Population cycles in the Tetraonidae

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This essay briefly reviews our present understanding of population cycles in the Tetraonidae (grouse family). A comparison of several studies of cyclic grouse populations shows different patterns of seasonal mortality. Despite this, we find that all studies of cyclic grouse are consistent with one unifying, and testable, hypothesis: cyclic grouse have the ability to respond to high density by changing their spacing behaviour so as to alter summer dispersal and winter losses in a compensatory manner. Evidence on summer dispersal is scarce as this has been neglected in most studies. Neither the period of the cycle nor the presence or absence of cycling is a necessary attribute of a given grouse species. A comparison of cyclic and non-cyclic populations of grouse and voles, and of cycles in other mammals, suggests that the distribution of the habitat (on a scale large in relation to a bird's home range) and the animals' dispersal are of key importance for cycling. We examine the literature on grouse cycles to see how they fit the main hypotheses put forward for animal population cycles in general. There is now a better mathematical understanding of the effects of time-lags on population processes that affect density, and this makes it unnecessary to postulate mysteriously regular external causes of cycles. Extrinsic changes in weather and food can affect densities in cyclic populations, but are not necessary for grouse cycles, though they may well bring neighbouring out-of-phase populations into phase. Cycles in predation or disease are likewise not necessary for population cycles. The most promising general explanation for cycles is that they are caused by changes in spacing behaviour which occur at high density.

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Introduction

The problem of how animal populations are limited is a central issue in ecology. Some populations change little in density from year to year, others fluctuate irregularly due to obvious external factors such as catastrophes in climate or food supply, and a few show fairly regular cycles.

The regularity of cycles was once regarded as a mysterious phenomenon which might be due to causes different from the causes of less regular or random fluctuations. The realisation that this is not necessarily so has come from a better understanding of time-lags (for a brief review see Krebs 1978). Time-lag effects on density can arise without any external environmental changes, provided that the mechanisms of population limitation operate in response to density, and that there is a delay before the effects of a response actually appear in the census data. Simple deterministic model populations may show stable equilibria, stable cycles, or chaotic fluctuations indistinguishable from random processes, depending on the relation between the time-lags in the density-dependent regulatory mechanisms that cause declines and the population's response or recovery time (Maynard Smith 1968, May 1976). As these examples show that cycles and random-like fluctuations can both stem from the same theoretical model, it is not necessary to postulate any regularly-recurring extrinsic causes of cycles. At the same time, such models do not exclude the possibility that extrinsic events cause population changes in cyclic species. If any time-lag model is assumed, whatever its precise form, the field worker's main task is to determine what the density-dependent regulatory mechanisms are and how they operate.

"Cycles" in animal populations do not have an invariant period. What is usually observed in "cyclic" species is a statistically significant tendency for fluctuations in numbers to be repeated at intervals which are more regular than would be expected by chance.

Apart from the intriguing nature of cycles, study of the subject has contributed useful insights into the principles of animal population dynamics, insights that would be more difficult to get by observing more stable populations. A step towards finding out what limits populations, cyclic or not, is to observe what happens when the system is perturbed. For example, what happens to rates of recruitment and movement when the death rate is altered? One advantage of cyclic populations is that such perturbations are repeated fairly regularly and so can be studied repeatedly. Another is that the changes in numbers are often big, and this has made it easier to measure the factors involved. Hence, even though the species known to cycle form only a small fraction of the animal kingdom, studies of cycles have contributed much to our understanding of population dynamics in general.

But what causes these fairly regular perturbations? In this essay we offer some ideas about the problem, based on studies of grouse (Tetraonidae) that show cyclic fluctuations. We use our own work (Watson & Moss 1972) on Red Grouse *Lagopus lagopus scoticus* as a basis for comparison with other species, some of the more important results on which are summarized in the Appendix. Mackenzie (1952) and Moran (1952, 1954) analysed bag figures from Scotland on Red Grouse, Ptarmigan *Lagopus mutus*, Black Grouse *Lyrurus tetrix* and Capercaillie *Tetrao urogallus* from over a century. Their conclusions were: (1) bags of Red Grouse show an oscillatory tendency with a period usually of 5—6 years, (2) bags of Ptarmigan, Capercaillie and Red Grouse are significantly correlated with one another, as are bags of Black and Red Grouse, (3) bags of the four species tend to be in phase but occasionally drift out of phase and then come sharply back into line, and (4) bags from local populations of Red Grouse within a few km of each other also sometimes drift out of phase for a cycle or two and then come back into phase. We can confirm from further bag data that these conclusions have continued to apply up till now. More recently, Williams (1974) has re-analysed Mackenzie's figures and also the bag figures of Middleton (1934), and confirms a 6-year cycle in the Red Grouse.

