

PERIOD LENGTH IN CYCLIC ANIMAL POPULATIONS

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Abstract. Although cyclic animal dynamics have long been a focus of scientific interest, the variable cycle lengths are poorly understood. Based on a review of the literature, we suggest that period length in animals showing multiannual cycles is related to the life span of their food plant rather than to any trait of the animal, such as mass or fecundity. We envisage that this pattern is brought about by a prolonged mobilization of induced defenses in longer lived plants, which can better afford periods of low reproductive output than can short-lived plants. On the basis of this hypothesis we expect animals with similar diets to show similar cycle lengths, irrespective of taxonomy and size. A path analysis, on the vertebrate herbivores, shows that 92% of the variation in cycle length is explained by food-plant longevity and that body mass adds little to this.

Key words: bird; cyclic herbivore populations; food-plant longevity; herbivory; insect; mammals; multiannual cycles; plant life span.

INTRODUCTION

In the hope of finding general principles in population dynamics, scientists have long taken an interest in species with cyclic population fluctuations. Apart from trying to find the factor(s) causing delayed density dependence that can produce cyclicity, efforts have been focused on periodicity in cycles, varying between three and more than 30 years. Attempts to explain cycle intervals have concentrated on maternal effects (insects; Ginzburg and Tanneyhill 1994), population growth rate (May 1981), and in vertebrates, body mass (Calder 1983). The logic behind these views is that fast-growing populations of small animals will pass through their cycles faster than slow-growing populations of large species, whatever the factor(s) causing the population change (Ginzburg and Tanneyhill 1995). Calder (1983) suggested that cycle length for herbivores, but not for predators, which presumably follow the cycle of their prey, is associated with the intrinsic rate of population increase (r), which scales with the 4th root of body mass. Peterson et al. (1984) found a very good fit between cycle length and body mass (exponent 0.26) in 41 species of herbivorous birds and mammals. However, the inclusion of a larger sample of herbivores decreased both the fit and the scaling exponent (Krukoni and Schaffer 1991), who also asked (p. 471) "If carnivores simply tag along after their food supply, why not herbivores after theirs?"

We explored this latter suggestion by assuming that traits of food plants rather than those of the herbivores determine cycle length, as a consequence of costs and benefits linked with grazing-induced delayed plant re-

sistance (Haukioja and Hakala 1975, Rhoades 1985). For such resistance to drive multi-annual cycles it is required that grazed plants show a delayed response by increasing defense substances/structures and that the relaxation of this response in the absence of grazing should take several years. These conditions were analyzed by Underwood (1999) in a mathematical model. For most plant species examined in this study (Tables 1 and 2) induced resistance has been shown (Karban and Baldwin 1997: Table 4.1), but information on relaxation periods is sparse. However, indirect evidence for long-lasting effects of induced resistance has been found: Haukioja and Neuvonen (1987) recorded significant reductions in fecundity of the moth *Epirrita autumnata* feeding on birches *Betula pubescens* defoliated up to four years earlier; Bryant et al. (1991) found a reduced palatability for snowshoe hares (*Lepus americanus*) in twigs of trees browsed three to four years earlier; and Baltensweiler (1985) reported an increased mortality level in larch bud moth *Zeiraphera diniana* caterpillars for several years following an outbreak. The benefit of an induced defense for the plant is a reduced grazing pressure, often for many years, which is balanced against its cost, a reduction in growth and seed production (Karban and Baldwin 1997). We suggest that short-lived plants demobilize their induced defenses sooner than long-lived plants, because the latter can better withstand lost growth and reproduction. In other words, one lost reproductive event, or part of it, constitutes a smaller fraction of the reproductive value of a long-lived plant compared to a short-lived plant, tipping the cost-benefit balance in favor of a longer-lasting defense period for long-lived plants. Therefore, cycles of herbivores that graze on trees will be longer than cycles of those grazing on herbs, irrespective of taxonomic affiliation, size of the herbivore,

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TABLE 1. Life history and cycle length of vertebrate herbivores and longevity of their food plants.

