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Hygnstrom, Scott E.; Vercauteren, Kurt C.; and Schmaderer, Thomas R., "BIOLOGICAL MANAGEMENT (CONTROL) OF VERTEBRATE PESTS-ADVANCES IN THE LAST QUARTER CENTURY" (1994). *Proceedings of the Sixteenth Vertebrate Pest Conference* (1994). 28.

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BIOLOGICAL MANAGEMENT (CONTROL) OF VERTEBRATE PESTS-ADVANCES IN THE LAST QUARTER CENTURY

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ABSTRACT: In 1967, Howard provided a review of biological control of vertebrate pests. The term "biological control" was borrowed from the field of entomology, where it has been traditionally defined as "the reduction in number or density of pests through biological processes such as predation, pathogens, habitat modification, and fertility control." Current philosophy in wildlife damage management advocates "the reduction of damage to a tolerable level" rather than "the reduction of the number or density of vertebrate pests." Therefore we abdicate the term "biological control" and encourage the use of a new term, "biological management" of wildlife damage. Advances in science in the past 25 years have led to the testing and potential development of several biological methods for controlling wildlife damage and nuisance problems. We provide a nonexhaustive review of research in the following areas: secondary plant defense compounds, morphological plant defenses, predator odors, predation aversion compounds, pheromones, habitat modification, introduced and endemic predators, micro- and macroparasites, and fertility control through chemosterilants, genetic manipulation, and immunocontraception. No methods have been fully developed or are without problems. Several constraints associated with the development of biological management strategies are discussed.

Proc. 16th Vertebr. PestConf. (W.S. Halverson& A.C. Crabb, Eds.) Published at Univ. of Calif., Davis. 1994.

INTRODUCTION

Scientists and managers have attempted to control vertebrate pests using a variety of biological processes, including habitat manipulation, predators, pathogens, and fertility control. In general, public support for "biological control" is high because of the perceived reduction in use of chemicals, associated natural processes, and "greenness" of the control methods. In reality, most applications have had only limited success and have in some cases had serious negative environmental consequences. Significant efforts have been made during the last 25 years to identify, refine, and develop biological methods that reduce damage and nuisance problems caused by vertebrate species, but a great deal more must be done. Our objectives are to 1) present a historical perspective of biological control, 2) suggest new terminology, 3) provide examples and a nonexhaustive review of research and developments in the past 25 years, 4) discuss current constraints, and 5) speculate on future advances.

HISTORICAL PERSPECTIVES

In 1967, Walter E. Howard presented a paper entitled "Biological Control of Vertebrate Pests" at the Third Vertebrate Pest Conference in San Francisco, California. In the same year, he authored a chapter on "Biocontrol and Chemosterilants" for a book on pest control, published by Academic Press. In those papers, Howard provided an overview of biological control methods that had been researched or employed to date. He defined biological control of vertebrate pests as

"an attempt to reduce the population density of a pest species (i. e., increase mortality, reduce natality, or cause a significant emigration) either by increasing predation, manipulating the conditions of the habitat, introducing or stimulating epizootics, or by the application of antifertility agents."

Howard also differentiated biological control from "conventional control," which includes exclusion,

frightening devices, repellents, toxicants, trapping, and shooting. To his credit, Howard recognized that the goal of vertebrate pest control is not to just reduce pest populations, but rather to alleviate damage. The term "biological control" is one that has been borrowed from the field of entomology, where it has been traditionally defined as "the reduction in numbers or density of pests through biological processes such as parasites, predators, or pathogens." In dealing with insect pests, such a definition is accepted, if not encouraged, as the public cries out for control campaigns against mosquitoes, flies, aphids, leafhoppers, and cockroaches. Such approaches, however, would not be acceptable in today's field of wildlife damage management. The axiom "to reduce the number or density of vertebrate pests" is now often insufficient or inappropriate. Today's directive in wildlife damage management is to "reduce damage to a tolerable level." Therefore, we encourage that wildlife biologists, vertebrate pest specialists, and pest control operators drop the old and borrowed terminology of "biological control" and adopt "biological management," a term that is more descriptive and better reflects the goals of contemporary wildlife damage management.