Continental North America is even better known for its "10-year cycle"

(Keith 1963, Bulmer 1974) of Ruffed Grouse *Bonasa umbellus,* Snowshoe Hares *Lepus americanus,* Lynx *Lynx canadensis* and other mammals, and data consistent with 10-year cycles have been found more recently in Ptarmigan in Alaska (Weeden & Theberge 1972) and Willow Grouse in Newfoundland (Bergerud 1970). There is some evidence that other grouse species in North America may show cycles (Williams 1954, Lack 1954, Ammann 1957, Keith 1963). We do not emphasise these other species here, either because long runs of population data are lacking or because the main documented changes in populations within areas areas sociated with habitat succession or other habitat changes, as in the Blue Grouse *Dendragapus obscurus* studied by Zwickel & Bendell (1972). Iceland has a 10-year cycle of Ptarmigan (Gudmundsson 1960). In Fenno-Scandia and northern Russia, 3—4 year cycles have been documented for Willow Grouse, Ptarmigan, Hazel Grouse *Tetrastes bonasia,* Capercaillie and Black Grouse (Siivonen 1948, Semenov-Tian-Shansky 1960), and there is some evidence that these tend to be in phase with one another (Siivonen 1948, 1954, Semenov-Tian-Shansky 1960, Moksnes 1972, Myrberget 1974).

In this essay we put more emphasis on intrinsic, as opposed to extrinsic, factors that affect populations, than they have received in the literature on tetraonids. This is deliberate as we think that the role of intrinsic factors has been underestimated and should receive more attention in future.

The problem

We concentrate on changes in density between years within areas, and shall not discuss what regulates mean density within areas or what causes differences in mean density between areas.

Some grouse populations cycle but others do not. This statement is based largely on statistical analysis of shooting bags from autumn populations. In cases where autumn populations cycle, population studies show that spring densities are consistent with the occurrence of cycles, and tend to fluctuate in parallel with autumn densities. Even within one species *(Lagopus lagopus),* cycles of period 3—4, 6 and 10 years have been documented (Appendix) in different populations, and a short study of one population of this species in western Ireland suggests that it does not cycle (Watson & O'Hare in press). The Ruffed Grouse apparently also has cyclic and non-cyclic populations (Appendix). Hence, neither the property of cycling nor the period of the cycle is a necessary attribute of a particular species. If one assumes that the local genotypes in different parts of the range of a species are adapted to their environments, it follows that the physical environment must play some role in determining whether or not a population cycles and also the period of that cycle.

From this starting point, how can a worker tackle the problem? In one lifetime he cannot do many replicated experiments on different cycles, as a physical scientist may be able to do in a few days. Also, so many variables are involved that each cycle is likely to be unique in some respects. He can use past associations of events to predict and then observe future events. Alternatively, he can experimentally change those factors thought to be important, classifying factors into those present in or absent from various cycles, and regarding factors which are always present as potential causes of cycles. These are then changed by experiment. The two approaches are not mutually exclusive, and the difference is mainly one of emphasis. But it can affect greatly how people spend their time, and what kind of results they get.

Whatever one's approach, the logical next step is to recognise that cyclic populations must show cyclic variation in recruitment, mortality, or dispersal, or some combination of them. Losses must exceed gains during the decline phase after a peak in breeding density, and vice versa during an increase after the trough. In cycles where the decline continues for two or more years, this implies that the proximate cause of cyclic changes in numbers shows "delayed density-dependence".

Do population data from cyclic populations show any common pattern?