Herbivore	Data source	Cycle length, median (yr)	Body mass (kg)	Plant species	Plant longevity, mean (yr)
<i>Lagopus scoticus</i>	Watson and Moss (1979)	6	0.6	<i>Calluna vulgaris</i>	25
<i>Lagopus lagopus</i>	Andreev (1988)	10	0.6	<i>Salix pulchra</i>	75
<i>Dicrostonyx groenlandicus</i>	Shelford (1943)	5	0.07	<i>Dryas</i> spp., <i>Salix</i> spp.	50
<i>Lemmus lemmus</i>	Framstad et al. (1993)	3.5	0.05	Poaceae, Cyperaceae	7
<i>Myopus schisticolor</i>	Eskelinen (1997)	3	0.03	Bryophyta (Poaceae)	15
<i>Clethrionomys rufocanus</i>	Krebs and Myers (1974)	4.8	0.04	<i>Vaccinium myrtillus</i>	15
<i>Microtus agrestis</i>	Myllymäki (1977)	3.3	0.03	Poaceae, Cyperaceae	7
<i>Arvicola terrestris</i>	Saucy et al. (1994)	6	0.15	<i>Trifolium pratense</i>	20
<i>Ondatra zibethicus</i>	Danell (1985)	4	1.4	Cyperaceae	7
<i>Erethizon dorsatum</i>	Spencer (1964)	32	5.5	<i>Pinus edulis</i> , <i>P. ponderosa</i>	450
<i>Lepus americanus</i>	Keith (1990)	10	1.5	<i>Betula</i> spp., <i>Salix</i> spp.	100
<i>Alces alces</i>	Messier (1991)	19	300	<i>Betula</i> spp., <i>Abies</i> spp.	210
<i>Odocoileus virginianus</i>	Fryxell et al. (1991)	24	100	<i>Quercus</i> spp., <i>Thuja</i> spp.	300
<i>Ovis aries</i>	Clutton-Brock et al. (1997)	3.5	40	Poaceae	7

Note: Plant longevity information is from Harper and White (1974).

or growth rate of its population. This pattern cannot be predicted by any other known hypothesis on population cycles than those involving plant defense, i.e., the grazing-induced plant-defence hypothesis and the mast-depression hypothesis (Selås et al. 2001).

The suggestion that a single factor, such as food, might explain most variation in multi-annual cyclicity may appear unrealistic. For example, it is hard to imagine that peak, but still relatively sparse, populations of cyclic grouse, feeding on very abundant plant species, could induce such strong and widespread defense reactions as required for a population crash. On the other hand, there are many herbivores, from mites and insects to birds and mammals that specialize on the same food plants. We believe that the combined grazing pressure from such a guild can mobilize a strong defense in plants, ultimately causing parallel cycles in all the her-

bivores specializing on that plant. By way of example, F. Schwerdtfeger's study on fluctuations in pine-eating moth populations over 46 years (in Varley 1949) show some co-variation ($K = 0.24$; $P < 0.001$) between four different species. Nevertheless, it is clear that other factors, such as predators (Krebs et al. 1995, Reid et al. 1995, Korpimäki and Norrdahl 1998) and parasites (Hudson et al. 1998) can also contribute to cyclic population fluctuations.

METHODS

To compare periodicity of cyclic animals and longevity of their food plants we needed information on both herbivore cycle length, species of food plants, and life span of these. Much data are available on herbivore cycle length but much less is known about relevant food plants and their longevity. Selection of data had

TABLE 2. Life history and cycle length of insect herbivores and longevity of their food plants.

