WILDLIFE POPULATION CYCLES: IMPLICATIONS FOR DAMAGE CONTROL PLANNING

Richard E. Griffiths[1], *US Army Environmental Hygiene Agency, Pest Management and Pesticide Monitoring Division, Aberdeen Proving Ground, MD 21010*

Animal population cycles are not a newly discovered phenomena. References to irruptions (sic, Leopold 1933 p. 50) of small rodents can be found in the Old Testament, the writings of Aristotle and in European histories (Orr 1963 p. 360). The wildlife literature is filled with descriptions and studies of the population fluctuations of numerous species. Despite the vast amounts of data collected and speculation engaged in, biologists only partially understand the reasons for these fluctuations (Archibald 1977, Chitty 1952, Christian 1950, Cole 1951, Frank 1957, Hoffman 1958, Swinton 1883 and many others).

Most biologists agree that, regardless of the causes, wildlife populations fluctuate in a cyclic manner at somewhat predictable intervals. This paper addresses some of the implications that these cycles have for wildlife damage control.

An annual cycle is exhibited by all species that reproduce seasonally. During the reproductive period, natality normally exceeds mortality and the population increases. When reproduction ceases, mortality exceeds recruitment and the population declines until the next breeding season. A population change of 2 to 5 fold is not uncommon during an average animal cycle. Factors which affect this pattern include immigration, emigration, adverse weather and habitat disruption. The cycle is most pronounced in species which produce only one litter of young per year (Rowan 1954). Those species which produce multiple litters during a prolonged breeding season or breed year-round also exhibit periods of increase and decline but they are less conspicuous than those of seasonal breeders (Blair 1940).

A short-term cycle, of about 3 years duration, is common in wild rodents. Typically, reproduction exceeds mortality through 2-3, sometimes more, annual cycles until the population reaches a peak from which it abruptly declines to a very low level. The cycle is then repeated. Occasionally, environmental conditions favor high reproduction accompanied by low mortality and the population increases to plague levels (Frank 1957, Siivonen 1948, 1954). Such irruptions can be difficult to predict and result in brief (usually one season) periods of intense impact on crops and native habitat.

The long-term cycle extends over approximately 10 years. This cycle is characterized by a slow population increase over 4-5 years followed by 3-4 years of rapid increase and then 1-2 years of sharp decline. During a cycle, the population may increase to 100 times its lowest level (Rowan 1954, Griffiths, unpublished).

The cause(s) of the 10-year cycle are not understood although many of its characteristics are well documented (Siivonen 1948 and others). Attempts to explain cycles have led biologists to look for relationships between cycles and such things as sunspots and solar tide (Balser pers. comm., Swinton 1883) moonrise (Archibald 1977) and random numbers (Cole 1951). Evidence has been found linking cycles to stress (Christian 1950, Chitty 1952) reproduction and juvenile survival (Green and Evans 1940, Hoffman 1958) weather (McKay and Verts 1978, Meslow and Keith 1971) disease (Green et al. 1939, MacLulich 1937, Murray 1967) food depletion (Cengal and Kirkpatrick 1978, Vaughn and Keith 1981) and predation (Lack 1954, Wagner and Stoddart 1972, Pease et al. 1979).

The most conspicuous long-term cyclic species are the muskrat, arctic and snowshoe hares, jackrabbits, forest and prairie grouse, and their predators: foxes, coyotes, hawks and owls. These species tend to reach their peaks and lows at about the same time over large portions of their range; the predators lagging 1-2 years behind their prey (Errington 1954, Rowan 1954, Todd et al. 1981, Brand and Keith 1979, Todd and Keith 1983, Hoffman 1958, Wagner and Stoddart 1972, Rusch et al. 1972).

Short-term cyclic species include voles, lemmings, other small rodents and their avian predators (Siivonen 1948, Baker and Brooks 1981). Small rodent populations may fluctuate independently of each other, with one species being abundant when another is scarce (Lack 1954, Wood 1965) often resulting in a somewhat constant total biomass on a given area. Sometimes rodent peaks coincide with those of a larger prey species, to the benefit of the predator that feeds on both species (Rowan 1954).

Disease is commonly believed, by laymen, to cause the abrupt decline which follows a population peak. Although disease may play an important role in some rodents (Murray 1967), it has not been identified as the principal cause of population declines in most species. However, disease is undoubtedly a contrib-

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uting factor in the decline of populations under stress from other factors associated with high densities (Lack 1954).

High animal populations provide a favorable environment for disease transmission and can lead to a buildup of parasites (and disease vectors) in the hosts habitat. When a parasite is the vector for a disease affecting humans, the high animal population is viewed as a threat to human health, especially if the host population is suddenly decimated (Murray 1967, Harrison 1956). rabies may pose a threat to humans and domestic animals when wild canid, or other predator populations are high (Rausch 1958). Interestingly, seasonal fluctuations have been observed in numbers of parasites as well as in their host species (Miller et al. 1977, Muul et al. 1973).