Most studies provide measures of spring density, clutch size, nest losses due to predation and nest desertion, the proportion of eggs hatching, and the proportion of hatched chicks surviving till late summer. Can we see in these data a pattern common to all cyclic populations? In particular, do the important changes in recruitment, mortality and dispersal occur at some particular season?

The simplest analysis is to separate the annual loss of potential recruits (i.e. "total loss", or K in a K-factor analysis (Varley & Gradwell 1970)) into two periods, production losses and overwinter losses. Production losses cover the period between the time when numbers are last counted in spring just before the hens begin to lay, and the time when the chicks are last counted and are almost fully grown in late summer or early autumn. Overwinter losses cover the rest of the year. Even at this level, there are obviously big differences amongst populations. Some workers (e.g. Bergerud 1970, see our Appendix) have concluded that overwinter losses remain relatively constant between years, and that the observed cycle is due largely to large variations in chick production. Other studies (e.g. Gudmundsson pers. commun., Appendix) show smaller variations in chick production, but large variations in overwinter mortality which is clearly the proximate cause of changes in numbers. Still others (e.g. Weeden & Theberge 1972) show delayed density-dependence in both production losses and overwinter losses, suggesting that both cause changes in spring numbers by varying in parallel.

Therefore, if summer and winter losses are causally independent, we must infer that there is no common cause of grouse population cycles. Alternatively, overwinter losses may be compensatory, i.e. normally high during a decline, but possibly low if heavy summer losses have already occurred. Compensatory overwinter loss is suggested by experiments in which the shooting of birds between autumn and spring does not reduce subsequent breeding densities. This has been done for Red Grouse (Watson & Jenkins 1968), Ptarmigan in Scotland (Watson 1965) and Alaska (Weeden 1972), Willow Grouse in Norway (Myrberget 1972), and Ruffed Grouse (Palmer & Bennett 1963). In such experiments it is useful to distinguish between compensation due to a) changes in dispersal, and b) changes in survival rate within a set of individuals. Point b) has been shown only in Red Grouse

(Jenkins, Watson & Miller 1963: Table 32, Watson & Jenkins 1968).

If we accept that winter losses are compensatory, it follows that factors in winter are the proximate determinants of spring density, even in populations where workers have found winter losses to be more or less constant. A constant winter mortality during a particular study is not necessarily good evidence that overwinter mortality is always constant and therefore non-compensatory. Firstly, the constancy may not have been repeated if the study were continued for a few more years. Secondly, it may be that total overwinter mortality during the study merely happened to be constant because compensatory mortality became adjusted to non-compensatory mortality in such a way as to produce a constant result. Thirdly, although a population may have the potential for compensatory mortality, it may not show it during a particular study; the only sure way to detect the presence or absence of this potential would be to increase non-compensatory mortality in an experiment (e.g. Watson & Jenkins 1968). Hence, even if population changes are highly correlated with previous production losses and are not correlated with overwinter mortality, compensatory mortality may still be determining spring densities. If so, the question becomes: what determines the compensatory part of overwinter mortality?

This is partly understood in Red Grouse. Here, most cocks with territories survive the winter, but virtually all birds without territories die before the spring, due to proximate causes such as predation and accidents. If territory owners are killed in experiments, they are replaced by formerly non-territorial birds (Watson & Jenkins 1968), which would have died if they had not gained territories, but which survive very well after getting them. So, the number of cocks left in spring is limited by the number taking territories in autumn. As Red Grouse are monogamous, female numbers vary largely in parallel with male numbers. In short, the number of territorial birds determines the density to which the spring population will be reduced by compensatory mortality.

This explanation raises two problems. First, not all tetraonids are territorial. For example, the Black Grouse in Scandinavia cycles in numbers, but is a polygamous, lekking species. However, we can extrapolate from Red Grouse to all tetraonids by suggesting that the essential feature determining overwinter losses is competition amongst individuals or groups. Competition need not be for territories, and may be for status, space, or other resources such as food.

Secondly, if competition determines overwinter losses, the intensity of competition in cyclic species must either vary cyclically (in populations where overwinter losses show delayed density-dependence) or would vary cyclically if summer losses were less variable (in populations where overwinter losses are fairly constant). In the latter case, there is the additional problem of why summer losses should vary cyclically. This question of summer losses has received most attention from researchers, and we consider it next.

