GRAZING AND DEFOLIATION

A BRIEF REVIEW OF THE EFFECT ON PLANTS AND PLANT POPULATIONS AND PREDATION ON SEEDS AND FRUITS

A BRIEF ANALYSIS

For: Dr. R. Turkington

Course : Bot. 527

By: R. Gardner
41389776

Introduction

As Harper (1977) points out in his introduction to the chapter on the Role of the Grazing Animal in the text, Population Biology of Plants, much of the present knowledge of the effect of grazing animals in the population biology of plants originates from agriculture where deliberate introduction of mammals has been made to natural or artifical grassland. However, a fairly considerable body of information has also been collected by workers in forestry, where the effects of both grazing and defoliation have long been of concern to the silviculturalist.

Although some very sophisticated models have been developed both of an applied and theoretical nature (some are discussed by Harper) to predict the impact of grazing on the carrying capacity of range land (e.g., Paulsen, 1975 and Thilenius, 1975) there would seem to be a place for a simple system that aggregates and portrays the general findings of many workers.

Such a simple system has been utilized for the collation of the references examined for this paper and is similar to that used for the original presentation. The basic concept is that, if the causal organism is first identified, it is then often possible to categorize the impact that it will have on any given species of vegetation, or collection of vegetation types.

To use an example discussed by Harper of the slug *Agriolimax reticulatus* in defoliating a grass species, (*Lolrum perenne*) it is possible to lay out the information in a simple sequence using the prompting words who?, does what?, to what?, where?, how much?, when?, for how long?, the outcome?, and the implication?. An example would read as follows: "Who? Slug, A. reticulatus; does what? chews through young shoots at ground level, eats meristematic region of the base of shoot, leaves leaves felled on ground; to what? grass species L. perenne; where? at the base of the plant; how much? various amounts depending on experimental protocol; when? at night; for how long?. one week; outcome? reduced yield (growth) and varying length of effect particularly when seedlings were young; implications? the lowest density of grass seedlings could not withstand even one slug and with more mature grass some plants were heavily damaged (though others were undamaged) and even after recovery their contribution to the yield of sward was minute compared with their numbers.

In this way it is possible to sort out the implications arising from grazing or defoliation. Although the system is fairly simplistic it can identify general rules and provide the basic ingredients to allow for more sophisticated assessments and judgments, and too, for the resulting information to be used for such tasks as preparing program management strategies or for integrated pest management.

Further, a number of the headings could be subdivided. For example, the damaging organizism might have a life table developed, as might the damaged plant. The prompting question does what? could be subdivided as to types of damage or types of feeding, and the question where? could be twofold, addressing where on the plant the damage occurred and where the plant grew in relation to the damaging organism and other plants. The question of how much, could be both qualitative and quantatative, while the when? could relate to both diurnal and seasonal timing. The question of outcome could be divided into morphological and physiological impacts while the implications obviously could be categorized as direct or indirect. The importance of this organized but in depth breakdown is seen when one considers the quantity of information that can result even from the most modest of experiments or field observations.

The following brief review of grazing and defoliation from a number of authorities is generally modelled around the simple system outlined above although the tedious use of the "prompting question" does not continue. From this review a number of specific and general conclusions are drawn and given in the last part of this paper.

Discussion

None of the authors consulted draw any significatnt separation between the terms defoliation and grazing. Although it might be concluded that defoliation is intrinsically a specific impact while grazing is more a complex of factors which would include defolialtion or partial defoliation but might also include direct effects such as trampling as well as more ecologically based changes such as diversification of grassland communities at one end of the scale and transition from grassland to desert at the other.

Much of the literature concenring grazing is related to that of large herbivores, particularly cattle either on open grassland or pasture and in forest situations.

Odum (1959) suggests that if range land productivity is to be ensured, only about one-half of the annual production should be consumed by cattle. He suggests that carrying capacity for grazing animals can be determined by considering (1) primary production of palatable species and (2) the percentage of the net productivity that can be removed annually while still leaving the grass plants with enough reserve to enable them to maintain future productivity. Of course, such factors as seasonaly distribution of rainfall, the quality of forage and season of growth would also influence such decisions. The undesirable impacts that can result from over-grazing are suggested as unpalatable annuals and shrubs invading but that before the overt effect is seen subtle changes in community structure, decreases in density and loss of vigor in sensitive species occur. In addition, in artificial pasture when animals are confined, soil can become compacted and "sod bound" with reduced productivity due to soil aeration. Cattle management and rotation of pasture would appear to be important conclusions to reduce excessive grazing pressure. Daubenmire (1947) notes that cattle grazing might injure a plant either because of the frequency or degree of removal of its photosynthetic organs curtails its assimilation or because of its susceptibility to trampling. Less direct, but more important consequences include the erosion and deposition that result when soil is exposed to wind and water. Damage may be magnified by drought (plant unable to cope with the combination of adverse conditions) or plants may be better able to withstand draught because the smaller plants that result from grazing make less demands on the water stored in the soil. Daubenmire also contends that grasses and sedges also withstand grazing better than forms since leaves are not destroyed when only distal segments are removed, because they have basal stems. (In fact stimulations may result from mild grazing). Vegetative bugs are also less injured by trampling because they are below ground level, protected by dense tufts of foliage. Palatable annuals could quickly disappear from an area that is grazed so much that they cannot set seed, while shrubs are less damaged by browsing than herbs, since browsing in normally confined to new growth, so that only a small portion of the shoots are removed; also there is greater longevity of shrubs and increased chances for survival of sufficient seedlings to replace old-age mortality. Perennials appear to be damaged most if the foliage is removed before the plant has re-stored part of its underground food reserves. The plant becomes weakened and killed as the roots become starved and inefficient. In the case of tall shrubs and trees, these eventually grow out of feeding range and thus are free of direct injury. Grazing observations in shrubby vegetation certainly indicate that the numbers and sizes of shrubs increase as competitive grasses are reduced, while grazing in herbatious vegetation results in sparser plant cover, consisting of fewer species, usually unpalatable, with a short life cycle so that live stock do not have sufficient feeding time to cause damage. Oosting (1956) observes that moderate grazing by cattle does not change the essential nature of the grassland community, in fact, under natural conditions, on North American grasslands, grazing was greatest when the buffalo ranged, feeding and trampling or destroying vegetation around waterholes, but since they constantly moved to where grazing was best, damage was minimal overall.

Spurr (1964) suggests that grazing animals change the vegetation to their selective feeding habits, and the differential ability of different plants to survive and prosper under these conditions. However, as the vegetation changes there is also the possibility of changed litter and soil biotic activity, causing changed site conditions (usually for the worse) with less palatable and more woody species usually decomposing more slowly. An indirect effect of grazing, however, is that natural manuring raises the nitroginous content of the surface soil layer which can be beneficial. Spurr also notes that direct effects, such as hooves, can pack the soil and break up the ground cover which may also have site implications, such as poorly airated soil, less water absorbing capacity and consequently sheet erosion with minimal biotic activity and degration of site quality. In this context, cattle are suggested as the worst offenders, since their sharp hooves and heavy weight, along with their tendency to congregate around water, salt or bedding areas, causes complete eradication of almost all but the most durable weed species.

Grazing can also arrest or reverse succession. Smith (1966) again in the context of buffalo, suggests that they control grass height be grazing on the taller species, causing the shorter species to become dominant. The example is also given of the effects of overgrazing by life stock in range lands in the south west of the United States, where erosion has resulted from reduced organic mat, periodic fires and decreased competition for grasses with dispersal of long-lived seeds through cattle droppings, producing such undesirable shrubs as mesquite. In the Wasatche plateau in Utah, virgin sub-alpine meadows were so over-grazed in the 1880's and 1890's that meadows were first overtaken by annuals and early withering perennials but later changed to virtual desert conditions. It is also noted in the context of timing that grazing too early in the spring causes plants to put on insufficient growth during the year and they cannot survive the following winter. Highly palatable plants disappear with big and little blue stem, prairie and tall drop seed and nitrogen-fixing legumes or forbes decreasing, while blue grass, side-oats, grama, daisey freebane and iron weed are freed from competition. As the grassland further deteriorates, weedy wheat grass, broom grass, little barley and annual drop seeds substantially increase in number, while the palatable grasses, such as blue stem, may decrease by up to 75% as grassland deteriorates from high grade to low grade pature. McNaughton (1979) suggests that grasses can recover quickly from local heavy defoliation for short periods, and that even fairly severe defoliation has little deleterious effect on grasses and often stimulates productivity but that the full impact is regulated by intensity and frequency of defolialtion,plant life cycle stage, the time of defoliation, the general vigor of the plant and environmental conditions although often the most abundant and desirable species are not adapted to sustained heavy grazing. Clary (1975), in extensive studies in Arizona, has observed that perhaps the most pronounced deterioration that occurs from continued heavy grazing of cattle as they exert a selective influence on herbacious plant community, is that the plant life forms of each of the successive stages are progressively shorter lived.