During the low point in a cycle, the cyclic species is found only in its most favorable habitat and may be so scarce as to be almost undetectable. As a population increases, individuals disperse into less favorable habitat and even into normally untenable habitat (Griffiths, unpublished). Greater competition for food, shelter and breeding partners requires the expenditure of more time and energy in filling these needs as the population increases. At peak densities, individuals may be active at all hours of the day and far from their usual haunts (Griffiths, unpublished). In some species, fighting becomes more frequent as the population density increases (Chitty 1952). Juvenile survival also declines due to intraspecific friction (Chitty 1952, Ozoga et al. 1982).

When populations are low and the habitat is favorable, reproduction is characterized by a long (relatively) breeding season, large litters and juvenile breeding. As the population increases, the breeding seasons become successively shorter, fewer and smaller litters are born and juvenile breeding ceases. During a population decline, the breeding season is short, litters are small and fewer in number, and juvenile survival may be lower. An increasing population contains a high proportion of juveniles in the fall, while the reverse is often true during a decline (Griffiths unpublished, Todd and Keith 1983, Brand and Keith 1979). Continuous, accurate monitoring of these indicators can facilitate population trend predictions.

High populations of species such as voles, hares, and even grouse place heavy demands on vegetation (Rowan 1954). In some situations, the animals may deplete vegetation to the point that the habitat can no longer support them (Pease et al. 1979, Vaughn and Keith 1981). However, this is not always the case (Clark and Innis 1982).

Predators respond to a growing prey base with larger litters and in increased pregnancy rate among adults and juvenile mammals and larger clutches in raptors (Clark 1972, Rusch et al. 1972). Unfortunately, predators are unable to monitor their prey and are still producing large litters when the prey begins to decline (Brand and Keith 1979, Todd and Keith 1983, Clark 1972). The high predator population puts heavy pressure on the prey (and its alternates) and may hasten the decline of the prey (Wagner and Stoddart 1972). The result is often a large number of predators which must turn to an alternate prey such as livestock (or livestock carrion) in order to survive (Todd et al. 1981).

Wildlife damage varies with season and population levels. The annual cycle in herbivores coincides with the growth and maturation of the vegetation they feed on; predator cycles correspond to the annual and long-term fluctuations of their prey (Blair 1940, Knowlton 1972). The greatest damage to annual crops by wildlife usually occurs at the peak of the annual cycle, (midsummer to early fall) when most of the annual investment (money and labor) in the crop has already been made and the crop is unlikely to recover from severe damage before the end of the growing season. Protection of annual crops from high pest populations should occur early in the growing season, usually before damage reaches its peak, if economic loss is to be minimized.

Locally severe depredations on livestock may occur in the spring when young animals (and fowl) are most vulnerable and the predators are struggling to meet the nutritional demands of their own young (Knowlton 1972). As the juvenile predators mature, demands on the prey base increase. In years of poor reproduction and high predation, the prey population may be depressed to a level which makes hunting that species impractical, thus causing the predator to seek alternate prey (Todd and Keith 1983). Conflict between man and predator arises when the alternate prey is livestock.

Damage to perennial crops, shrubs, orchards and forest regeneration is usually greatest during the fall and winter dormant period, when available wildlife foods are most limited (Parker 1941). The damage is often greatest when hare and rodent populations are high (Oxford University 1937) although exceptions have been reported (Parker 1941).

In addition to following the annual cycle, wildlife damage also fluctuates with the longer cycles. Damage is seldom a problem when populations are low. During peak years, damage may become severe and require frequent, intensive control efforts to prevent destruction of the affected crop.

Weather is often a factor in wildlife damage. If wildlife populations are high, damage increases markedly during a dry growing season but damage to crops is reduced during years when native forage is readily available. While jackrabbits may or may not increase in actual numbers during dry years, they concentrate on croplands and appear to be more numerous (Tiemeier 1965). During a hard winter, hungry wildlife may cause locally severe damage to woody vegetation and stored crops, whereas damage tends to be light during a mild winter even though the damaging species is abundant. However, high survival as a result of a mild winter also means more animals available to cause damage during the next growing season. Abundant food supplies as a result of favorable growing conditions promoted fall breeding and a high rodent population the following spring in Michigan (Jameson 1955). Weather can enhance or suppress breeding and juvenile survival in rabbits and hares (Meslow and Keith 1971, McKay and Verts 1978, Jacobs and Dixon 1981). An extremely dry summer in Utah may have caused an early fall dispersal of black bear cubs beyond their normal habitat (Fair 1978).