Herbivore	Data source	Cycle length, median (yr)	Plant species	Plant longevity, mean (yr)
<i>Strophiingia ericae</i>	Whittaker (1985)	6	<i>Calluna vulgaris</i>	25
<i>Melolontha hippocastani</i>	Schwerdtfeger (1968)	4.5	Poaceae	7
<i>Lochmaea saturalis</i>	Nielsen (1986)	6	<i>Calluna vulgaris</i>	25
<i>Diprion pini</i>	Geri (1988)	17	<i>Pinus sylvestris</i>	200
<i>Neodiprion sertifep</i>	Kangas (1963)	17	<i>Pinus sylvestris</i>	200
<i>Pristiphora erichsonii</i>	Jardon et al. (1994)	25	<i>Larix laricina</i>	180
<i>Acleris variana</i>	Morris (1959)	8	<i>Abies balsamea</i>	200
<i>Choristoneura fumiferana</i>	Royama (1984)	33	<i>Abies balsamea</i> , <i>Picea glauca</i>	250
<i>Choristoneura occidentalis</i>	Swetnam and Lynch (1993)	33	<i>Pseudotsuga menziesii</i> , <i>Abies concolor</i>	500
<i>Choristoneura pinus</i>	McCullough (2000)	9	<i>Pinus banksiana</i>	180
<i>Zeiraphera diniana</i>	Baltensweiler and Fischlin (1988)	9	<i>Larix decidua</i>	200
<i>Bupalus piniarius</i>	Varley (1949)	8	<i>Pinus sylvestris</i>	200
<i>Epirrita autumnata</i>	Tenow (1972)	9	<i>Betula verrucosa</i>	120
<i>Malacosoma californicum</i>	Myers (1988)	8	<i>Alnus rubra</i>	110
<i>Coloradia pandora</i>	Speer et al. (2001)	30	<i>Pinus ponderosa</i>	450
<i>Hyloicus pinastri</i>	Varley (1949)	13	<i>Pinus sylvestris</i>	200
<i>Orygia pseudosugata</i>	Myers (1988)	22	<i>Pseudotsuga menziesii</i>	600
<i>Cerapteryx graminis</i>	Danell and Ericson (1990)	7	Poaceae	7

Note: Plant longevity information is from Harper and White (1974).

to be based on knowledge of both these variables and also had to consider the risk of phylogenetic pseudo-replication, not only for the herbivores but also for the food plants. We restricted the analysis to monophagous animals or those feeding on a few plant species of similar longevity. Information on food plants and cycle length was usually from the same study, but in some cases, such as the microtines, muskrat (*Ondatra zibethicus*), snowshoe hare, moose, and white-tailed deer (*Odocoileus virginianus*), diet data were from other work in the same or nearby areas.

Further, because our hypothesis is based on responses of individual plants we considered only periodicities for local populations, unless there was synchrony in cycle dynamics over vast areas. For polyphagous vertebrate herbivores we considered only food plants of the limiting period of the year, i.e., winter for the species in Table 1. Difficulties in defining the limiting period for polyphagous grouse species forced us to omit these, despite the fact that many of them show distinct multi-annual cycles, often attributed to between-year variation in breeding success. If so, the relevant food could be that of the laying hen, the newly hatched chicks (often insects), older young, or a combination of these.

Finally, to avoid selection bias, most data on food-plant longevity were taken from the study by Harper and White (1974). As stressed by these authors their longevity data represent "normally attainable age," best regarded as that at which dominant individuals die, i.e., when senility sets in. Length of the defense period is presumably related to such an age.

Choice of species and time period

Comparative analyses like our present study often are accused of being biased in favor of suitable species and/or time periods. We therefore discuss some important groups in terms of data selection:

Rodents.—To our knowledge, all long-term (>3 cycles) studies of cyclic small rodents (microtines) show short cycles (3–5 years). The microtine diet consists mainly of green plant parts, usually of graminoids and mosses. Typically, shoots of preferred grasses and mosses are shortlived, 5–10 and 15–20 yr, respectively (Harper and White 1974, Jonsdottir and Callaghan 1988, Økland 1995; E. Heegaard, *personal communication*). The exception to this general pattern is the collared lemming (*Dicrostonyx groenlandicus*), which often feeds on herbs and willows that attain ages of 50 years, but also to a large extent feeds on short-lived graminoids and mosses (Klein and Bay 1994).

To avoid pseudoreplication we give data for one species each in the microtine genera *Lemmus*, *Dicrostonyx*, *Myopus*, *Microtus*, and *Clethrionomys*. We stress that choice of species does little to change the overall picture of Fig. 1. In addition, we show data for water vole (*Arvicola terrestris*), muskrat, and porcupine (*Erethizon dorsatum*), all rodents. The porcupine data are

based on dendrochronologic analysis and encompass three cycles.