The effects of cattle can, of course, also be seen in upland and forest situations. Lawson (1966) suggests that heavy cattle grazing in heathland, normally dominated by heather (calluna bulgaris) particularly in areas of moderate to high rainfall, with well-drained acid soils and strong winds, can completely prevent the establishment of calluna and result in grassland, thus interfering with normal plant succession. In the USDA Year Book of Agriculture (1949) it is observed that live stock can readily browse young hardwood trees to the point of destruction. Not only does heavy grazing destroy the trees but also the forest soil structure and eventually lowers site potential. In addition, wet weather trampling can compact the soil, or when drying breaking up the litter cover, exposing mineral soil to excessive drying. This makes seedling survival growth difficult. Further, cattle tend to ride down young trees, to graze on them or to brush off flies. The Year Book stresses that it is important to avoid over grazing, to maintain satisfactory watershed conditions. In the past cattle have been turned loose to roam over any unfenced land, even in winter, when the range consisted of dead grass of low nutritive value. Stock was often so cheap and poor that owners could not afford other winter feed. A late winter fire would be used to remove the dead foliage and be followed by fresh growth of grass which would tide the animals over. With the coming of fenced, improved pastures, however, herds of good quality and fewer cattle are seen in woodland areas. Under protected conditions, there are twice as many species and numbers of plants as in over-grazed woodlands, contributing to there being twice as many kinds of birds with nests on or near the ground, and twice as many kinds of small mammals. Furst, writing in 1893, was one of the original foresters that observed that cattle have an extremely damaging impact on woodland. He observed that although cattle usually eat woody plants only when grass is scarce, they do considerable damage. Although occurrence and extent of the damage depended on the type of cattle grazed, species of tree, nature of woodland, soil and climatic conditions, management practices and number of animals. Broad leaved species seemed to be preferred over conifers, but conifers suffered much more seriously from grazing injury. High value crops, such as beech, chestnut, ash, elm, oak, maple and sycamore were favoured, followed by aspen, willow and limes, with alder and birch being least preferred. Amongst the conifers, silver fir, spruce and larch seemed to be attacked first, while the pines generally suffered the least damage.

Miles and Kinnaird (1979) in a study of grazing in the Scottish highlands, found that cattle grazing, browsing, trampling and bark stripping were important determinents of tree and shrub establishment and development and thus of species composition in woodland, but that large herbivors of all types also had a positive role in promoting re-generation through the creation of micro-sites for seedling establishment. as a result of trampling, close cropping and occasional tearing up of vegetation. For example, a preponderance of *Betula* species and *Pinus sylvestris* seedlings were found in an area trampled by red deer, sheep and cattle, while cattle grazing benefitted regeneration of *P. Jeffreyi* and *P. Ponderosa* which cannot survive severe competition when young since seedling growth is minimal at the low light intensities found under deep moss and litter layers common to woodland. It was also found that *Betula* species occurred only in open patches amongst *Calluna vulgaris* and *Pteridium* and *Aquilimum* canopies since damping off of both seedlings occurs in the shade. It was also found that some undesirable woodland species, such as bracken, often difficult to control by normal practice, was much more susceptible to mechanical damage than other species with abundance and vigor of fronds substantially reduced in grazing areas. In heavily browsed areas it was found that compaction was severe in soils high in clay or organic matter, and that this impeded both root development and penetration of radicals germinating from herbacious seeds. It was generally concluded that apart from fire and windfell, grazing animals were probably the most important natural agency in creating conditions for tree regeneration, but conversely, browsing by domestic stock had prevented regeneration of the original woodland cover in the highlands with tree saplings becoming increasingly susceptible to browsing as they emerge from the field layer.

In the case of deer, probably the next most important herbivor effecting plant populations, Furst (1893) observes that not only do deer bite off the buds and young shoots of most species of trees, killing younger plants and crippling or stunting older ones, but that they also eat acorns and beech nuts for example, substantially reducing reproduction. Daubenmire (1947) notes that in the main, deer prefer shrubs and that they browse rather than graze with species being classified readily from very palitable to quickly avoided. Despite the roaming nature of deer, this can have rapid implications for the plant stock in given areas with the unpalatable species escaping injury, benefitting from the release from competition, and significantly improving their competitive position. Oosting (1956) suggests that this feeding can cause the complete destruction of young woody plants, particularly in areas of winter browse. as the deer population increases. Spurr (1964) carries through this argument and notes that over-population of deer, through elimination of predators and restricted and inadequate hunting, has resulted in the development of park-like forests, free from undergrowth in parts of the Appalachians, Lake States and

Western Europe. If the deer population is not reduced long enough to permit regeneration to grow up past the browse line, establishment of a tolerant understory is prevented and eventually an open and grassy woodland develops. Smith (1966) reports that in the Ottawa National Forest, yellow birch, basswood, hemlock, white cedar and aspen have been almost eliminated by deer browsing and that in much of the mixed northern hardwood-hemlock stands, only sugar and red maples have survived browsing, with the basswoods and hemlocks being almost completely eliminated. Black, as early as 1954, long before the concept of sustained yield was accepted, noted that in Michigan and Pennsylvania deer browsing was so severe that it was removing regeneration at a rate faster than surviving trees could replace the timber being cut for commercial purposes.

Sheep are less important than cattle or deer in influencing plant population. Harper (1977) refers to the classic experiments by Jones where sheep grazing rapidly and dramatically a composition of plants in pastures that had apparently retained their stable composition for many years previously. Although not a natural system, and further complicated by the use of fertilizers and different grazing times, it can be clearly seen that palatability, timing, grazing pressure and original composition play extremely important parts in determining the competitive leverage of certain species and eventually, of course, the management practices adopted for pasture use.

A number of authors refer to the impact that goats have on plant composition. Furst (1893) suggested that goats do considerable injury, appearing to prefer grazing on foliage, buds and young shoots of woody fibrous plants rather than on grass and weeds. Since they can stand quite high on their hind legs, even the crowns of sturdy saplings can be readily grazed. Money (1965) observes that in Europe, in areas where goats have predominated, the form of woodland has been replaced by a mixed deciduous-evergreen scrub, with shrubby herbs and geophytes. Spurr (1964) echoed this observation and notes that goats are by far the most destructive of forest regeneration, with over grazing causing elimination of palatable species from the ground to the browse line, compaction of forest soils and eventual conversion of the forest to an open scrub of unpalatable species or to grassland.

Rabbits have long been seen as a factor in affecting plant population. Oosting (1956) notes that in localized areas with high concentrations of jack and cottontail rabbits they can seriously damage young seedlings of almost all species of range land plants and even trees, by eating the bark. Daubenmire notes that jack rabbits can affect wide areas uniformly since their range is extensive as they depend on speed for safety, not on burrows. Specific impacts on individual species are not discussed and recourse to original literature that deals with these animals would be required to generate specific information on their feeding habits and impact on plant populations. Much the same is true of such animals as prairie dogs, which may consume all of the forage for some distance around their villages. Smith (1966) suggests that these animals can reduce the proportion of annual grasses and forbes while increasing the number of peremmial forbes in an area. Moreover, in areas where there are tall and short species present, prairie dogs effectively develop and maintain a short grass prairie. Sporadic references are made by some authors to the effects of large mammals in the African setting and their varying effects on the composition of plants in the Savanna. There is no doubt a considerable body of literature that examines the seasonality and type of foraging of such animals as zebras, gazelles, wildebeast and elephants. Much in the same way there is a whole body of literature that examines the impact of such animals as porcupines in the forest setting, however, in this brief paper the examples so far discussed probably provide a representative picture and certainly underscore the general premise that grazing animals have a significant impact on plant composition.