While biological control had been quite effective with several insect and weed pests, applications to vertebrate pest problems had only limited success and in some cases had serious negative consequences. Howard was able to report on a few successful applications in 1967. During the past 25 years, a significant number of studies have been conducted in the areas associated with biological management of vertebrate pests. Regrettably, there are still few refined methods in regular practice.

RECENT ADVANCES IN BIOLOGICAL MANAGEMENT

To generate information on this subject we conducted key word computer searches of the following library data bases: AGRICOLA, BIOSIS, Commonwealth Agriculture, Commonwealth Zoology, Current Contents, FWRS, IRIS, and Wildlife Review. Through these searches we

generated 560 titles related to biological management since 1967. In addition, we used a bibliography entitled "Biological Control of Vertebrate Pests" by Marsh (1979) and browsed the Literature Cited or References sections of most papers on biological management that we obtained. We have taken a rather liberal view of the definition of biological management so as to not exclude any pertinent studies. As a result, some readers may feel that some methods should be considered only as contemporary control methods. Although the review presented here is not exhaustive, we do intend to develop a complete annotated bibliography on biological management in the near future.

HABITAT MANIPULATION

Substantial research has been conducted on habitat manipulation through biological mechanisms. We identified 42 papers that could be included in the following categories: chemical plant defense, morphological plant defense, animal predator odors, dispersal pheromones, and physical manipulation.

Chemical plant defense. Several secondary defense compounds have been identified and isolated that affect the susceptibility of plants to herbivory. Most are alkaloids or phenolic compounds such as tannins and turpenes. Wildlife species regularly exhibit strong selective behavior for or against certain woody plant species, varieties, and even individuals within species (Radwan and Crouch 1974, Dimoc et al. 1976, Chiba 1977, Rousi 1983, Pigott 1985, Mole and Waterman 1987). Researchers have isolated several chemical compounds that affect the susceptibility of woody plants to herbivory (Radwan and Crouch 1978, Bryant et al. 1985, Palo 1985, Reichardt et al. 1987, Greig-Smith 1988, Rousi et al. 1988, Sinclair et al. 1988, Joiga et al. 1989, Crocker 1990, Jakubas and Gullion 1990, Reichardt et al. 1990, Vainiotalo et al. 1991). Some selective breeding for damage resistance and varietal testing has been conducted (Chiba and Nagata 1969, Chiba et al. 1982, Knudson et al. 1992) and lists of damage-resistant plants have been assembled (Cummings et al. 1963, Fargione et al. 1991, Marsh 1991). Vertebrate-resistant varieties, however, have yet to be genetically engineered and marketed. In addition, scientists have questioned if secondary plant defense compounds are a part of static defense or are actively induced by herbivory (Haukioja and Neuvonen 1985, Bryant et al. 1988). Both mechanisms are important factors regarding the genetic development of damage-resistant plants.

Morphological plant defense. Morphological features such as spines, thorns, barbs, pubescence, and other growth forms can increase damage resistance to herbivory. Research on physical mechanisms of plant defense in agricultural crops has focussed primarily on reducing susceptibility to insect damage. Limited research, however, has been conducted on resistance of corn, sorghum, and sunflower to vertebrate damage. Morphological features thought to increase damage resistance in sunflower include concave heads, heads that face the ground, long head-to-stem distance, long bracts, and seeds with tough fibrous hulls (Parfitt 1984, Hagen

and Hanzel 1992). Genetic backcrossing and isolation of the germplasm that codes for these morphological features is underway. Similar work has been done by researchers working to improve trees for timber production (Raulo 1981, Rousi et al. 1988).

Dispersal agents. Research has been conducted on materials that cause dispersal of various vertebrates from an area. Most of these are predator odors that stimulate herbivore dispersal. Early anecdotal accounts illustrate the use of lion and tiger urine and feces in gardens and orchards. The idea of using predator odors and sociochemicals as dispersal agents for crop protection was championed by Shumake (1977) and Muller-Schwartz (1983). Sullivan and colleagues isolated odors from the stoat (*Mustella erminea*), ferret (*M. putorius*), and red fox (*Vulpes vulpes*) and successfully used them to disperse voles (*Microtus* spp.) and pocket gophers (*Thomomys talpoides*) from orchards (Sullivan et al. 1988a,b). The researchers also synthesized predator odors and developed delivery systems for the most effective materials (Sullivan et al. 1990a,b). More recently, Swihart (1991) reported that bobcat urine reduced woodchuck damage to fruit trees by 98.3%. Predator avoidance is innate and potentially adaptive, which would lead to the selection of individuals that respond in a positive manner (Gorman 1984).

