occupying a one to four tree area intrarow. This observation was expanded on by Sullivan (1977) who found that an average of about 40 percent of the pine voles were captured in more than one row of trees, and 13 percent in more than two rows with linear, intrarow movements of up to 120 feet.

While pine voles spend a considerable time underground, they are easily trapped from surface runways. Activity periods are about equally divided between day and night but are subject to modifications related to extrinsic conditions (Miller and Getz 1969, Paul 1970).

Limiting Habitat Factors. Hardy (1945) found that soil texture had a distinct effect on the local distribution of mammals, especially the burrowing or fossorial forms. Although opinions vary, a consensus indicates that soil type (light soils and humus), rather than the composition and density of the vegetative understory, is the most important factor in determining the occurrence and distribution of pine voles (Hansen 1946, Jameson 1949, Neill and Boyles 1955, Foreman 1956, Paul 1970). Studies by Fisher (1976) suggest that pine voles require soils with greater than 35 percent gravel, 20 percent clay and 25-48 percent sand.

Miller and Getz (1969) concluded that the distribution of pine voles was essentially restricted to moist, well drained sites. Paul (1970) also explored the possibility that soil moisture was a critical factor in site selection by pine voles, i.e., areas where trap success was high during wet periods yielded poor trap response during the dry season. Benton (1955) and Paul (1970) attributed this low trap success to vertical downward migration. However, it is possible that natural mortality and/or lateral migration might also have occurred.

Food Habits Preferences and Nutrition. The literature on pine vole food habits dates back over 100 years; however, to the present day, few if any long-term studies have been conducted to develop a comprehensive picture of inter-intra-orchard diets, preferences, nutrition and seasonal variation in the diet. Initial investigations (Audubon and Bachman 1851) mentioned peanuts and seeds of grama grass (*Bouteloua* spp.) as dietary components. Underground plant parts are frequently mentioned as preferred foods (Quick and Butler 1885, Hahn 1908, Schmidt 1931). Perhaps the first reference to bark damage was noted by Kennecott (1857). While some authors felt that pine voles fed mainly on succulent roots and tubers (Hamilton 1938), more recent additions to the literature show that diet is more variable, including both above- and below-ground plant parts. Indications of opportunistic feeding were described by Gifford and Whitehead (1951) who reported voles with stained abdominal walls from eating pikeberries, while the flesh of another group of voles smelled strongly of wild onion (*Allium* spp). Benton (1955) stated "the orchard pine mouse appears to subsist largely on grass roots and stems during the summer, fruit and seeds during the fall, and bark, roots and possibly stored food during the winter." Benton also reported that the normal diet contained only small amounts of animal matter, yet Sim (1934) found that voles readily accepted larvae of Japanese beetle (*Popillia japonica*). Various sources indicate that apple tree roots are not a preferred food. Kirkpatrick and Noffsinger (1977) found that pine voles feed primarily on above ground vegetation (grasses and forbs) and feed on roots only when other foods are in short supply. They found some root (apple tree) fragments in the stomachs throughout most of the year but larger amounts (7 to 14 percent of the identifiable epidermal material) were found only during the January-March period. This observation tends to isolate the winter months as the major period of apple tree damage by pine voles.

Evidence of food caching by pine voles is conflicting, but most authors tend to agree that pine voles cache rootstocks, stems, and leaves in both orchard and natural habitats.

Recent studies by Noffsinger (1976) and Estep et al. (1977) indicate that well-managed orchards provide pine vole populations with an ideal habitat from the standpoint of nutrition. They found that while body fat levels were not consistently different between managed and abandoned orchards, there was a marked decline in fat stores during the autumn months in abandoned orchards. The dry weights and percent digestible energy of the stomach contents were markedly lower in voles from abandoned orchards, especially during the early autumn.