Before leaving this topic a brief mention should be made of the impact of defoliators, particularly in forestry. McNaughton (1979) in discussing spruce budworm notes that the larvae are usually present at low densities but periodic outbreaks occur in which needles, buds and flowers of spruce and fir are entirely consumed, causing massive tree damage. Low diversity of mature forest allows rapid spread of the insects. Wet, cold summers, which are typical of coniferous forests, can cause poor larvae survival, sometimes interrupted by a short series of dry sunny summers causing tremendous increase in the budworm populations. They in turn attack mature trees with declining vigor, causing recycling of nutrients in dominant plants (into the general environmental pool) where they can be used by the younger plants with a potential for more vigorous growth. Certainly tree death opens up the forest canopy and tree seedlings and sapplings are released from the light limitations imposed by the mature trees. This then changes community composition, nutrient cycling, and microenvironments in the forest ego system, allowing a more dynamic, uneven aged, and diversified flora. Thomson (1979) found in examining the impact of spruce budworm in British Columbia that tree mortality due to defoliation by budworm was relatively limited, but reduced radial and height growth, die-back of previous height growth and deformation of the main stem resulted in a non-commercial future for many of the stands observed. Miller (1975) studying the same problem, provides a chronology of the years it takes for an endemic population to grow to the level that causes noticeable defoliation. At pre-outbreak density, only five larvae were found per tree. After four years 2000 larvae were found per tree, causing noticeable defoliation of new shoots. In 6 to 7 years 20,000 larvae were found per tree, stripping all of the current needles as well as some old needles. This caused the tree to decline in vigor, becoming less attractive as an adult oviposition site. After 8 to 9 years there were enough larvae to strip new shoots and top killing became evident with even understory reproduction killed. After 10 years some dominant trees began to die, and after 14 years the epidemic population had caused 80% of the merchantable stand to die. It was found that stand composition influenced rate and degree of damage. Susceptibility or more properly described, probability of attack, seemed to involve site factors such as local climate, stand age, proximity of heavily infected stands. Vulnerability, on the other hand, that is the prbability of tree mortality, was governed almost exclusively by stand age and composition, with over-mature pure fir stands being highly vulnerable. Young fir stands, although highly susceptible, were not very vulnerable. It was found that white and red spruce were less susceptible to mortality than fir, and that black spruce was almost immune to spruce budworm defoliation. Baskerville (1975) in also examining this insect found that when the budworm reaches epidemic levels and destroys the host species, the population declines rapidly, ensuring the development of a new stand, eventually of host species suitable for future generations of budworms. Thus the budworm and particular forests are an integrated self-regulating system. In the interim, a budworm killed forest is highly prone to fire. When fire occurs, there is a tendency for the forest composition to move away from susceptible species to black spruce, jackpine and aspen as evidenced by the position of more intolerant species such as white spruce and birch in previously attacked and burnt areas.

Wickman (1978A) (1978B) found in studying Douglas fir tussock moss (*Orygia* and *pseudotseugata*) large patches of saplings and pole-sized trees were completely stripped of needles by late summer and that tree mortality occurred in heavily defoliated areas. Mortality tended to be concentrated in patches and severe, (up to 84% within each patch). Examination of possible changes in overstory species composition, in a 10 year period, was attempted by comparing the standard plant ecology perimeters of density predominance and frequency. Various firs, pondorosa pine and Western juniper all occurred on the site. Surprisingly, little change appeared for the firs and pine in their relative values, especially since the fir suffered over 30% stand mortality. The largest change in the 10 year period was with western juniper whose relative values tripled.

So it can be seen that defoliating insects can have substantial effects on stand composition in forest situations particularly when insects reach epidemic populations. Forest composition is altered not only by the loss of trees but as Harper (1977) notes, defoliation can have significant effects on reproduction of the affected species, radically diminishing their ability to re-establish their climax position even when only partially damaged.

Conclusions

It is clear from the previous brief review that there are some general conclusions that can be drawn from the observations of these authors. At the plant's specific level, it seems that the removal of leaves or roots from individual plants in a population may damage that plant's position in a competive heirarchy and reduce their reproductive output. Conversely, it is possible in some species that partial compensation for lost parts or leaves is possible through more active stimulation of advantitious or dormant buds, or in the case of leaves through increased assimilation capacity of the remaining leaves.

In most cases, defoliation or grazing, as long as it is not too long and sustained, leaves sufficient plant parts capable of regeneration to remain and to allow for regrowth and/or reproduction. It is only when the plant is irreparably damaged or weakened to an extent that secondary organisms can enter, that it is killed out. It is clear that in many cases some individual plants within a species are more prone to defoliation or grazing. This seems to depend on factors of selection relating to palatability or to pre-disposition caused by morphological or phsyological considerations. Even with this, most plants have considerable powers of recovery or compensation, such as increased photosynthetic activity to accommodate loss of leaves or, under more severe duress, cessation or contraction of the integrated activity of the plant, such as lower transpiration rates and reduction in their growth. (Harper 1977). This author also suggests that the loss of mineral nutrients may have a more damaging effect on individual plants than the simple loss of carbon products.

Timing of the impact on plants also appears to greatly influence the degree of damage. Young tissues, and particularly young leaves (Harper suggests that almost all "predators" take young plant tissues preferentially) seem vulnerable, especially when a plant is very young, although obviously the impact would differ between epigeal and hypogeal species.

On the broader scale, grazing animals can certainly influence the relative abundance of different species in a habitat. Although the influence of grazers is in part due to partial or complete defoliation, their physical impact, both on the plant community and on the environment, ranging from micro-climatic changes to changes in soil conditions, are extremely important. On balance, it seems that the grazing animal, as long as its grazing pressure is in moderation, is a diversifier of plant communities, creating locally different micro-environments for seedling establishment and subsequent growth, thus continutally initiating regeneration cycles on a small scale within the community. Where the impact is more pronounced, as with some defoliators who may damage apical miristems, or,in the case of the base of trees, actually remove cambrian the effect on individual plants can be devastating. When these species make up a high proportion of a plant community, there can be rapid and dramatic changes in community structure. Typically, monophagous feeders will have their live cycle tightly synchronized with plant life cycles and really cause larger scale plant extinction, and even then, their effect is to cause major purturbations in their own population numbers until similar conditions again exist in the plant community. Polyphages, on the other hand, are less sufficient but can cause low extinction of plant species rather than species regulation. The time of defolialtion is critical in determining the type of plant response. Depending when leaves are removed, this can impact reproduction, upsetting the evolved synchronization of phenology with climate. Moreover, smaller seeds from defoliated plants have smaller food reserves, produce smaller seedlings and eventually affect survival and community composition.

In summary, it can be said that grazing and defoliation play an import role in influencing species composition in both natural and agronomic or forest plant communities. It would be a mistake, however, to draw too many sweeping conclusions and then apply them to any specific case, since the dynamics and interdependencies of flora, fauna and elements of the supporting environment are still, for the most part, poorly understood. As the need to manage all areas of our finite world rapidly increases, however, it also becomes increasingly important that a better understanding of the interactions between plants, animals and man be seen as a key to our future survival.

References

Anon., Trees.

The Year Book of Agriculture, 1949, U.S.D.A. Washington, D.C. U.S. Government Printing Office.

Baskerville, G.L., 1975; Spruce Budworm : Super Silviculturist in Sprucewood Budworm : How it lives and what it does Forestry Chronicle 51:4, 1-26.

Black, J.D., 1954, Biological Conservation, McGraw Hill Book Co.

Clary, W.P., 1975, Range Management and Its Ecological Basis in the Ponderosa Pine Type of Arizona : A Status of our Knowledge U.S.D.A. Forest Service Research Paper RM-158.

Daubenmire, R.S., 1947, Plants and Environment, A textbook of plant autecology, John Wiley & Sons.

Furst, H., 1893, The Protection of Woodlands, David Douglas.

Harper, J.L., 1977, Population Biology of Plants, Academic Press: 385-456.

Lawson, T., 1966, Textbook of Botany; Revised by E.W. Simonds, K.J. Dormer and J.N. Hartshorne, University Tutorial Press.

Miles, J. and Kinnaird, J.W., 1979, Grazing : With Particular Reference to Birch, Juniper and Scotch Pine in the Scottish Highlands; Scottish Forestry, 33:4, 280-289.

Money, A.C., 1965, Climates, Styles and Vegetation, University Tutorial Press.

Miller, C.A., 1975, Spruce Budworm - How it lives and what it does, Forestry Chronicle 51 :4, 1-26.

McNaughton, J.S. and Wolf, L.L., 1979, General Ecology, Holt , Rinehart and Winston.

Odum, E.P., 1959, Fundamentals of Ecology, W.B. Saunders Company.

Oosting, H.J., 1956, The Study of Plant Communities, W.H. Freeman and Company.

Paulsen, H.A., 1975, Range Management in the Central and Southern Rocky Mountains. A Summary of the Status of Our Knowledge of Range Ecosystems, U.S.D.A. Forest Research Paper RM-154.

Spurr, 1964, Forest Ecology, The Ronald Press Company.

Smith, R.L., 1966, Ecology and Field Biology, Harper and Roe.

Thilenius, J.F., 1975, Alpine Range Management in the Western United States - Principles, Practices and Problems : The Status of our Knowledge, U.S.D.A. Forest Research Paper RM-157.

Thomson, A.J., 1979, Evaluation of Key Biological Relationships of Western Budworm and its Host Trees, Pacific Forest Research Centre, Victoria, B.C.

Wickman, B.E., 1978A, A Case Study of a Douglas Fir Tussock Moth Outbreak and Stand Conditions 10 Years Later, U.S.D.A. Forest Service Research Paper PMW-244.