Other dispersal agents include predator aversion compounds and species-specific pheromones. Kanehisa et al. (1989) extracted taste aversion compounds from insects and effectively repelled sparrows from an area. Muller-Schwartz (1983) examined the behavioral significance of a variety of mammalian pheromones and speculated on their uses as damage management agents. Stoddart (1988) provided a review of rodent behavioral responses to pheromones and other odors.

Habitat Modification. Modification of habitat is often considered a "conventional" control method, however, where biological mechanisms are involved, those practices could be considered as biological management. For example, Hlavachick and Sullivan (1981) reported that black-tailed prairie dog (*Cynomys ludovicianus*) colonies could be reduced substantially by deferring livestock grazing for one year to allow tall-grass species to grow tall and rank. The opposite strategy was used by Long (1989) in Wyoming, where parcels of public land were burned, sprayed, and fertilized to attract elk (*Cervus elaphus*) away from sensitive agricultural areas.

PREDATORS

The role of predators in controlling vertebrate pest populations has been questioned extensively during the past 25 years. We found 94 papers that dealt with the active introduction of exotic species or the encouragement of native predators. A rather dim light was cast over the exotics, but management of native predators may still play a role in controlling vertebrate pests (Howard 1967a,b, Newsome 1990). Unfortunately, not enough is known about the roles and interactions of vertebrate predators and pests in natural systems.

Introduced exotic predators have not consistently reduced damage or pest populations, and in several cases

have become pests themselves by preying on desirable vertebrates (Howard 1967a,b). A classic example is the mongoose (*Herpestes anropunctatus*), introduced to control rats (*Rattus* spp.) on Jamaica in 1872 (Laycock 1966). Although initially successful in reducing rat populations, mongooses were not particular about their prey, and nearly extirpated four species of ground-nesting birds. Nearly 20 years later, the mongoose, originally considered very beneficial, came to be regarded as the greatest pest ever introduced to Jamaica.

Today there are regulations and significant social pressures against the importation of exotic predators because of the impacts they may have on nontarget wildlife, livestock, and concerns about human safety. Although attempted occasionally by individuals, the most recent government-sanctioned program dealt with the importation (parachuting) of domestic cats in an ill-fated attempt to control rodents on Pacific islands (Harrison 1965, Pomerantz 1971).

Predator-prey relationships among native species relative to population control applications were studied extensively in recent years. All authors reported that predators took pest species, but none were able to ascertain whether they controlled or regulated pest populations. Hall et al. (1981) found that artificial perches significantly increased raptor numbers in agricultural areas. In a related study, Howard et al. (1985) reported that there were no measurable reductions in rodent pest populations in agricultural crops, nor of pest birds in vineyards, where raptors were encouraged with artificial perches. Similar results were reported by Askham (1990). Researchers in Chile reported that rodent pests in pine plantations were controlled by avian and mammalian predators (Murua and Rodriguez 1989, Munoz and Murua 1990). Perch sites were provided and habitat modification increased prey vulnerability. Barn owls provided limited reduction of prey species in Israel (Kahila 1991). Native predators may exert some control over prey species in certain situations, but they are unpredictable, and cannot be relied on to prevent or control wildlife damage. Vertebrate pests have evolved with endemic predators and their numbers often fluctuate in synchrony with predator populations. Often it is the number of prey present that determines the number of predators, not vice versa (Marsh 1984).

Finally, predators do not necessarily have to reduce prey populations to be effective at reducing damage. Falconry has often been used as a hazing technique to disperse other birds from airport runways (Erickson et al. 1990).