Behavior. Basic and applied studies of pine vole behavior are almost nonexistent. A sampling from the literature shows that all behavioral research is keyed to two phenomena--inter-species associations (Fitch 1958, Calhoun 1959, 1964, Paul 1970) and intra-species antagonism (Kimball 1972).

CONTROL METHODS

Little effort was expended to develop ways and means to control pine voles (or damage) until 1934 when the U.S. Fish and Wildlife Service initiated a program to evaluate toxicants, baits and baiting techniques. Much time and effort has been spent on this avenue of research by the Federal government and other agencies and groups with few efforts made to gain a better understanding of the pine vole/orchard problem. In recent years the initiative for basic and applied research and the development and evaluation of new control methods has shifted from the USFWS (DWRC) to other agencies, primarily state universities and Cooperative Wildlife Research Units in the problem area.

Many publications detail ways and means of controlling pine voles with poison baits, most utilizing materials such as zinc phosphide, chlorophacinone (Rozol) and diphacinone (Ramik Brown) on either grain or cubed apple carriers (O'Neal 1977, Byers 1977). When properly carried out, these methods can be effective, offering temporary relief (Tietjen 1969, Byers 1977). However, field trials employing these agents indicate that, while they are effective if used on a consistent basis, they all suffer from certain common weaknesses--(1) time-cost economics, (2) lack of trained and dedicated applicators, and (3) inherent use limitations (if applied mechanically). These shortcomings restrict general acceptance and use of toxic baits in many areas.

The development of endrin as an area spray for controlling pine voles (Horsfall 1954, 1956) has also received much publicity--at least 95 publications dealing directly with the pros and cons of its use in orchards and conifer plantations. The technique has met with questionable success. Hayne (1970) concluded that endrin ground spray for the control of pine voles . . . "may on occasion reduce activity in orchards." The reasons for the failure of endrin under certain conditions are not readily apparent; however, both endrin resistance in some populations (Webb and Horsfall 1967, Byers 1977) and the characteristics of the vegetative ground cover (Webb and Horsfall 1969) have an impact on the effectiveness of this contact toxicant. Horsfall further speculated that the occurrence and abundance of pine voles is regulated by ground cover type, and that endrin spray treatment is ineffective in heavy grass cover because grasses are not a preferred food. Additional difficulties with endrin may be encountered in the form of residues on fruit and hazards to nontarget species. Numerous recommendations against its use in orchards appear in the literature (Eadie 1957, Hamilton 1966, Small 1958, Fitzwater 1953, MacNay 1965). In spite of the many problems associated with the use of endrin, many growers feel it provides their main (and only) line of defense against pine vole damage and it is still used in some apple growing regions during the dormant season. However, the future of endrin is in doubt since it is under Rebuttable Presumption Against Registration by the EPA (Markley 1977), and other methods of control are urgently needed.

New control techniques have been under evaluation in recent years and include the use of anticoagulant-treated baits (e.g., chlorophacinone {Rozol}, diphacinone {Ramick Brown}, ICI 581, and LM 637), anticoagulant area sprays, selected herbicides to eliminate preferred foods (Byers 1977, Young 1977), and various cultural techniques modifying orchard flora to destroy or enhance vole habitat (e.g., establishment of buffer foods).

RESEARCH NEEDS

Vital quantitative information about the pine vole problem is lacking because past research has emphasized chemical control. The long-heard contention by some orchardists and scientists that research need only provide an effective chemical to kill pine voles has in recent years been largely replaced by the recognition that the pine vole problem may be very amenable to nonchemical control methods. Only within the past few years has the Service provided funds to universities for studies on the ecology of the pine vole problem. These studies, though limited in scope, suggest that nonchemical control methods may be very promising.

The limited and disrupted distribution of pine voles, both seasonally and geographically, indicates that this species is not readily adaptable to a wide range of habitat types or conditions. If there are certain factors that are limiting the occurrence and abundance of pine voles, and they can be detected, we may be able to exploit this knowledge to adversely affect pine vole populations by manipulating their habitat. Future pine vole research, therefore, should be broad in scope and include studies of the economics of damage, pine vole biology, physiology, behavior, movements, and habitat requirements, as well as the development of control methods.