Wickman, B.E., 1978B, Tree Mortality and Top Kill related to Defoliation by Douglas Fir Tussock Moth in the Blue Mountains Outbreak, U.S.D.A. Forest Service Research Paper PMW-233.

AN OUTLINE OF TWO CANADIAN VERTEBRATE PESTS IN THE FOREST SYSTEM

North American Porcupine
Erethizon dorsatum

and

Red Squirrel
Tamiasciurus hudsonicus

ABSTRACT

A profile is given of two ubiquitous vertebrate forest pests in Canada; The North American Porcupine, Erethizon dorsatum and the Red Squirrel Tamiasciurus hudsonicus. These two pests with cosmopolitan distribution were chosen from the group of fourteen major vertebrate forest pests in order to briefly assess their importance in the Canadian Forest system, to illustrate the magnitude of their impact, and to review the biology of the two animals. The changing pattern of forestry in Canada is discussed in the context of the overall importance of forestry to the Canadian economy. The types of damage inflicted on the various developing stages of the forest resource by all vertebrate pests is reviewed and the injuries caused by Red Squirrel and Porcupine noted in greater detail with appropriate references. A complete profile of each animal is presented after an outline developed by Sadleir (38) and including a review of the rational for classifying each animal as a pest, the specific nature of the damage, the biology of the pest and the response alternatives reported to negate or contain the impact of injury.

INTRODUCTION

The forests of Canada cover nearly half the country's total area. About one half of this forest land contains merchantable timber - 8% of the worlds total timber resource (59). Potential forest land is calculated as 805 million acres (61) of which approximately one million square miles are presently carrying productive forest. Stanton in a recent publication on Canadian Forestry (45) notes that the present annual demand for timber is 4.5 billion cubic feet which will rise by the year 2000 to 7.6 billion cubic feet. Present demand represents 2.25 million acres harvested annually. Since the mid 1950's active programmes have been pursued to replant cut-over areas; four million acres have now been artifically restocked and it is expected that this will rise to ten million acres in 1985 (59). It is estimated that 290,000 acres are planted annually with a further 60,000 acres directly seeded from collected seed. Greater emphasis is being placed on the genetic improvement of growing stock and much of the seed collected is from superior seed sources. In addition some 30,000 acres of forest plantation are being fertilized annually. In addition to the direct income from forestry and the employment which it provides, 250,000 people in B. C. alone (64) some 5.3 million dollars worth of christmas trees and some 13 million dollars of maple syrup products are produced annually (45).

In recent years recreational use of the forest has grown enormously as the mainly urban dweller seeks peace and pleasure in the countryside. There are now 28 national parks, one park reserve and 1,800 provincial parks across Canada, encompassing some 85 million acres of forest land utilized by some 42 million visitors in 1972 (62). Howard (24) however has noted that many urban citizens need a more enlightened outlook on man's relationship with wildlife and that an effort should be made to obtain a more objective treatment and training about wildlife and resource management in public education and school programmes, giving adequate attention to wildlife damage problems as well as stressing the asthetic and beneficial values. Just as important it would seem is the need to stress the economic impact of vertebrate pests to the forest profession in Canada. Three indicators point to this conclusion; virtually all of the literature over the past 15 to 20 years concerning vertebrate pests in North American Forests is the work of researchers in the United States. In the last major Canadian survey (63) only 50% of the respondent regions mention vertebrate pests and the Canadian forest service unlike other countries (57) (65) has apparently no publications dealing specifically with vertebrate pest management. Perhaps one of the reasons for this, has been the difficulty in providing reliable data on economic losses caused by vertebrates, (24) although for one forest company in the American Pacific Northwest it has been estimated to exceed one million dollars annually (22). Certainly recognition of the problem has been more formal with the formation of a Forest Wildlife Problems Committee under the aegis of the Northwest Forest Pest Action Council. This group has been responsible for a handbook used extensively in this review (31). In addition in the early 1960's the American Wildlife Society formed a Committee on Economic Losses caused by vertebrates which was, along with other goals, charged with developing a standardized technique for measuring losses and values and for reporting such data (24).

Since the depression years of the 1930's, Canadian Forestry moved into a second phase - the cutting of second growth timber since most of the economic virgin timber had been completely depleted. The high cutting rates mentioned earlier in this paper indicate that a third major phase will be entered by the late 1980's; that of intensive forest systems. This will be the only way that Canadian Forestry, particularly in the west, can continue to be competative on world markets. As labour and processing costs rise there will be an increasing trend toward mechanization. In turn this will require the more specialized intensive land use associated with plantation forestry. Here the degree of vertebrate pest damage, perhaps tolerable in the open forest system, is unacceptable. Further the Red Squirrel and Porcupine are both vertebrates capable of inhabiting the climax forest thus perpretrating their damage through all phases of growth of the forest plantation from initial seeding to harvest of the mature timber. A more specific outline of the stages in plantation development is given in table II, but is briefly: cone and seed losses, seedling and sapling injuries and mature tree injuries. A complete review of the damage caused by all types of forest vertebrate pests is given in table III, while a definition of the types of damage, for example barking, clipping etc., is given in table I.

In summary then, the trend towards increased cutting of forest resources continues unabaited. Ontario for example has recently introduced a policy which will allow for 911 million cubic feet of timber to be cut by the year 2020. The challenge for forest regeneration is formidable. In addition to the 2.25 million acres of forest land harvested annually there is almost as much again lost to fire and there is an estimated backlog of 42 million acres inadequately regenerated in the Canadian forest system (45). In 1962 D. H. Janzen then Director, Bureau of Sport Fisheries and Wildlife U.S. Department of the Interior, noted that some of the most difficult damage problems in the forest system from the point of view of control are those related to the smaller mammals (27). It was noted however that it was with great difficulty that the wildlife biologist came to any firm assertion as to the acceptable population levels for any animal. Research, was nevertheless being undertaken in three concurrent directions: effects of timber management practices on wildlife populations was being examined; methods of preventing wildlife populations from reaching pest proportions in the forest were being developed and a major programme was devoted to testing potential repellents in order to lessen vertebrate pest injury in high value stands without radically altering population balance. Sadly it appears that Canada is unwilling to embrace a similar coordinated management approach to what must be an existing and potential problem of considerable dimension.

The following is a synoptic report of Porcupine and Red Squirrel as important forest pests.

American Porcupine, Erthizon dorsatum

The American porcupine is considered one of the most important mammalian forest pests since it attacks both trees less than six inches in diameter at B.H. and merchantable timber (3). Complete girdling may result in the death of the tree, but even spot damage may seriously effect growth and timber value (18). Banfield (3) indicates that Ponderosa and Lodgepole Pine, Eastern White and Red Spruce are of prime importance while Eastern and Western Hemlock, Balsam Fir, Tamarack, Sugar Maple, American Beach and Baswood are all severely damaged. In addition Caras (8) adds to this list Cottonwood, Willow, Aspen, Jack Pine, Elm, orchard trees and their fruit. Peterson adds White Birch as an important food source. Indirect damage includes the eating of wooden tool handles left in the wood because of salt attraction, the gnawing on buildings, picnic tables and latrines for the same reason. The chewing of rubber tires and also in forest recreation areas-the danger of pets being attacked and requiring veterinary attention for quills in the mouth (4) (8) (23) (36). Wood lot areas near agriculture can allow for porcupine harbourage and damage to corn, alphalfa and clover (18) and in recreational areas the pungant and annoying odor of urin (31) and the animals perchant for eating forest signs (60) further defines their pest status. Fletch writing on the infectious diseases of wild mammals in (10) indicates that porcupine may be a vector of foot and mouth disease.

While economic thresholds are poorly defined, some studies have attempted to quantify actual losses due to porcupines. Banfield, quoting a study from 1940 indicates 11.5 to 36¢ per animal per year damage in Maine, 45¢ to $1.10 in Colorado and a $1.66 in Montana. If we allow for a 480% inflation rate since 1940 (66) this provides a range of economic impact of $1.72 to $7.96 with a mean of $5.00. Banfield also notes studies indicating 6 to 8 animals per square mile in New Brunswick, up to 20 to 28 animals per square mile in Maine. If we take a mean of ten animals per square mile on one million square miles of forest in Canada, we have an indicated figure of some 10 million animals. This figure of ten million animals on 650 million acres corresponds well with the known animal habitat requirement of approximately 6.5 acres. This would indicate that porcupines may be responsible for up to 50 million dollars worth of damage in the Canadian forest system per year. In another study (30) in the Great Lakes region it was found that porcupine damage accounted for 20.8¢ per acre per year or 5.2% of the board feet growth and 8.3% of stumpage values. There is little doubt that damage can be severe (15 (63)

More specifically, direct damage includes barking injury to seedlings and saplings with broad prominent inciser marks in exposed sapwood and feeding on older trees which appears to be confined to the unplated bark of the upper bole where top girdling produces characteristic bushy crowns. There is also feeding on young full size trees, in particular Douglas Fir and, at denning time, branch cutting to feed young (31). Clipping of leaders, multi-leaders and stag heading along with bleeding of resin from wounds is also recorded (4). Exposure to disease and insects especially cankers and borers would seem likely. Costs are associated not only with loss of increment and top growth, but with reduced yields per acre and in younger stands labour and tree costs for replacement, and future management problems resulting from uneven stocking.