Grouse.—In many tetraonid species chick survival/recruitment appears to be crucial for population density in the next breeding season (Moss and Watson 2001), but for Willow Grouse (*Lagopus lagopus*) in Siberia the proportion of adult birds breeding, varying between 38 and 100%, seems to be the factor determining population size (Andreev 1988). Winter and spring diets of these grouse are dominated by twigs and buds of a willow (*Salix pulchra*; Andreev 1988), a species often attaining an age of 75 years (K. Danell, *personal communication*). *Vaccinium* spp. and other shrub species figure prominently in the spring and summer diet of many tetraonids (Savory 1977, Spidsø 1980, De Franceschi and Boag 1991), suggesting an intermediate cycle length in these birds. However, since knowledge of the limiting period/diet in polyphagous grouse is inadequate (see above) we have omitted these species. In addition, most studied tetraonid populations have been subject to shooting, a factor Moss et al. (1996) found important in shaping, if not preventing, the multi-annual cycle in Red Grouse (*Lagopus scoticus*).

Ungulates.—We have included three species of ungulates in Table 1, two browsers with long between-peak periods (one and two cycles for white-tailed deer and moose, respectively) and one grazer, the Soay sheep, with a temporal pattern and diet similar to a microtine rodent. For white-tailed deer Turchin (2003) reported historical data covering a longer period with similar periodicity to that recorded by Fryxell et al. (1991). It appears that regular fluctuations occur only in northern deer populations, for which tree browse above the snow is the most important winter food. Caribou populations in the High Arctic appear to undergo extremely long (30–50 yr) oscillations (summarized in Caughley and Gunn [1993]). This fits well with the high longevity of their main winter food, lichen of the genus *Cladina*. Yet, these cycles may have less to do with induced resistance of food-plants than with sheer overgrazing, apparent from the lack of lichen in intensely grazed caribou winter pasture. This is one of the few herbivore–plant interactions often leading to dramatic food depletion. Usually, cyclic herbivore populations in the decrease phase are associated with only slight signs of overgrazing.

Insects.—Most long-time series are of pest species, in particular of moths feeding on forest trees. We have omitted some well-known forest pests such as *Lymantria* spp., *Hyphantria cunea*, and *Heterocampa guttivitta* that feed on a range of plant species of widely different longevity. On the other hand, we have included some closely related species that, in contrast to the rodents mentioned above, show no overlap in food plant choice.

RESULTS AND DISCUSSION

Variation in life-span of food plants explains 72% of the variation in herbivore cycle length (Fig. 1). Cor-

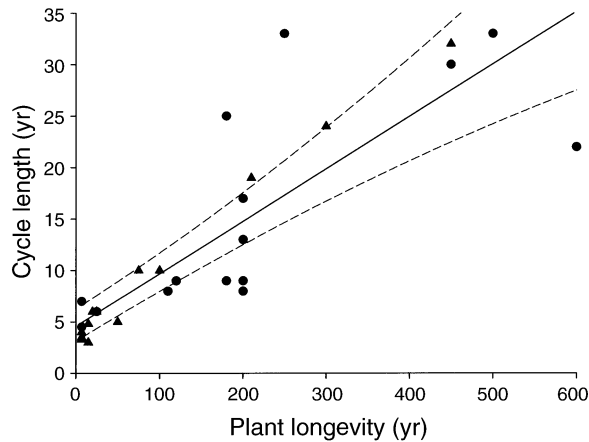


FIG. 1. Cycle length for herbivorous insects (●) and vertebrates (▲) in relation to food-plant longevity. Dashed lines show 95% confidence intervals calculated from 1000 resamples using bootstrapping techniques. The line is described by the equation $y = 0.05(x) + 4.58$ ($F_{1,30} = 77.6$, $n = 32$, $r^2 = 0.72$; $P < 0.001$ for both the F test and the r^2 correlation).

responding figures for vertebrates and insects are 99% and 56%, respectively. The lower value for insects may be due to the varying methods of documenting cycles in this group, adding to the variance in estimates of cycle length. Except for the porcupine, all periods of vertebrates were based on counts of individual animals, but for insects, period lengths were calculated from studies of tree-ring data, counts of individual insects, and the extent of damage on host plants, both on a local and regional scale. Also, some insect species with less clear cycles, e.g., *Orgyia pseudotsugata*, *Bupalus piniaria*, and *Pristiphora erichsonii*, may have become outliers because of difficulties in correctly estimating time periods between population peaks. Finally, most insects in Fig. 1 feed on trees, which often barely survive herbivore attacks (Jardon et al. 1994). Such morbidity, sometimes lasting for decades, paves the way for continuous insect attacks, possibly biasing records towards shorter cycle lengths.