PATHOGENS

The most active research in biological management techniques has been in the area of competitive pathogens and much hope is held for advancement in this area (Dobson 1988). Pathogenic agents must meet several criteria, however, before they can be used for biological management (Shingleton and Redhead 1990, Spratt 1990). Criteria include: 1) high host specificity, 2) direct life cycle, 3) transmission by aerosol or highly mobile vectors that can flourish throughout the range of the target species, 4) pathogenicity that is density dependent, 5) inexpensive to maintain in the laboratory, 6) all national

import regulations must be met if they are non-endemic, 7) little genetic resistance in target species, and 8) pathogenic effects must meet minimum animal welfare considerations. We found 385 papers that dealt with the etiology and ecology of viruses, bacteria, and macroparasites, and their role in controlling vertebrate pest populations. Most of the papers, however, dealt with one disease—myxomatosis.

The *Myxoma* virus was introduced to Australia in the 1950s to control European rabbits (*Oryctolagus cuniculus*). Initially, the virus was very successful in reducing rabbit numbers, but soon, the virus attenuated and genetic resistance appeared in the rabbit population (Fenner and Ratcliffe 1965, Fenner and Myers 1978, Fenner 1985). Myxomatosis was not effective in controlling rabbit populations in New Zealand because of insufficient populations of arthropod vectors (Howard 1965). Recent literature has dealt primarily with reviews of applications of myxomatosis in other environments (Ross et al. 1989, Lutz et al. 1990) and in the examination of perceived limitations of myxomatosis as a management technique. Most studies dealt with virus attenuation (Parer et al. 1985), resistance in rabbits (Ross and Sanders 1977, Sobey and Conolly 1986, Williams et al. 1990), arthropod vectors (Boag 1988, Parer and Korn 1989), and dynamics of rabbit populations (Ross and Tittensor 1985, Dwyer et al. 1990).

Several authors have discussed the merits of using other microparasites to control vertebrate pests (Gibbs 1985, Bykovskii and Kandybin 1988, Redhead and Shingleton 1988). For example, a feline parvovirus was used to control a population of feral cats on Marion Island—cat density was reduced by 80% over 5 years (Howell 1984). In addition, "salmon poisoning disease," which involves a fish host, trematode vector, and a rickettsial disease agent; has been suggested as a means of controlling coyotes (*Canis latrans*) (Foreyt et al. 1982, Green et al. 1986).

Pasteur and Mechnikov were the first to suggest the use of bacterial pathogens to control vertebrate pests in the mid-1800s. In the late 1800s, *Salmonella enteritidis* was used to control rats in Europe (Wodzicki 1973). Unfortunately, this highly virulent bacteria also infected humans. Several people became ill or died from *Salmonella* poisoning during initial testing of the bacteria for its rodenticidal effects. Subsequent research focussed on the development of less virulent strains (Issatchenko and 5170) that are safer to humans and domestic livestock. A pesticide formulation of *Salmonella*, known as Bacterodenticide, was developed and used extensively in Russia in 1988 to control mice and voles (Bykovskii and Kandybin 1988).

Work with macroparasites has also increased in recent years. Murphy (1991) examined the effects of a cestode (*Vamirolepis straminea*) on reproduction in house mice (*Mus musculus*). He found that the bile duct tapeworm delayed production of the first litter, but had no effects on the size or number of litters, and therefore would likely be ineffective at regulating house mouse populations. Researchers in Australia have examined the use of a hepatic nematode (*Capillaria hepatica*) to affect the mortality and fecundity of house mice (McCallum and Shingleton 1989, Shingleton and McCallum 1990, Spratt

1990, Barker et al. 1991). Shingleton has provided a thorough review of their work in another paper in this conference proceedings.

Herman (1964) suggested that there have likely been many unreported attempts to control wildlife populations with disease-causing organisms. Research on competitive pathogens has been limited because of the hazards such materials present to humans and non-target organisms, and the potential for introduced, widespread epizootics. Epizootics are complex phenomena. Before pathogens can become an important tool in the control of vertebrate populations, there must be a full understanding of the causative agents, hosts, vectors, and other associated biotic and abiotic interrelationships involved. It is likely that substantial work has been conducted in these areas under government contracts for military and defense purposes. Most information of this nature, however, is confidential and unavailable for practical applications. In addition, public acceptance of "biological" or "germ" warfare is likely to be very low, without the strictest assurances and most active educational programs.

Genetic engineering holds much promise in the area of biological management. Through recombinant DNA procedures and gene splicing, pathogens may be refined to increase host specificity and virulence, while reducing persistence in the environment. In addition, for years we have bred plants and animals for increased disease resistance. It certainly seems plausible that we could breed pest species to increase their genetic predisposition to disease agents and infection.