What causes summer losses? The most obvious causes of variations in clutch size, nest losses and chick survival are bad weather, inadequate food and heavy predation. First, we discuss clutch size. There is little evidence on what causes variations between years in a population's clutch size, although variations in food have been suggested (e.g. Jenkins, Watson & Miller 1963). In different studies, clutch size shows inverse delayed density-dependence, inverse direct density-dependence, or no clear relationship with spring density (Appendix). In all cases, however, differences amongst years in the production of full-grown young are largely due to changes in nest losses and chick losses, not differences in clutch size.

Nest losses are due largely to predation and desertion. Obvious suggestions are that predation is heavy when predators are more numerous or when a predator's alternative prey (e.g. rodents, Myrberget 1972) becomes scarcer. Jenkins, Watson & Miller (1963) found that desertion and predation in nesting Red Grouse both increased in years when the birds' food had been damaged by desiccation and many breeding birds were dying in poor condition. In most studies, nest losses are higher in years of decline than in years of increase.

Several workers have correlated the proportion of young in hunters' bags (i.e. an index of chick production) with the previous summer's weather, but without separating chick production into nest losses and chick losses. In northern Russia, Semenov-Tian-Shansky (1960) noted that chick production in Capercaillie was correlated positively with temperature and inversely with rainfall during June, when hens were incubating. He attributed this to nest losses. Slagsvold (1975) noted a similar correlation between June (incubation period) temperatures and the ratio of young to old Willow Grouse shot in Norway, and Dorney & Kabat (1960) found a correlation between May temperatures (when hen Ruffed Grouse are laying and incubating) and the number of juveniles per adult male in shooting bags. In these cases, no direct evidence on nest losses was given. Such correlations of chick production with temperature in the incubation period are therefore open to two interpretations. Either low temperature increases nest losses directly, or warm temperature hastens the phenological development of plants and insects that are important foods for chicks (Slagsvold 1975).

In all studies, hatchability is high and varies little between years. In one cycle in Red Grouse (Jenkins, Watson & Miller, 1963) it showed delayed density-dependence, but in other studies bore no systematic relation to the phases of the cycle. We shall therefore not consider it further.

In studies where nest losses and chick losses have both been measured, what causes variations in chick losses? Cold, wet weather in the first days after hatching is an obvious idea, which has been suggested for Capercaillie (Marcström 1960) and Willow Grouse (Höglund 1970). However, workers who have studied chick survival and compared it with weather data during the post-hatching period have found no correlation (e.g. Jenkins, Watson & Miller 1963, Bergerud 1970, Myrberget 1972). There is evidence in Red Grouse and Ptarmigan (Jenkins, Watson & Picozzi 1965, Moss, Watson & Parr 1974) that chick mortality is partly pre-determined before the eggs hatch; some chicks are inherently more vigorous and more likely to survive than others. The explanation offered is that the laying hens' food varies, partly due to variations in spring weather (Siivonen 1957, Moss, Watson & Parr 1975): as a result, the eggs vary in quality.

Whatever the proximate mechanism, the proportion of chicks lost is usually higher in years of decline than in years of increase (Appendix). The same applies to production losses (nest losses and chick losses combined). There is much evidence that at least some of this variation in summer losses is environmentally determined, by bad weather or poor food. Hence the fact that summer losses are cyclic might suggest that the physical environment is also cyclic and causes the changes in chick production.

Alternatively, although changes in the environment do occur and can cause some losses of nests and chicks, the main causes of summer losses may be intrinsic factors within the birds themselves. Two such possible causes for cyclic summer losses are cyclic variations in the quality of parental care or in the chicks' inherent vigour. Such cyclic variations might result from changes in the population's quality analogous to those found by Wellington (1960) in Tent Caterpillars *Malacosoma pluviale*. Inferior grouse individuals may proliferate during the increase phase, when recruitment is easy and selection relaxed. This may result in poor breeding performance until the selection imposed during the decline phase leaves only superior individuals in the breeding population. Or, the stress of the decline itself may cause poorer reproduction. Or, it may be adaptive for individuals to put less effort into rearing young during the decline and to put more into surviving the decline.