Economics of Damage/Damage Assessment

Economic data on the impact of pine vole damage to apple orchards are incomplete; however, we do know that pine voles are causing intolerable losses to orchardists. Current loss figures probably are conservative, since they are based primarily on the costs of tree replacement and do not reflect declining yields from vole-damaged trees over the several years prior to replacement. This lack of quantitative damage data is due to inadequate techniques for measuring declining yields resulting from subterranean damage to tree roots. The development of a technique to assess damage prior to replacement, possibly by physio-electric measurement of tree vigor, is needed. Such damage assessment data would provide: (1) more reliable estimates of losses, (2) a basis for determining cost-benefit ratios of new control methods, (3) a method by which the orchardist and researcher could determine the extent of infestation within an orchard before extensive tree loss occurs, and (4) a measure of efficacy of experimental and currently used methods of pine vole damage control.

Ecology

Pine Vole/Meadow Vole Relationship. Because pine and meadow voles often occupy the same orchards, the relationships between the two species is of particular interest. Field studies are needed to determine what occurs when one of these species is eliminated from an orchard. Data are needed on the interactions between pine and meadow voles and on the changes in the numbers and distribution of these species that may occur throughout the year. Without knowledge of the interdependencies of these species, control measures may result in an even greater problem by improving the habitat for the surviving species. For example, the control of meadow voles in some orchards may have resulted in more severe pine vole problems.

Habitat. Research findings indicate that cultural practices, soil type (e.g., amounts of clay, gravel, sand, and humus), and composition of understory vegetation are correlated with the occurrence and distribution of pine voles. The occurrence of pine voles also has been observed to be virtually restricted to active apple orchards, and that their numbers are greatly reduced or they are absent in abandoned orchards. Comparative inter- and intra-orchard studies are needed to better define vole habitat requirements. Such information may provide clues to ways of reducing pine vole populations.

Food Habits. The meager data available about pine vole food habits indicates that pine vole density declines in orchards treated for several years with herbicides. Grasses, when available, constitute the bulk of the vole diet. The dependency on grasses also may be the cause of a decline or disappearance of pine voles in abandoned orchards, which generally exhibit increased forb density and a decrease in grasses. The relationship between high pine vole densities and the ratio of grasses to forbs required to maintain these high population levels is not clear and requires study. Studies of vole food habits and the effects of herbicides on orchard vegetation are needed in a wide variety of orchards with diverse vegetative composition and cultural practices. Such research has good potential for producing low-cost control methods.

Distribution of Voles in Orchards. The distribution of pine voles and associated vertebrate fauna in orchard habitat is not well documented. For example, pine and meadow voles do not usually inhabit the basal area of the same tree. Knowing the distribution of both species in orchards, together with damage and population data, would provide a basis for optimizing control techniques.

Behavior and Physiology

We are handicapped by our lack of knowledge about the behavior and physiology of pine voles. The limited habitat and fossorial existence of pine voles indicates a finely tuned physiological-behavioral order. The disturbance of this order could result in a reduction of this pest species. Sensory systems, such as olfaction, perhaps in relation to reproduction or the identification of foods or of other inhabitants within the community, would seem to offer a reasonable starting point for such investigations. The sporadic activity of voles may be cued by environmental factors. The identification of these behavioral cues may show that they are amenable to disruption. This area of inquiry is so broad and unexplored that virtually any point of investigation could lead to the development of control methods.

Movements

Seasonal. Although daily movements and home ranges have been fairly well determined, seasonal movements have not been investigated. Theories regarding the vertical and horizontal movement of pine voles in response to climatic stresses (summer and winter) are speculative. However, it seeems reasonable that extremes in soil moisture/temperature, and climatic conditions could be important in initiating movements. Data on the influence of climatically induced stress and its resulting effects on the pine vole, whether it be movement, mortality, or other behavior, will yield valuable knowledge about the periods of greatest vulnerability to control.