Although birds are able to move more readily than mammals, both respond to changes in habitat and food availability. Concentrations of raptors are not uncommon on areas where rodent or lagomorph populations are high (Baker and Brooks 1981). Seasonal movement of waterfowl and blackbirds often results in concentrations of these species on ripening crops in late summer and early fall (Boudreau 1967). Problems associated with fall-winter concentrations include blackbird roosts in urban areas (Good 1978) and deer (and elk) damage to haystacks, nursery stock and forest plantings during periods of heavy snow (Nielsen et al. 1982, Wilkins 1957).

Several features of wildlife cycles are important to damage control planning. Animal numbers normally reach their lowest levels in late winter. During this period, just prior to planting most crops or turning livestock onto pasture, animals are stressed by low food availability and the energy demands of reproduction. Control at this time, before the young have been produced or become self-sufficient removes not only those adults remaining after the normal fall-winter mortality, but also the young those adults might have produced. The net effect is a reduction in the number of animals available to cause damage later in the year (Knowlton 1972). It is also possible that late-winter control of a rising population over a broad area could delay a peak or prolong it.

Although bait acceptance during late-winter should be excellent due to a lack of competing food, the target population will be dispersed throughout its habitat making effective bait placement a challenge. One of the problems associated with the use of baits containing a reproductive inhibitor has been getting the chemical into enough of the breeding population to significantly suppress reproduction (Linhart et al. 1958). It is also difficult to justify control during a period of little or no damage unless the wildlife manager can show that it will prevent future losses (Spitz 1978).

From late spring through the summer is often a time of abundance; abundant growing vegetation, birds and animals. It can also be a time of abundant damage. The annual population peak is reached when the last litter of the season is born although the visible peak in the population does not occur until later in the year when the adults and their young concentrate on unharvested crops and crop stubble. When pest populations are low and rainfall adequate, wildlife damage is seldom serious. However, when poor growing conditions coincide with a population peak, the loss to wildlife combined with reduced production often brings loud demands for relief. The readily available native vegetation and growing crops (young livestock for predators) are usually more attractive than toxic baits. Effective damage control during this period depends on careful selection of attractive bait materials and proper bait placement. The preferred food or crop may not be the best bait (Griffiths unpublished).

Population control of multiple litter species during the summer may require frequent repetition as the animals removed are rapidly replaced by the young from subsequent litters and by dispersing juveniles from adjacent non-control areas. In some situations, rapid carcass disposal must be effected to control the potential odor, fly and other problems associated with large numbers of dead animals.

From late summer into winter is a time of dispersal for the current year's juveniles. This large segment of the fall population is extremely susceptible to all forms of mortality as it moves into unfamiliar territory (Bowman and Robel 1977, Knowlton 1972). Although control at this time may result in a high kill, it is probably justified only to prevent immediate economic loss. The adults of shortlived species are reaching the end of their lifespan; natural and human induced mortality (without control) will reduce the population to the spring low. Control may be warranted to protect perennial vegetation or stored crops such as hay, especially from a species which is in the increase phase of its cycle. Bait acceptance during the fall dispersal is still affected by the availability of natural foods but is generally better than during the summer months.

Following fall dispersal (and mortality), animals establish themselves on the territories or home ranges they will occupy during the coming reproductive season. At this time populations have declined to their annual low, but survival of the remaining individuals is relatively high barring extreme weather or food complications. Bait acceptance during the winter months is generally good and control at this time depresses the populations reproductive potential during the coming spring.

In addition to annual cycles, many species have longer cycles that span from 3 to 11 annual cycles. During the cycle lows, damage levels are usually negligible, even at the mid-summer peak. This is in sharp contrast to peak populations which may cause significant damage year-round. Seasonal vulnerability and bait acceptance follow the annual pattern. However, the competition for food at high densities tends to increase bait acceptance.

In addition to annual and longer cycles, weather effects, and seasonal damage, economics should also be a factor in wildlife damage control planning. The "economic threshold" in wildlife damage control is the degree of damage which justifies control. Below this threshold, the cost of controlling a problem animal exceeds the probable loss that animal could cause and control is not economically justifiable. When losses exceed the threshold, control results in economic benefit. The economic threshold may not be applicable to situations where aesthetic or public health concerns are the predominate reason for control.

Prediction or forecasting of damage is based on determining when pest populations will reach a level at which control becomes necessary in order to prevent economic loss. Control is difficult to justify when a population is very low but it may be imperative when the population reaches its peak. Accurate prediction of population trends can help wildlife managers reduce unnecessary control efforts when populations are low and allow them to plan in advance for the control needed during population peaks. In today's socio-political climate, control without a knowledge of damage potential is difficult to justify.

One feature of the long-term cycle is its predictability. By monitoring the population trends of a long-term species, it is possible to predict damage as much as 3-5 years in advance. This knowledge makes it possible to plan for control measures well in advance of the actual need. Species such as voles which follow a shorter (3-4 year) cycle are less easy to predict. Local weather and agricultural practices may affect reproduction and survival enough to suppress or prolong a population peak. Prediction is still practical, but it needs to be based on the local situation (Jackson 1978, Frank 1957, Spitz 1978).