In short, summer losses in tetraonids can be caused by extrinsic factors such as bad weather, but the emphasis on this in the literature may be because most workers have concentrated on this aspect. The possibility that intrinsic factors cause summer losses has scarcely been considered.

What causes winter losses? In most studies, winter losses are calculated on the assumptions that all hens present in the spring will breed and that almost all are still on the study area in late summer. In recent years we have become more aware of the importance of summer dispersal of Red Grouse, Ptarmigan and Capercaillie in Scotland. Emigration of adult Red Grouse can be substantial shortly before nesting, and when the young are at various stages from day-old to full grown. Also, areas with no grouse in spring can gain adults and chicks in summer, whereas other areas at higher density can lose birds over the same period (Watson & O'Hare in press). Estimates of the late-summer population based on the spring density and the late-summer chick/adult ratio can be wildly incorrect. Before the late-summer count, some of the birds may have left the area or extra birds may have come in from outside. It is therefore essential that a total count of full grown chicks and adults is done on each study area in one day. In addition it is possible that the fraction that moves may have a different chick/adult ratio from the fraction that stays. Estimates of winter loss based on incorrect late-summer figures will also be inaccurate. This comment applies to our less intensively studied areas with Red Grouse, the papers of Watson (1965), Bergerud (1970), Weeden & Theberge (1972), Myrberget (1972), Bump et al. (1947:359), and Dorney & Kabat (1960).

We must therefore treat the term "winter loss" with caution, as it may include some summer emigration or immigration. So, overwinter loss may not be constant in studies where a "constant winter loss" is recorded. Over an area very much larger than the usual study area, this may be numerically unimportant as summer emigration and immigration may cancel out. But the occurrence and incidence of summer dispersal in different years may be a vital clue to important behavioural changes in the population. An ancillary point is that most workers (including ourselves) have usually chosen areas of high grouse density on which to work. Such areas are atypical, and more emigration than immigration is likely. Even more atypical are populations on islands, which have been study areas in at least three major studies. There, summer dispersal is likely to be more difficult than on the nearby mainland.

As data on summer emigration or immigration are lacking in most studies, we can only continue to compare these studies by using a parameter which we shall continue to call ”winter losses” but which may include an unknown proportion of summer emigration or immigration.

So far we have concluded that winter losses can be compensatory and may be caused by intraspecific competition. They either vary cyclically or add to cyclic variations in summer numbers. Hence the degree of competition over winter may well determine spring densities. Why should it vary cyclically? Either competition is varying (1) in response to some cyclic environmental resource such as food, or (2) within the population for reasons not connected with cycles in the environment.

Consider (1) first. There is no published quantitative evidence in grouse that the winter environment does vary cyclically in a manner corresponding with grouse cycles. But in all populations studied, declines in numbers are associated with relatively poor chick production. The suggestion made by Watson & Moss (1972) for Red Grouse is that birds compete more in winters following seasons when environmental variations cause poor breeding.

One may distinguish suggestions (1) and (2) by changing the environment experimentally. This has been done for Red Grouse by fertilizing and burning the Heather *Calluna vulgaris* on which the birds feed (Miller, Watson & Jenkins 1970, Watson & O'Hare 1973, Watson et al. 1977). Red Grouse respond to an improvement in the quality of their environment when the experiment is started during years with low or moderate densities. However, recently we failed to halt a big decline from high density by fertilizing an area (unpublished), and Krebs & DeLong (1965) reported a similar finding in the vole *Microtus californicus*. This supports suggestion (2), but more experiments are required to test this fully.

Predation has been found to be the main proximate cause of winter loss in the only studies where such data are available (in Red Grouse and Ruffed Grouse (Bump et al. 1947, Eng & Gullion 1962, Jenkins, Watson & Miller 1963, Rusch & Keith 1971)). But we can ask whether this high predation is a result of cyclical variation in the environment (which could be changes in the number of predators) or in the grouse themselves. Although some workers have emphasised the numerical importance of winter predation in limiting grouse numbers (e.g. Rusch & Keith 1971 for Ruffed Grouse), the view that predation is a necessary cause of cycles is not supported by experiments (Bump et al. 1947) done to find wether numbers of Ruffed Grouse would be increased by the absence of predators, nor by other observations (see Current General Hypotheses).