Specific damage thresholds are not readily calculated. In particular there seems to be some difficulty in obtaining exact figures on investment in plantations. Even ignoring the fixed costs associated with tasks outlined in Table II, and using only costs for seedlings and transportation (9), planting, and supervision (28)-there is approximately $75 invested in every site re-planted with 400 2 + 1 seedlings. The net disconcounted revenue on forest investments is relatively low ranging only from 1 to 3% (28). On a $75.00 investment 1% at 10 years equals $83.00 at 2% $91.00 and at 3% $101.00. The gain therefore at even the best rate of investment, is only $26.00. A damage rate of 10% in conifer plantations appears quite common (13) (30) but may rise as high as 90% (63). For such a small return on investment, it would appear that little damage at this level can be tolerated. However there is an obvious need for more detailed studies under Canadian conditions and on a wider scope before reliable figures can be developed.

The porcupine is the only member of a typically South American group of rodent that crossed the Isthmus of Panama during the Pleistocene era and invaded North America of its own accord (4). The Old World porcupine Hystrix belongs to another family, though illustrates convergent evolution.

Distribution in North America is from Northern Mexico to Alaska and from the Atlantic to the Pacific and in Canada all of continental Canada north to the tree line and in Northern Quebec, Labrador, Northwest Territories and the Yukon. The porcupine is not found in Newfoundland and Anticosti, Prince Edward Island, Cape Breton, Grant Manon or Campobello Island in the East or on Vancouver Island or Queen Charlotte Islands in the west (36) (4) (33) (8).

Porcupine belongs to the Order Rodentia and suborder Caviomorpha. It is in the family Erethizontidae and is of the species Erethizon dorsatum. There are four sub species whose name and distribution is given in Figure I. Common names include porcupine, porky, quill pig, and in French, Porc-épic.

Subspecies dorsatum is the typical form in Eastern Canada and is found also in the Prairies east of the McKenzie River and in the Northwest Territories. Epixanthum is found in the short grass areas of Alberta and Saskatchewan and has paler greenish yellow tip guard hairs than the cream tips found in dorsatum. Myops is brownish colour with long rusty yellow tipped guard hairs and is found in the Yukon, west of the McKenzie River, northeast B. C. and northwest Alberta. Nigrescens is blackish hair with rusty yellow tips and is found in B. C. and the Rocky Mountains (4) (34). Comments on habitat appear to differ, Banfield notes that the animal is found in both deciduous and coniferous forested areas. In summer it may be found far from trees in Eastern farm land. Mc T. Cowan and Lawrence note that it is rarely found in the Coastal Douglas Fir forest. It is however abundant where there is broken rock and cliffs which occur with Pine forest. Caras also add Poplar woodland to common porcupine habitat.

Caras in describing the porcupine,gives it as a flat footed, deliberate, robust, short legged, clumsy rodent. It has a small head, short ears and beady eyes, its muzzle is blunt and his tail short and muscular. The animal is reported to have good hearing and smell but poor eyesight. His fur is long, soft and wooly,he walks with a shuffle leaving pigeoned toed tracks. Banfield notes that his Pelage is composed of sensory hairs with a dense wooly brown undercoat, long cream tufted guard hairs and stiff quills. The hairs are arranged in transverse rows, the quill rows are separated from the rows of coat hairs. Quills are located on head, neck, rump and tail, the longest is about 60 millimetres, the shortest 30 millimetres. The quills are easily pulled out and may grow one half a millimetre per day and may be replaced in ten days to four months. The tip has a backward projecting scale preventing withdrawal and may cause the tip to work inwards in flesh. There are about 30,000 quills per animal. Ventral surfaces and legs are coated with hair, the underbelly with soft down. Coat hairs are moulted annually between Spring and late Summer from nose to tail. Broken quills can be shed. The short strong legs are equipped with long curved black claws,four toes on the forefeet and five on the hind. Soles of the feet are flesh
Albino porcupines occur fairly often.

The porcupine is Canada's second largest rodent after the beaver. Its weight is given by Banfield as 11.2 kilograms and a length of 91 centimeters as against 18 kilograms and 101 centimeters by Caras and 10 kilograms and 78 centimeters by Mc T. Cowan. These differences may accounted for in the different sub-species. Hind foot is noted by the the latter author as 9.8 centimeters.

The behaviourof porcupines appears relatively well documented. It is noted as a solitary and cantankerous animal which pairs only for mating, it has dens or ground shelters particularly in winter. Rocky tallus slopes, quarries, caves and rocky road fill appear suitable denning sites as do road culverts, hollow logs, brush piles and wind blown trees. One author (34) notes that the base of trees with branches to the ground are often used. Snow tunnels appear common in the winter (4). Porcupines can climb extremely well (20) and will swim without effort (4). They are primarily nocturnal and spend much of the daylight hours resting in loafing trees, normally a bushy confier (31). They are active throughout the winter (4) (8) (23) (31) (36). The front teeth keep growing and actively need to be worn down (8). The porcupine is an easy animal to approach. When threatened it puts its unguarded snout between its forelegs often near a log or rock, lowers its body, arches its back and spines,and moves around to keep its rump towards an enemy. It can lash its tail leaving quills in the attacker (4) (8) (36).

Home range appears to be from five to six acres although some animals may wander considerably further, 30 acres in a 30 day tag study being recorded (4). It is common for porcupine to have regular paths to and from feeding areas (8).

Most authors note that there are marked seasonal changes in the feeding patterns of porcupine. In summer Banfield notes that leaves of the yellow Pond Belly, Aspen, White Birsh, various shrubs and forbes are consumed. In winter the cambium of all species and new twigs and buds are eaten while in the spring unfolding Poplar and Baswood leaves and branches are consumed. Caras specifically notes the Cottonwood twigs as winter food. Lawrence notes that in spring and summer suculent herbaceous vegetation is consumed and porcupines are attracted to moist meadows and stream banks. In Fall and Winter the bark and foliage of conifers preferably Ponderosa and Lodgepole Pine but White Fir, Sugar Pine and Juniper are also eaten. Taylor (48) indicates that Douglas Fir and Spruce may be injured while this author and Horn (26) note that dwarf Mistletoe is sometimes eaten.

Eadie in a comprehensive study of the porcupine in 1954 notes that the animal has a large daily food requirement approaching 10% of its body weight (13) which equates to 2.7 to 3 pounds (.3 to 1.3 kg.) per day. If the same rough figure of 10 million animals in the Canadian forest system is used this is equivalent to 5,000 tons of green matter a day using a median one pound consumption rate per animal. Even assuming that most summer feeding is not on woody plants this is still a considerable impact on forest productivity. Banfield also notes that there is a high demand for salt, already mentioned under damage and bones and antlers found on the ground are consumed for mineral content.

Mating occurs in November and December according to Banfield and September to December according to Lawrence. Patterson favours November and December but notes that mating may take place in January or April. Mc. T. Cowan records November as the principal month in British Columbia. There is a highly developed mating ritual and females may mate with a number of males, however it appears that males require prolonged association with the female before mating and are normally restricted to one female per season (4). Gestation data is quite varied, Mc T. Cowan indicating 112 days while Paterson, Caras and Banfield give figures of 209 to 217 days. The weight at birth according to Banfield is .53 grams while Patterson extends this up to 1.5 kilograms. Length is on average 22 to 28 centimetres. Birthdate is mainly mid May to the end of July or in later conceived young October. There is normally one and rarely two offspring.

Young porcupines are unique among Canadian rodents, born at an advanced stage of development and are precocious. Eyes are open and they can walk within an hour of birth. The young are covered with long black hairs and 10 to 25 millimetre quills which although soft at birth harden within an hour. They are playful but exhibit defense turning very quickly. Banfield indicates that weaning takes place after two weeks however Peterson indicates nursing may continue up to four months and Caras up to five months. Sexual maturing for both males and females appears to occur between two and two and one half years old. (4) (34)

Population studies by Spencer (67) indicate that porcupine populations have fluctuated in past centuries in the Central United States. There were population explosions well documented by Dendrochronology in 1845, 1885, 1905 and 1935. Earlier population increases are indicated for 1716, 1746, 1785 and 1815.