FERTILITY CONTROL

Fertility control through chemosterilization, genetic manipulation, and immunocontraception is the newest and perhaps most promising field in vertebrate pest management. Humans are quite familiar with the concept of birth control and are therefore likely to be receptive to its use in the environment. Fertility control is often perceived as a more humane and socially acceptable alternative to conventional population control because it acts on reducing birth rates rather than increasing mortality (Marsh and Howard 1973). Natality, however, is only one part of the population equation. Compensatory mechanisms are present in most vertebrate populations that may actually stimulate population growth in response to reduced natality. Therefore, continued application of antifertility agents will likely be necessary to maintain populations below prescribed levels. In accordance with integrated pest management principles, fertility control should be used in conjunction with other population reduction and habitat modification techniques.

Research on vertebrate fertility control in the 1950s and 1960s focussed on chemical contraceptives for humans. Through the 1970s and 1980s, new technologies were applied to domestic and wild animals (Bell and Peterle 1975, Matschke 1980, Kirkpatrick and Turner 1985). In 1990, Bomford reviewed 14 chemical antifertility compounds that have been used to alter the fertility of offspring produced, reduce the number of offspring produced, or cause permanent or temporary sterility in either sex. Most chemosterilants act on the hypothalamic-pituitary-gonadal axis and affect hormone release or reception. To date, none of the products

provide environmentally safe, permanent, humane, and nontoxic sterility in both sexes of target wildlife species, and few can be effectively delivered in the field. Two chemosterilants were registered for use in the United States by the Environmental Protection Agency (EPA) during the 1980s: Epiblock (alpha-chlorohydrin) for male Norway rats (*Rattus norvegicus*) and Ornitrol (20,25-diazocholesterol hydrochloride) for female pigeons (*Columba livid*). Both products were only marginally effective in field applications and their registrations were recently cancelled by the EPA.

Several genetic syndromes have been identified that affect fertility and survival in rodents (Stanley and Gumbreck 1964). Genetic manipulation to promote such syndromes would require the alteration of the normal gene pool, either by the introduction of genetic material or mutagenic agents that induce genetic alteration. As a result, animals would become less harmful or less successful in the environment through developing some form of weakness that increases their susceptibility to other natural regulatory factors or by some self-destructive mechanism or behavior (Marsh and Howard 1973). Environmental selection dictates that phenotypic responses that lead to reduced damage must have selective advantages so they are not diluted out of the population. Relatively little work has been done regarding genetic manipulation, yet it holds great potential for future applications in biological management.

Fertility control through immunocontraception is the newest field in vertebrate pest management. The concept involves exposing an animal to a foreign substance (antigen) that will stimulate the animal's immune system to produce antibodies that will attack and eliminate the antigen. Once exposed, an animal will often retain a compliment of antibodies to ward off future exposures. Using these principles, scientists have successfully developed vaccines to combat polio, rabies, and several other diseases. The same approach can be used to stimulate an immunological response that will inhibit reproduction in vertebrates. Several hormones associated with reproduction, as well as proteins from sperm, zona pellucida, embryonic tissue, and fetal tissue may serve as reproductively-antagonistic antigens.

Kirkpatrick and Turner (1985) reported that female horses exhibited a decrease in gonadotropins and ovarian function when immunized with luteinizing hormone (LH), LH-releasing hormone (LH-RH), or follicle-stimulating hormone (FSH). Males experienced testicular atrophy and a decrease in gonadotropin and testosterone production. Several other hormone pathways are possible candidates for use in immunocontraception. The major reservations associated with using hormonally-induced immunization are 1) behavioral and physical side effects, 2) movement of hormones through the food chain, and 3) administration to the animal (Turner and Kirkpatrick 1991).

Sperm antigens have shown promise in the development of immunocontraception. Testicular germ cells and spermatozoa are unique cells that express several gene products that are not found on cells elsewhere in the body (Anderson and Alexander 1983). Some of these molecules are potent autoantigens, but they are isolated from the immune system of males by a blood-

testis barrier system. Pregnancies in female rabbits were significantly reduced when they were immunized with an isozyme of lactate dehydrogenase (LDH-C₄), found only on male rabbit germ cells (Goldberg 1973). The LDH-Q, antigen stimulated the production of antibodies in the females that agglutinated or lysed sperm cells that were introduced into the females. Infertility was reversible in one to two years and could be continued with booster injections. Ovulation cycles continued throughout the infertile period and there were no apparent side effects.