To sum up this section, we suggest that the effects of dispersal on population changes should be considered more fully in future studies; and that experiments are needed to distinguish the effects of extrinsic and intrinsic factors on winter losses and to find whether compensatory mortality is operating overwinter.

What causes synchrony of cycles over large areas?

The fact that different populations and species of tetraonids fluctuate partly in phase over large geographical areas clearly implicates some very large-scale aspect of the birds' environment as a synchronising factor. One view is that large-scale cycles in weather or vegetation are a necessary cause of these fluctuations (see Current General Hypotheses). Alternatively, irrespective of extrinsic causes, local populations may fluctuate with similar periods but independently of each other, and be brought into phase by random but widespread events such as particularly good or poor weather (Leslie 1959, Chitty 1969). Other synchronising factors operating on a smaller scale than weather may include dispersal of avian predators from declining prey populations (Keith 1963) and also dispersal of grouse from declining populations.

Comparisons of cyclic and non-cyclic populations

Do cyclic populations show features not shown by non-cyclic ones? If so, can these help us understand why cyclic ones cycle? In many cyclic species or populations, cock and hen breed in their first year, winters are cold and snowy, the area of breeding habitat varies greatly with the extent of thaw, the winter food largely comprises only a few species, and other possible competitors for this food may abound. However, none of these distinguishes cyclic from noncyclic populations.

Dispersal in relation to habitat distribution. As a starting point it is useful to consider voles (*Microtus* spp.), where more work has been done than on grouse. When *Microtus californicus* came on to an island and increased, Lidicker (1973) found a regular annual peak of summer numbers and a two-year, low-amplitude cycle of winter numbers, whereas nearby mainland populations had a 3—4 year cycle. The island had no mammal predators, less space for dispersal, and a drier climate which reduced the food supply; the island voles had a low reproductive rate and slow population growth. He suggested that 3—4 year cycles required mammalian predators, and that shorter, 2-year cycles would occur on the mainland if very good food led to better reproduction and so to faster population growth. Another revealing case is Tamarin's (1978) study. Mainland populations of *Microtus pennsylvanicus* cycle, whereas an island population of the closely related, more slowly-reproducing *M. breweri* (only doubtfully a separate species) does not. Tamarin attributed the lack of a cycle to the island not being enough of a "dispersal sink", because of ineffective predation due to having no mammal predators. Although Pearson (1966) suggested that *Microtus* does not show cycles without predators, inability to disperse is an equally good possibility. When Krebs, Keller & Tamarin (1969) fenced an area to stop dispersal, voles built up extremely high densities, overgrazed the vegetation, and declined due to starvation even though predators were present. This suggests that space to disperse, not predation, may be necessary for vole cycles. However, predation and dispersal may merely be two proximate aspects of the same ultimate process (i.e. mechanisms by which animals which fail to remain on their natal area are lost from the population). Fundamentally, the difference between island and mainland populations of voles is a part of the more general question that the structure and heterogeneity of the environment may be an important determinant of the amplitude and temporal pattern of population changes (e.g. den Boer 1971, Birch 1971, May 1976).

How does the observation that some island populations of voles do not cycle fit the tetraonids? Consider the White-tailed Ptarmigan *Lagopus leucurus,* which appears to be non-cyclic and on most study areas fairly stable in numbers to judge from the short studies so far done (Choate 1963, Braun & Rogers 1971) in Montana and Colorado. In North America it occupies high mountain tops rather like islands. Similarly, at the southern edge of its boreal-forest range, the Ruffed Grouse occurs in small, isolated patches left after forest clearance for agriculture. Leopold (1931) noted a lack of big fluctuations in numbers on the remaining pieces of such habitat in the mid-western United States, and suggested that Ruffed Grouse there may have cycled originally when the habitat occurred in big continuous tracts. More recently, Graham & Hunt (1958) gave some evidence from one isolated patch that birds there did not show big fluctuations, let alone cycles, and Ammann (1972) has also made the same point. Again this resembles an island-like situation. Perhaps dispersal plays a similar role in both grouse and voles.