The population density of porcupines have been reviewed by a number of authors (4) (8) (18) (23) (30). On average there appears to be something in the order of ten animals per square mile each with a home range of five to six acres. Diurnal movement is about 80 metres and nocturnal movement up to 130 metres.

Mortality is not great. Porcupines exhibit a high ratio between conception and Embryonic survival indicating few complications occur during pregnacy. This is coupled with a high post natal survival rate and precocious young contribute to the high biological potential for porcupines dispite their low birth rate (18). Banfield gives a life span of eight to ten years and Caras five to six years. Natural predation includes the large carnivors Wolvarine, Fisher, and Bobcat all of which may search for winter denning places and have developed the skill to turn porcupines over to avoid the quills. Caras notes that when other food is unavailable wolves, coyote and foxes may also attack porcupine.

Control programs in Canada are poorly recorded and as is often the case those programs noted (4) (18) have concentrated on chemical elimination of the problem. Biological control is not recorded by any authors but perhaps could be investigated with the use of palatetable herbaccous or woody plants interplanted in single species conifer plantations. Physical control seems to have included clubbing; shooting-where it is suggested that after sunset; along forest roads is the most successful denning and electrical fences (4) (8) (18). Denning would appear to be a fairly successful method as the winter dens are readily identifiable (19). The electric fences are suggested only for the potection of agricultural problems (8). Two chemical control methods are recorded (4) (18) and appear to have been relatively successful. One has involved using strychnine in a salt bait and the other sodium arsenite in apple baits. No integrated management methods are reported in the literature and cost effectiveness of any method is poorly reported. A report from Oregon (56) indicates that poison baiting of porcupines has not been particularly successful since the animal prefered to chew the plywood structure used to protect the bait rather than eat the bait itself.

The benefits from porcupine appear to include the use of quills for decorative work their providing food for desireable carnivors; some thining of weed trees; such as Balsam and Poplar.

There are, as is so often the case, no cost/benefit analysis covering the impact of this animal on the productive forest system.

Red Squirrel, Tmiasciurus hudsonicus

The damage caused by red squirrels may be seen in two catagories: that of cone and twig cutting, and girdling or barking injury to the upper bole of mature trees. Lawrence (31) notes that conifer seed is the principal food of red squirrel especially during winter months. Heavy cone cutting in late summer in order to store cone crop may result in as high as 85% of the current cone crop being removed and 9% of all developing cones being taken before they have the opportunity to mature Squillau (47). Lawrence notes that there are considerably more twigs cut and eaten, while Lutz (33) records cutting of branches on Black Spruce. Adams (2) reports bark and branch tips cut from Ponderosa Pine which also destroys developing cones. Schmidt (39) records red squirrel as taking 66% of mature cones in the Ponderosa Pine forest, while Smith in a quite detailed study (43) indicates that a single squirrel may cut between 12 and 16,000 cones in a normal heavy crop year. Brink (7) indicates 144 cones being cut per squirrel per day from Picea glauca in Alaska. Zaitsev (54) in a study on a European squirrel species notes an 80% destruction of Larch cones.

In the second class of damage; that to mature trees, Viidik (53) noted decapitation of the leader and branches of the first Whorl or in some cases removal of lateral buds. Lawrence noting that much of this damage occurs in the 20 to 60 year age class, states that considerable damage can be sustained by Douglas Fir and Ponderosa Pine, that small strips of bark may be removed in order to lick the sapwood or completed girdling may take place. This later damage can be confused with that of porcupine.

In addition to direct damage to the forest resource a number of indirect problems or potential problems occur. As far back as the mid 1800's squirrels extracted a considerable toll on nursery stock especially Spruce (17). In hardwood or mixed forest there is the problem of disease introduction after winter or spring feeding especially in Maple where virulent canker may later result (41) and in Oak where a wilt fungus may be transmitted by the animal (16) An important side effect of feeding preference in red squirrel on fertilized plantations is discussed by Asher (1) which could have significant impact on forest management practice in the plantation forests (see also Straton) (45). In recreational forest areas squirrel can cause damage to camping food, clothing and bedding (4) but more importantly may be the vectors for western and eastern equine encephalitis (10) and in the Sierra Nevadas at least, as a carrier Bubonic plague. For example a park directive dated August 1976 lists five precautions of which the first suggests to avoid all contact with squirrels, including not feeding the rodents, and the fifth "should one become ill within one week of visiting a park, a physician should be immediately contacted." It is thought that such advise can only but depress park attendance. Finally red squirrels exert some preda ion pressure on smaller forest wildlife and in particular gamebird eggs and broods may be effected.

The red squirrel belongs to the order Rodentia and the family Sciuridae which includes five species of chipmunk, one woodchuck, three marmots, five ground squirrels, one black tailed prairie dog, three regular squirrels and two flying squirrels. The red squirrel however belongs to a separate genus than other squirrels and has two closely related species-the red squirrel Tamiasciurus hudsonicus and the douglas squirrel T. douglasii. The North American red squirrel should not be confused with the European red squirrel <u>Sciurus</u> vulgaris leucourus. North American red squirrel is a highly plastic species which has been divided into 15 geographic sub-species across its Canadian range as outlined in Table II.

The habitat of the red squirrel indicates that it is more versatile than the grey. Boreal coniferous forest is its principal habitats and it is one of the few mammals to inhabit climax conifer forest. Preference appears to be for mixed forest with White Pine and Hemlocks on cooler north facing slopes (4) However it is found in the Eastern hardwood deciduous forest (36) and in immature hardwood forest (32). On the westcoast it is common throughout the Ponderosa Pine and Douglas Fir cover types (31) (35) (68).

Distribution in North America includes the broad forested belt from Atlantic to Pacific, south in the Rocky Mountain region almost to the Mexico border It does not occur in the south of Manitoba or the southeast of Alberta nor in the central plains or deep south of the United States (4). As noted before it has 15 Canadian sub-species which differ in size, length of tail and colour.

Peterson provides general descriptions as follows: a rusty olive tail with bright yellowish, orange rusty or deep red tips of long tail hair which is white to pale orange. In winter there is a reddish band on the back and tail. Also in winter the black line on the side separating the upper and lower body colours is lost. Feet are bright reddish in summer with thin hair turning heavy grey in winter. Mc T. Cowan indicates that upper parts are grey to olive brown with a reddish wash heaviest along the mid line. Under parts are white to greyish white. Tail is as long as the body, flatish but bushy. The tail upper colour is the same as the body while the lower side is lighter, tips of hairs in the tail are black sometimes the tail tip is black. There is again a black line bright in summer which separates body colour. Ears in the winter have pencils of hair from the tips. Banfield in a more detailed description opens with a notation that there are black vibrinae prominant on the side of the nose, eyebrows and cheeks that are also tactile hairs on the forearms and abdomen. The main coat is glossy olive brown flecked with white with the back of the ears cinnamon, white eye rings and black flank strip separating the body colours. The tail is rufous red with black subterminal black border and tips and grizzled grey. Ear tuffs identify sub-species and may be red or black. The normal palage in winter produces longer more silken fur with a thick leaden grey to buff tipped undercoat. Albinos, part albinos and melanisic types are recorded.

There are two annual moults from March to July starting at the nose and feet working towards the rump; in most individuals this moult will take two months either April, May or May, June however pregnant females will not moult until late Autumn. The second moult occurs in August to December lasting only one month starting at the tail, which only moults once per year, moving from the rump to head and lastly to the feet (4).

Description of size and weight though differing among the sub-species is reported by most authors to be in the range of 350 to 400 millimetres for length (4) (8) (31) although Mc T. Cowan notes the British Columbia sub-species columbiensis - to be somewhat smaller in the range of 300 to 320 millimetres with a tail length of 125 millimetres Hind foot is recorded as being 50 millimeters in diameter. Banfield notes a similar length for tails and 25 millimeters for ears though this varies depending again on sub-species. Weight of a full grown adult which does not appear to differ between males and females ranges between 140 and 250 grams. The head is short and broad, there is a thick glandular area around the anus where two orifices can discharge a musky fluid used for marking (4).

Movement of the animal is, surprisingly, rather poorly documented by Caras indicated that the animal will normally be found within 200 yards of a single nest tree and over a season may range over an area of some five square miles. Other authors (55) (32) indicate the home range to vary from 2.73 to 6.03 acres. Density is reported to be from 0.28 to 1.85 per acre depending largely on food availibility (4) . Various authors indicate that the squirrel normally dens alone except in extremely cold weather, it is normally a solitary animal intolerant of strange individuals of its own or other species. It exhibits fierce territoriality at feeding station and dens however, it may form a (loose attachement) during the mating season.