Egg antigens may also play a role in immunocontraception. The zona pellucida, a noncellular glycoprotein layer that surrounds the mature oocyte, plays an important role in sperm binding and protection of the egg during fertilization and early development. Several species have exhibited reduced fertility in females by active immunization with porcine zona pellucida (Turner and Kirkpatrick 1991, Turner et al. 1992). Infertility is the result of blockage of sperm receptor sites on the ovum, altered ovarian follicle growth and function, and possibly autoimmune activity associated with the ovary itself.

Research will continue to isolate antigens through the use of monoclonal antibodies, to construct antigens through recombinant DNA, and to develop a better understanding of the physiological processes of immune systems. In addition, the efficacy of antigens will continue to be improved by experimentation with antigen dose, adjuvants, routes of administration, and immunization schedules (Anderson and Alexander 1983). Ecological studies must also be conducted to determine the impact of immunological strategies on population dynamics and social structures of candidate species.

One of the primary barriers to fertility control is the lack of feasible delivery systems. Many of the fertility control agents currently available require repeat doses to be effective. The delivery of multiple doses to a high proportion of a population is expensive and difficult. Timed-release microencapsulation may serve as a means of administering such agents. Oral administration can be unreliable and requires frequent ingestion of the agent. Oral dosing is often confounded by the attractiveness of the bait and the taste, smell, appearance, or action of the agent. Implants require capture or immobilization, which is expensive and potentially dangerous to the animals. Materials that require implants or frequent injections will only be suitable for small accessible populations. Equipment currently used to remotely deliver materials (dart guns and blowpipes) have limited range and their use is labor intensive. Additional work is necessary to develop single-dose antigens, passively contagious antigens, and other delivery systems.

Social acceptance of immunocontraception will likely be high because contraception is perceived as being nonlethal and it is a relatively familiar form of population control to humans. Miller provides a more thorough review of immunocontraception elsewhere in this proceedings.

CURRENT CONSTRAINTS

Few if any biological management techniques have been developed, refined, and put into practice during the past 25 years. Delays in development have been partially

caused by individual and institutional bias in favor of conventional control methods. Perhaps more important, however, are the ecological and economic constraints associated with biological management. The following factors must be considered for any biological management strategy: 1) the biological complexity of vertebrate damage problems, 2) uncertainty associated with predator and pathogen activity, 3) concern for environmental safety, 4) regulations and costs associated with development and registration of materials in relation to market scale, 5) effective application methods, and 6) human dimensions of dealing with vertebrate damage problems. Pimental et al. (1984) provided a useful review of environmental risks associated with biological management. Although these points may be viewed as constraints, they also represent guidelines that will ensure safe, cost-effective, and socially acceptable management outcomes.

THE FUTURE

Although there have been few new biological management techniques developed in the last quarter century, we feel the stage is set for significant advances in the near future. Discoveries in microbiology and genetic engineering will likely lead to the development of new techniques associated with chemical and morphological plant defense, dispersal agents, competitive pathogens, genetic manipulation, and immunocontraception. In fact, it may simply be a matter of applying what we already know to vertebrate pest systems. It is essential that new methods of biological management be evaluated based on their ability to reduce damage to a tolerable level, rather than simply controlling population levels. Population reduction alone may only stimulate compensatory mechanisms that lead to higher pest populations and increased levels of damage. We need to gain a better understanding of the roles and interactions among components of natural landscapes, such that natural processes maintain vertebrate pests below damage tolerance levels. Biological management methods should be incorporated into integrated pest management systems that enlist a variety of effective damage management techniques.

ACKNOWLEDGMENTS

Much of the text in this paper was adapted from Hygnstrom and Johnson (1992). We thank R. D. Curaow and L. A. Paulik, Denver Wildlife Research Center, for conducting computer searches of their library data bases. Funding was provided by the University of Nebraska Integrated Pest Management Program.

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