Evolution of cycles. Another useful approach to understanding complex biological phenomena is to ask how they evolved. We shall start by assuming that a selective advantage accrues both to animals that cycle and to other animals that do not cycle. What selective advantage might cycling offer? One general idea is that rapid changes in numbers can be advantageous. Declines to very low numbers allow rapid selection to occur, and Elton (1930) thought that this might play an important role in the evolution of voles and other mammals that show periodic cyclic declines. Another possibility is that cyclic populations have evolved in relation to predator populations, so that the numbers of predators will be reduced periodically due to declines in the prey population, which then outstrip the predators during the increase phase by breeding faster. However, such ideas imply group selection, which is currently unfashionable. We now propose an explanation in terms of current ideas on evolutionary strategies involving individual and kin selection. Obviously such evolutionary explanations cannot tell us what the mechanisms of population regulation are, but they can be useful in suggesting possible lines of research on such mechanisms.

The basic assumption is that an individual attempts to increase its contribution to a species' gene pool (i.e. its genetic "fitness"). It can do this by producing each year many surviving offspring, by living long, and by reducing its competitors' fitness. It is of no benefit to produce young which are not recruited. Young with little chance of being recruited into their natal population may have a better chance of breeding if they disperse. Hence dispersal becomes more probable when competition for space or other resources on the natal area increases, and when there is other habitat available into which an animal can disperse with a better chance of survival and recruitment than if it stayed at home. But we suggest that populations need not cycle when dispersal is continuously high, as severe competition for space is thereby avoided. Such a situation is likely to occur when new habitat is continually becoming available. We would expect much dispersal in Blue Grouse, for example, where large blocks of new habitat are continually being created by fire and the birds do not cycle.

Obviously, such a high-dispersal mechanism is not the same as in Tamarin's (1978) suggestion that populations do not cycle when dispersal is very low, as on islands with voles and possibly on island-like patches of habitat with White-tailed Ptarmigan and some isolated populations of Ruffed Grouse. However, any association between low dispersal and population stability has presumably arisen for a set of evolutionary reasons different from an association between high dispersal and stability. Firstly, if an individual's young do not disperse from an "island", it will be disadvantageous for that individual to become more aggressive and cause a decline in numbers, as it would then be competing with its own offspring. Secondly, if dispersal is low (because it is disadvantageous to disperse out of the island of suitable habitat), then an individual will have more competitors, and may reduce rather than increase its own fitness by attempting to oust them and then failing. Thirdly, if the occupied patches are very small and isolated, such local populations are more likely to become extinct. Behaviour that causes big fluctuations in density would be selected against, because extinctions would be even more likely at troughs in density.

If we can have stable populations with high or low dispersal, where do cyclic populations fit? Such populations may occur where the habitat makes the individual's decision to disperse or not dependent on population density and on the degree of social interaction. At locally high densities, the probability of recruitment is low and so dispersal becomes relatively more advantageous than staying. We also suggest (based on observations of Red Grouse) that it may benefit the most dominant individuals to reduce their non-kin neighbours' fitness by starting to take as much ground as possible at high density and thus excluding their neighbours. If they, or those of their offspring which do not disperse, can survive till the trough, they will then produce young with a high chance of being recruited during the increase phase. The longer the individual or kin can keep up the severe competition, even in years after density has already dropped greatly, the more benefit they should gain when the cycle turns to the increase phase, as even fewer competitors will then be left.

Predictions from these comparisons. In studies of several grouse species, some big differences in numbers between years are related to plant succession after fire. This occurs for apparently non-cyclic populations, as in the Blue Grouse studied by Zwickel & Bendell (1972), and in cyclic populations of Ruffed Grouse (Gullion 1970a). Hence cyclic fluctuations (if any) may be superimposed on changes in density caused by habitat changes. However, if our foregoing deductions are correct, some habitat changes may be sufficient not only to change mean densities, but also to cause populations to switch from cyclic to non-cyclic modes.