The sample of cyclic animals in Fig. 1 is diverse, encompassing four orders of insects, four birds, and mammals up to the size of moose (*Alces alces*). Clearly, with sheep (*Ovis aries*) and Red Grouse (*Lagopus scoticus*) having short (3–6 yr) cycles and several insects extremely long (>30 yr) cycles, body mass contributes little in explaining cycle length across taxa. In a sample of vertebrates, path analysis shows that although 99% of the variation in cycle length is explained by the combined effects of herbivore body mass and food-plant longevity, only the latter factor contributes significantly and accounts alone for 92% of the variation in periodicity (Fig. 2).

The notion that populations of cyclic herbivores to a large extent are regulated by induced plant defense and consequently that cycle length is determined by plant longevity may help explain some general phe-

nomena associated with population cycles. For example, older trees suffer higher mortality than younger ones during insect outbreaks, a fact compatible with the lower reproductive value of old trees, perhaps leading to a premature demobilization of their defense and increasing their vulnerability to renewed attacks by the herbivore. Generally, we would expect long-lasting outbreaks to induce a stronger and longer defense mobilization compared to shorter attacks. This appears to be the case in the tree-ring study (600 years) by Speer et al. (2001) on pandora moths defoliating ponderosa pine: out of 11 sites nine show a positive ($r = 0.15$, 0.28, 0.33, 0.44, 0.44, 0.50, 0.76, 0.86, and 0.94) and only two a negative ($r = -0.40$ and -0.47) correlation between duration of attack and interval to the next defoliation. Similarly, as pointed out by a reviewer, the severity of an attack should be reflected in a stronger response and a longer defense period. For example, the loss of bark and twigs could be considered more severe for a plant than the loss of annually renewed leaves/needles, and could result in longer cycles than expected. Indeed, Fig. 1 shows this to be the case with all the twig/bark-eating herbivores (the two grouse species, snowshoe hare, moose, white-tailed deer, and porcupine) being above the regression line. Also, the northwards increasing cycle length of microtines in Fennoscandia may be associated with a longer life-span of northern and alpine plants (Harper and White 1974) as compared with southern and lowland species.

Another prediction from this hypothesis is that herbivores feeding on the same plant species should show the same periodicity. This is clearly borne out by the three specialists on heather *Calluna vulgaris* (see Tables 1 and 2), which all have cycle lengths of six years despite differences in taxonomic affiliation (one bird, one beetle, one psyllid), size, and population growth rate. On the other hand, herbivorous insects on Scots pine *Pinus sylvestris* show a less constant period length, varying between 8 and 17 years.

Finally, different herbivore species in the same area may peak asynchronously depending on food-plant species in the diet. For example, Boutin et al. (1995) found snowshoe hares and voles to peak in different years and two lemming species, one eating herbs and willows and the other graminoids, showed asynchronous cycles locally (Pitelka and Batzli 1993). In con-

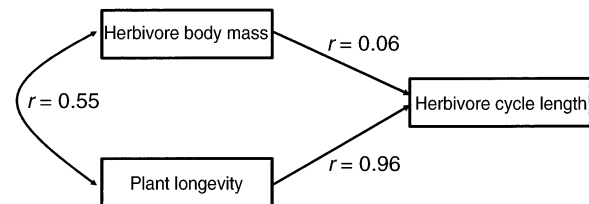


FIG. 2. A path diagram showing the joint effects of herbivore body mass and plant longevity on cycle length of herbivores; r values show the strength of the correlation.

trast, herbivores eating the same food plant should peak in parallel, irrespective of taxonomic relationships. Unfortunately, data are few except for some closely related species such as forest moths (see above), microtines (e.g., Framstad et al. 1993), and grouse (e.g., Lindström et al. 1997).

We conclude that data reviewed here are compatible with predictions from the hypothesis of herbivore-induced plant defense. This does not, however, mean that we exclude other factors as important in shaping cyclic dynamics. Experimental evidence for such effects has been reported for parasitism in red grouse (Hudson et al. 1998), predation in microtines (Korpimäki and Norrdahl 1998, Reid et al. 1995), and a combination of food and predation in snowshoe hares (Krebs et al. 1995). The latter study shows that both food and predation contributed to the cyclic pattern but their relative importance is difficult to evaluate.

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