Inhabit

The red squirrel is recorded as being a bold inquisitive animal, an extremely agile climber able to travel up to 15 miles an hour both up and down the trunk of trees. Further, it both hops and walks on the ground and can leap some five feet if startled. It is quite at home in the trees where it is judged to be the most arboreal of the squirrels being able to jump up to 15 feet and drop from heights of 30 feet without injury. (34) (8) (4) (36) The red squirrel is generally durinal but may be out in moonlight nights in summer and autumn. During the day it may sleep or sun itself in high branches though seek shade during high sun. It dislikes, cold, rain, snow and high wind (8). The tail is extremely sensitive to wind currents and is used for balance, for shade or for heat in cold weather (8). It has an extremely keen sense of smell, sight, hearing and can swim strongly (4). Activity peaks occur two hours after sunrise and just before sunset with the balance of the day being spent sleeping or basking in the sun. Winter activity is restricted to only the warmest part of the day (8) and the animal does not hibernate (31) (8) (4).

Nests, probably called drays, are constructed both for living and reproduction. Finely shredded plant material is used to line burrows, cavities in trees or on sheltered basil branches within six to eight feet of the trunk (34). Caras notes that hollow trees are often used while Peterson suggests that nesting in trees is more common only in the south of the red squirrels range. Banfield indicates the use of tree cavities, woodpecker holes, birds nests, rock piles, fallen trees and from five to sixty feet above the ground in living trees. The dray is normally up to one foot in diameter with a five inch cavity in the inside. It may only be used in the summer in northern parts of the squirrel's range in Canada. In this situation long winter tunnels may be constructed at ground level.

Feeding of the red squirrel is most varied. Lawrence includes fungi, berries, buds and bark of conifers, branch tips, ripening pollen buds and of course conifer seed. Peterson includes cones, nuts, buds, flowers, fruits, mushrooms, sap, other herbaceous plants, insects, small birds and eggs and small mammals. Mc T. Cowan also specifies leaf buds of Poplar and Birch and dead flesh while Caras suggests corn and commercial berry fruits. Banfield concurs with these authors and notes that the poisonous Sly amanita mushroom may be eaten with immunity and that mice, voles and young cottontails may be predated. Of the conifers White and Red Spruce, Balsam Fir, Douglas Fir, Hemlock, Larch and Cedar are included in the conifers and in the hardwood forest nuts, catkins, and slashing of bark especially on Sugar Maple is reported. Other authors (3) (7) (35) (39) (43) (46) (54) (68) list a variety of different conifers severly attacked. A most interesting indication came from the review of feeding literature,in that five authors (1) (14) (45) (53) indicates that there is very distinct preference exhibited in squirrel feeding. Edlin for example indicates that the squirrel is able to judge when seeds are ripe and that unripe or infertile cones are not attacked. Smith and Viidik indicate that specific trees are more susceptible to attack. It would seem that the squirrel has the ability to maximize its energy budget. In mid summer cone collection starts with climbing to the crown and cutting of terminal twigs that have green cones. These cutting sautes will last up to two hours and from ten to 100 cones will be allowed to fall to the forest floor. These are then cached in piles from one to many bushels, up to four yards in diameter and a yard in height. These middens are normally in a damp place so that cones do not open and disperse the seed before the squirrel can eat it. Food consumption is given by Caras as 100 pounds of food a year which is approximately four and one half ounces per day. Repeated attempts have been made to obtain figures on the value of forest seed but without success in time for this paper (25). It is known however, that Hemlock produces 0.61 kilograms of seed per bushel, Douglas Fir 0.52 , Lodgepole Pine 0.18 and Spruce 0.45. By knowing the number of bushels cut by and individual squirrel and population density it would be possible to calculate an approximate loss per acre figure, however, in terms of total consumption if it is assumed that there is only one squirrel per ten acres on the 650 million acres of the forest land some three and one quarter million tons of food per year would be consumed.

In the southern part of its range the red squirrel is polyoestrous with oestrus occuring in February, March and again June or July in northern Canada, however, only one litter is born per year. In the male the testes develop in February and then the animal is in breeding condition until August. The testes are withdrawn from September to mid January. Mc T. Cowan indicates that April is a common mating month. There are mating chases as with other squirrels (8) (4) (31). Births seem to predominate in the months of April, May and August, September, jestation is 40 days and litter size from one to eight. The newborn are altricial, virtually hairless, toothless, and with the eyes closed for the first month. The first hair appears at seven days and well defined by ten days. The external meatus of the ear develops in 18 days and by 38 days the young can play together. They are weaned at seven to eight weeks and appear outside the den by ten weeks old at which time they are about one third grown. The young squirrels will train with the mother for up to 18 weeks and then disperse (4) (49). The young have a soft rufous coat which they moult at the age of 11 months. They are sexually mature as yearlings.

The newborn are 65 to 75 millimetres in length and five to eight grams in weight (4). Young born in spring may spend the summer with the mother or in the case of fall born young have a complete winter (8).

Predation plays the most important role in the control of squirrel numbers as conversely the squirrels do in the population of predators. As one of the most abundant herbibores the squirrel is preyed on by Redtailed, Red Shouldered, Broadwing and Cooper's hawks. In addition the Goshawk, Sparrow, and Marsh Hawks may also take small squirrels. The Barred and Great Horned owls may prey on squirrels especially at dusk. The marten, fisher, bobcat and linx are predators of the squirrel in trees while weasel, coyote and wolf will attack the animal on the ground. In many areas vehicles take a heavy toll on squirrel populations. Man is also a direct predator mainly for the fur bearing industry. The squirrel has developed extremely good eyesight and the defense reaction of freezing on a tree so that its movement does not draw attention. Its life span is given variously from eight to ten years however Caras indicates that 50% of all young squirrels do not reach their first birthday.

Not withstanding the considerable toll in the forest crops the squirrel does have some important benefits; it is credited with consuming many forest insects and by providing some reforestation by leaving seeds in the ground in caches which are not eaten. It provides an important buffer prey species, removing predator pressures from other more desireable species. It has provided food and "sport" in the field of recreation and is used fairly extensively for lining and edgings of winter clothing especially in the north. In 1971-72 390,884 pelts were sold at an average value of 54¢ which equals $217,971 (4).

Responses in Canada to squirrel population are not well documented in the literature. Certainly modification of habitat does not seem a likely or profitable persuit since the animal is extremely adaptable. It may be that control measures are only warranted in high value crops; some plantations, seed orchards, and Plus Tree seed collection sites. Specimen trees may warrent some protection. The types of control include the encouragement of habitat for predators and perhaps research into natural disease mechanisims which control red squirrel populations. Coccidiousis is certainly reported to have controlled squirrel populations in Europe (52). Physical controls include live baited traps (57) the Imbra trap (42), the common Havahart trap and tree bans which expand with the tree and when attached to the trunk preclude climbing (29) (70). The common practice in Europe has been drey-poking (42) however this may not be particularly successful in Canada where ground burrows form a significant proportion of the nesting sites. Chemosterilants are not mentioned in the literature and surprisingly only one repellant (58) is reported. The most common method of reducing squirrel populations has been shooting the animal, often supported by bounties (37) (42) (50) (51). In the past very substantial numbers have been taken by this process. For example in the period 1903 to 1933 in Scotland the Hyland Squirrel Club shot some 82,000 European Red Squirrels (45). In the United States where squirrel hunting has been popular, records indicate that over 2 million squirrels were killed in one season in North Carolina on an area less than 52,000 square miles while in West Virginia the numbers killed range from 750,000 to 1,500.000 (51). These later programs were however directed to the grey squirrel.

In Canada where there is history of extensive squirrel shooting it could be expected that such policies would be publically unpalletable. In fact their usefullness is probably suspect. Without better definied economic criteria it is not possible to form any reasonable conclusions. It can however be said that squirrel do present a potential problem in high valued crops and that this potential will increase with the continuing trend toward intensive forest systems.

REFERENCES

1. Asher, W. C., 1963 Squirrel Prefer Cones From Fertilized Trees U. S. Forest Service, Southeast Forest Experiment Station Bulletin #SE3

2. Adams, L. 1955, Pine Squirrel Reduce Future Crops of Ponderosa Pine Cones Journal of Forestry 53; 35.

3. Backhmann, P., 1971 Barking Damage by Squirrels in 1969 in Canton Berne Schiviez. Z. Forstiv 122 (4) 164 - 180.

4. Bankfield, A. W., 1974, The Mammals of Canada. National Museums of Natural Science of Canada.

5. Baranyayja, 1968 Squirrel Feeding on Dwarf Mistletoe Infections bi-monthly research notes Canadian Forest Service 24 (5).

6. Brandu, R. B., 1973 Life history notes on the porcupine in Hardwood-Hemlock forest in upper Mich. Mich. Academician 5: (4).