The population monitoring method chosen should be simple, reliable and repeatable from year to year. Standardized damage measurement procedures can be developed to determine the economic threshold for various wildlife damage stiuations (DeGrazio 1969). Periodic sampling of population trends by non-capture census methods or by changes in hunting and trap success is commonly used to monitor many species. Data from captured animals such a pregnancy rate, litter size, breeding season length and adult/juvenile ratios can also be used to determine trends. Efforts to develop means of forecasting wildlife population trends as an aid in damage prediction and control have been underway for many years in Russia and more recently in European countries (WHO 1974, Spitz 1978).

Monitoring requires sampling during those periods or seasons when the appropriate data may be collected. Ideally, accurate damage predictions should be available before the growing season. Unfortunately, the optimum sampling period may not occur at a convenient time for predicting or preventing damage, i.e., before the damage occurs, as the reproductive season coincides with the growing season.

Long-term monitoring of such indicators as age ratios and reproductive parameters will often reveal patterns which, when compared over time, enable prediction of cyclic highs and the associated wildlife damage before it occurs. The development of a continuous monitoring program with a sound data base can enable a wildlife manager to predict damage and plan control with a greater degree of confidence than has existed in the past. Until this occurs, we may have to make our predictions based on less accurate data in order to provide the advance warning needed for effective control preparation (Spitz 1978, Jackson 1978).

Preventive control is most effective against long-cycle species where damage can be forecast well in advance of its occurrence. When this is possible, nonlethal controls such as physical barriers, repellents, habitat modification (Jackson 1978) and planting of resistant crops may be employed. Pre-damage population reduction by hunting or the use of toxicants is useful to keep some cyclic wildlife species below economically significant levels. Advance knowledge of potential damage is helpful in scheduling the procurement of toxicants, baits, personnel, or chemical registration that may be needed for damage control.

Seasonal control is applied during the actual damage season, most commonly for those species that are a problem only during part of the year and may not need to be controlled on a year-round basis. Knowledge of population trends is desirable for predicting the amount of control and control materials that may be needed. Neither seasonal nor preventive control should be employed unless damage can reasonably be expected to exceed the economic threshold.

Migratory species, usually avian, cause seasonal damage. However, they are often beyond the reach of practical (or legal) control methods outside of the damage season. Damage can be reduced by altering the period of prey or crop availability. Since migrant bird damage is highly seasonal and dependent on crop maturity, early or late maturing crops may be unattractive or unavailable to the migrants when they arrive on the area. Preventive controls for migratory mammals include barriers and repellents. Although migrant population levels during the damage season may be difficult to predict, the damage period remains fairly constant and predictable.

Some of our most serious wildlife damage problems have resulted from the introduction of exotic (non-native) species into new environments which lack the restraints on population growth that are found in the species' native habitat. Once established, the introduced species tends to increase rapidly, often displacing native wildlife and altering the vegetative complex, until it reaches or even exceeds the carrying capacity of the habitat. Following this initial surge, (and the discovery of its damage potential) the exotic species declines to a "normal" population level and develops a cyclic pattern in harmony with its new environment (Lewin 1971, Howard 1964).

As the exotic species expands into suitable habitats from its point of introduction, it follows this pattern of rapidly increasing to plague levels and then declining to a more or less stable population level. Demand for control is extremely high during the initial irruption phase of the invasion but declines as the pest and its environment return to equilibrium and humans learn to live with the invader (McNeil 1962).

Continuous control methods research is necessary if biologists are to keep up with changes in land use, toxicant resistance and environmental constraints on toxicant use. Since all pest wildlife is cyclic to some degree, both annually and over longer periods, it is important for researchers to be aware of these cycles when evaluating test results.

The degree of population reduction and/or damage control achieved in a given test can vary seasonally from year to year (Matschke et al. 1982, Stehn et al. 1980). Any tests of control methods should incorporate replications of both the treatment and control within the same habitat and season. Multiple replications are even more important when comparisons between seasons or even years are made, since nonexperimental variables such as population cycles may make it almost impossible to draw valid conclusions.

A knowledge and awareness of cycles is an important part of integrated pest management. Since most pest populations are cyclic, monitoring population trends makes it possible to predict damage and plan appropriate control measures. Monitoring is necessary for predicting when damage will exceed the economic threshold and for scheduling effective preventive control.

Control should be initiated when the cyclic trends indicate that it will be necessary to prevent economically unacceptable damage. It should be timed, whenever practical, to take advantage of a species most vulnerable periods. Control during the fall dispersal is usually unnecessary and uneconomical. When cycles are accounted for in control planning, the planning is simplified.

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