Immigration/Emigration. We do not know the extent and distances involved in vole immigration and emigration into and from stable (non-controlled populations, areas where populations are suppressed, or areas adjacent to suppressed areas. The inter- and intra-behavior between pine vole residents and immigrants is not known. Knowledge of movements and associated behavior would provide data for determining the frequency of application of control methods and for determining the need for either separate or simultaneous control of pine voles and/or meadow voles.

Population Dynamics

Population Density/Damage Potential. Orchards have been observed where high vole populations do not cause significant damage. Conversely, in other orchards, major problems have been caused by only a few animals. Studies are needed, therefore, to determine the relationship between pine vole densities and the amount of vole damage at various seasons of the year.

Cyclic Patterns. Some investigators attribute a cyclic population pattern to pine voles, as is common to other microtine rodents. This basic aspect of pine vole biology is of intense interest in the development of control methods because if this species is predictably cyclic, we could predict damage trends and thus optimize control strategies.

Reproduction. Data are needed on pine vole reproduction potential in various habitat types. This research is essential if we are to be able to determine factors that affect reproductive potential and the long-term efficacy of new control methods.

Mortality. Knowledge of natural mortality rates in pine vole populations is needed to aid in the development and evaluation of control strategies. Further, this information would be of value in developing population models having a predictive value in the development and application of control methods. The limited literature on pine vole longevity indicates that only about 20 percent of a population lives longer than 4 months. If this short life span is truly representative of the species, it may be possible to identify and utilize causative agents within the environment to adversely affect vole life span.

Repopulation. Recovery of pine vole populations after successful reductional control may result from accelerated reproduction in the residual population, and also, in part, to invasion from adjacent areas. This little-known aspect of pine vole population dynamics should be studied in order to evaluate proposed control methods.

Control Methods Development

Cultural Practices. Most investigators concur that pine vole density decreases when orchards are abandoned. Observations also show that pine voles do not occur in some active orchards, but will occur in large numbers in adjacent active orchards. These observations suggest the possibility that certain cultural practices are detrimental to vole populations. Although the gathering and interpretation of these data would be a formidable task, it is essential that it be done.

Physical Barriers. The most economically expedient control, in some rodent damage situations, has been to physically restrict access to the depredating species. This might involve installing voleproof exclosures around the perimeters of orchards. Physical barriers may offer complete and economical protection over an extended period, and, as such, are a control technique to be explored.

Chemical Control Agents. In view of problems associated with direct chemical, e.g., hazards to nontarget species, high registration costs, chemicals may be the least promising approach for controlling pine vole damage. The history of the Service's role in pine vole research has followed a single basic course consisting generally of the development of lethal baits. This approach has been only marginally successful. Chemical control research should not receive undue emphasis but should be an essential part of an overall research program. Research on chemicals should be broadened to include studies of the physiology of target species to determine if physiological uniqueness is present that could be exploited in the development of highly selective chemical stressing agents.

EPA Registration

The development of a new chemical control agent to meet EPA registration requirements currently costs from $4 to $6 million per chemical. In view of these enormous costs, and the fact that such chemicals have a limited market and produce little profit for the chemical industry, most of the future costs of chemical development must be borne by the FWS.

PROJECT REQUIREMENTS

The proposed research should be planned and implemented so that the various components are of high priority and will comprise a balanced and integrated research program. Research should be identified that would seem to offer the most direct route to problem solving, and that would yield data relevant to the entire program. Once priorities are set, research documentation should be prepared for each major area of research--problem definition, ecology, behavior and physiology, population dynamics and control methods development. The scope of the program will permit simultaneous research on each major area of interest and provide ample funds for Service pertinent contract research. The primary goal should be the development of species-specific integrated control programs that can be used throughout the range of the pine vole.

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