7. Brink, C. H., 1966 Spruce seeds as food of red squirrel and flying squirrel in interior of Alaska. Journal Wildlife Management.

8. Caras, R. A., 1967 North American Mammals, Galahad books.

9. Coney, M. G., 1976 Nursery crop costing report for year ending June, 1976 British Columbia Forest Service.

10. Davis, J. W., 1970 Infectious diseases of wild mammals, Iowa State University Press.

11. Davidson, A. M. 1969 Red squirrels in Thetford Chase, quarterly Journal of Forestry 63 (3).

12. Daniel, T. W., 1959 Thinning in a young stand of Lodgepole Pine. Proceedings Society of American Foresters 159 - 163.

13. Deusen, J. L. 1962 Porcupine damage in immature stands of Ponderosa Pine in the Black Hills. Journal of Forestry 60 (11) 811-3.

Dadie, W. R., 1954 Animal control in field, farm and forest, MacMillan, New York.

Edlin, H. L. 1956 Tree injuries there cause and prevention, Thimes and Hudson.

15. Cottrell, C., 1974 Forest Insect & Disease Conditions Canadian Forest Service Pacific Forest Research Centre.

16. Engelhard, A. W., 1960 Squirrels as possible vectors of oak, wilt fungus in Iowa. Plant disease reporter 44 (3) 192-6.

17. Furst, H., 1893 The protection of woodlands against dangers arising from organic and inorganic causes, David Douglas.

References (Continued)

18. Faulkner, C. E., 1962 Control of Porcupines in New England, Journal of Forestry 60 1 Part 1, 36 - 37.

19. Gill, D., 1972 Habitat Preference of Porcupine in Southern Alberta Foothills, Canadian Field Naturalist (4) 349 - 355.

20. Gordon, D. T., 1959 Ten year observations on pruned Ponderosa and Jeffrey Pine, research note, Pacific Southwest range experiment station Report #153.

21. Grossest, A., 1964 A squirrel trap, quarterly Journal of Forestry 58 (2).

22. Heacox, E. F., 1962 Industrial Foresty & Wildlife - The Northwest, Journal of Forestry 60 1 Part 1 10 - 12.

23, Hoover, E. F., 1971 The Porcupine in Oregon, its life history and control research paper Oregon Forestry Research Laboratory #10 22 pp..

24. Howard, W. E. 1962. 1961 report of the Wildlife Societies Committee on Economic losses caused by vertebrates, Journal of Forestry 60 1 Part 1 45 - 46.

25. Hamilton, M. 1977, Personal communication from the British Columbia Forest Service Seed Laboratory Duncan, B. C.

26. Horne, E. E. 1925, Studies relative to economic control of porcupines, U. S. Bureau of Biological Survey at the southwest forest experiment station 25 pp.

27. Janzen, D. H., 1962, Wildlife and the Forest, Journal of Forestry 60 1 Part 1 6 - 9.

28. Jones, R. 1977, Personal communication from Reid, Collins & Associates, Forestry Consultants, Vancouver, B. C.

29. Krugman, S. L. 1963, Modified tree banned to foil cone harvesting squirrels, U. S. Forest Service, research note Pacific Southwest Forest Range Experiment Station #PSW-35.

30. Krefting, L. W. 1962, Porcupine Timber Relationships in the Great Lakes, Journal of Forestry 60 (5) 325-30.

31. Lawrence, W. H., 1961, Guide to Wildlife Feeding Injuries on Conifers in the Pacific Northwest, Western Forestry and Conservation Association Portland, Oregon.

32. Lynch, G. R., 1968, Distribution and Habitat of Red Squirrel in the North Central States, proceedings Iowa Academy of Science 75.

33. Lutz, H. J. 1958, Effect of Red Squirrels on Crown Form of Black Spruce in Alaska. Technical note Alaska Forest Research Centre Report #42.

34. McTaggart Cowan I., 1956, The Mammals of British Columbia handbrook #11, British Columbia Provincial Museum.

References (Continued)

35. Pike, G. W., 1934, Girdling of Ponderosa Pine by Squirrels, Journal of Forestry 32 98-99.

36. Peterson, R. L., 1975, Mammals in Profile Parts I and II. Cerebrus Press Inc..

37. Ritch, I. E., 1931, Beasts and Birds as Farm Pests, Oliver and Boyd.

38. Sadleir, R. M., 1976 Format for information on vertebrate pests, Department of Pestology, Simon Fraser University,

39. Schmidt, W. C., 1971, Ponderosa Pine Seed - For Animals or Trees, U. S. Forest Service Research Paper, Intermountain Forest & Range Experiment Station Report #112 14 pp.

40. Shearer, R. C., 1970 Natural Regeneration in Ponderosa Pine Forest in Western Montana, U. S. Forest Service Research Paper Intermountain Forest Research Experiment Station Report #86 19pp.

41. Shigo, 1964, A canker on Maple caused by fungi infecting wounds made by the red squirrel, plant disease reporter 48 (10).

42. Shorten, M., 1962 Squirrels. United Kingdom Ministry of Agricultural Fisheries and food Bulletin #184 HMSO.

43. Smith, M. C., 1968 Red squirrel responses to Spruce cone failure in interior Alaska. Journal Wildlife Management 32.

44. Smith, C., 1970, The coevolution of pine squirrels and conifers, Ecology monographs 40 (3) 349-71.

45. Stratton, C. R., 1976 Canadian Forestry-The View Beyond the Trees, Environment Canada, MacMillan of Canada and MacLean-Hunter Press.

46. Stillinger, C. R. 1944, Damage to Conifers in Northern Idaho by the Red Squirrel Journal of Forestry 42 143-145.

47. Squillace, A. E., 1953, Effect of Squirrels on the Supply of Ponderosa Pine Seed, U. S. Forest Service, Northern Rocky Mountain Forest and Range Experiment Station, Research note 131.

48. Taylor, W. P., 1935 Ecology and Life History of the Porcupine, Erethizon epizanthum as related to the forests of Arizona and South Western United States, University of Arizona Biological Science Bulletin #3 177 pp.

49. Taylor, J. C. 1970, The Influence of Arboreal Rodents on their habitat and man. Publications Du L' OEPP #58 217-223.

50. Taylor, K. D., 1963 Some Aspects of Grey Squirrel Control. Anals Applied Biology 51 (2) 334-8.

51. Uhlig, H. G., 1955, The Grey Squirrel; its life history, ecology and population characteristics in West Virginia, Pittman-Robertson Project 31R Conservation Commission, West Virginia.

References (Continued)

52. Vizoso, A. D., 1969 A Red Squirrel Disease, published in Diseases in Free Living Wild Animals, Editor Ancdiarmid Academic Press.29-38.

53. Viidik, P. 1973 The Effect of Squirrel damage on Norway Spruce, Canadian Forest Service Bi-monthly Research Notes 29 (2) 14.

54. Zaitsev, V. S., 1974, Effect of Squirrels on Seed Production of Larix sukaczewii in the Pine Forests of the Trans Urals Forest-Steppe Ekologyia #1 102-103.

55. Zirul, D. L, 1971, Winter Fluctuations in the Size of Home Range of the Red Squirrel, Tamiascrurus hudsonicus, transactions North American Wildlife and Natural Resource Conference 35; 115-27.

56. Anon, 1964, Summary report on the United States Forest Abstracts 25 (4).

57. — 1967, Squirrel Control Forestry Commission Leaflet #56 HMSO.

58. ?

59. 1965, Forestry & the Environment, forestry information section Canadian Forest Service.

60. 1972, Equipment tips, Porcupine Resistant Forest Signs, Missoula, Montana, U. S. Forest Service Equipment Development Centre 4 pp.

61. 1973, National Forest Inventory for Canada, Canadian Forest Service, Department of the Environment.

62. 1974, Annual report, National Parks Branch, Department of Indian and Northern Affairs for Canada.

63. 1975, Annual report of the Forest Insect & Disease Survey, 1974 Canadian Forestry Service.

64. 1975, Forestry Statistics for British Columbia, Pacific Forest Research Centre, Canadian Forest Service Environment Canada.

65. 1975, What's New in Forest Research #22 and 27, Forest Research Institute, Rotoru, New Zealand.

66. 1977, Consumer Price and Price Indexes, Catalogue 62-101, computer print out, Statistics Canada.

67. Spencer, D. A., 1964, Porcupine Population Fluctuations in past centuries revealed by Dendrochronology Journal of Applied Ecology, Oxford 1 (1) 127-49.

68. Mitchell, J. E., 1950, Wildlife-Forest Relationships in the Pacific Northwest region, Journal of Forestry 48; 26-30.

69. 1976, Wild Rodent & Bubonic Plague Caution Handout. Vector and Waste Management Section California Department of Health.