An example may be the Ruffed Grouse. Another is the Red Grouse. In Co. Mayo in western Ireland, densities are much lower than formerly, associated with overgrazing, habitat deterioration, and heavy predation. The evidence from a short study of one such population is that it does not cycle; winter losses are directly related to density, as in Blue Grouse, and so are summer losses (Watson & O'Hare in press). Areas vacant of grouse in spring are common, and over the summer such areas tend to gain birds, whereas areas at higher density in spring tend to lose birds. This suggests movement from areas of higher density. If the density in such birds were to increase so that vacant areas became uncommon or absent, we think that the population would show cycles. During 1876—1939, when Red Grouse were much more numerous than now, bags from Co. Roscommon in western Ireland showed a cycle similar to that in Britain (figures from Lord de Freyne).

We suggest these speculations for the sake of giving a more complete framework for thinking about cycles. Although ideas about genetic fitness are not directly testable, their value is that they suggest predictions which can be tested by experiment.

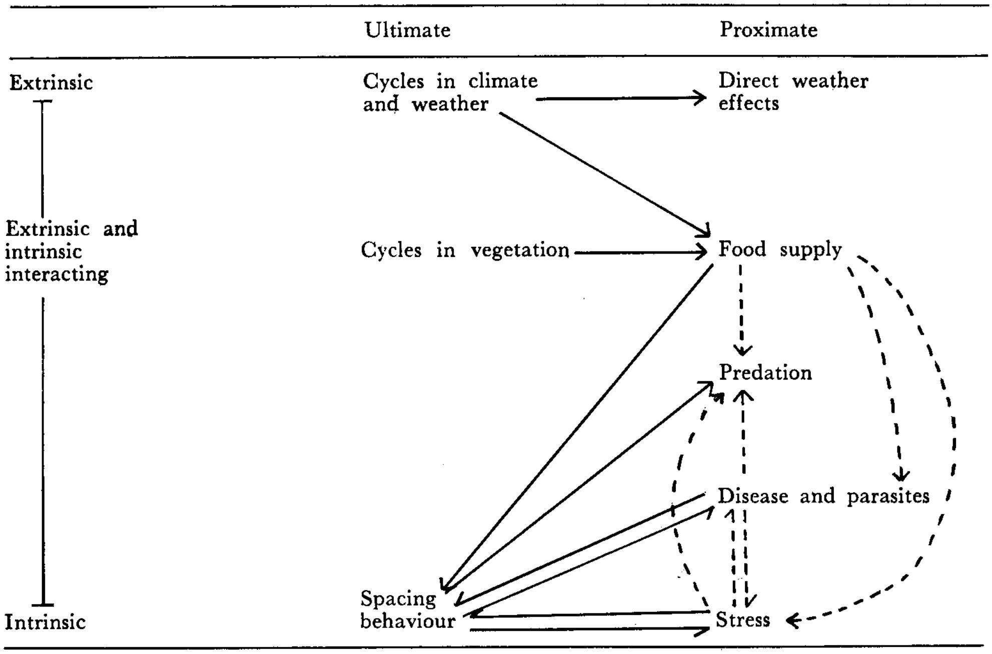
Current general hypotheses

Fig. 1 classifies the processes which have been suggested as causes of cycles.

All the processes in the second and third columns of Fig. 1 play some role in determining grouse numbers. Some obvious examples are: Capercaillie eggs freezing in cold weather (Semenov-Tian-Shansky 1960), Ruffed Grouse dying after their food has been iced over by freezing rain (McGowan 1969), Gyr Falcons *Falco rusticolus* eating Ptarmigan (Gudmundsson 1970), louping-ill virus *Flavivirus* group) carried by Sheep Ticks *Ixodes ricinus* and killing Red Grouse (Duncan et al. 1978), Red Grouse which have failed to get territories dying in good condition and without any obvious proximate cause except social stress (Jenkins, Watson & Miller 1963, Watson 1970), and Capercaillie cocks killing each other at their display grounds (Boback 1952). As all the processes in Fig. 1 are likely to be operating on some populations at some time, this might be regarded essentially as the "holistic, synthetic and multifactorial" systems "model" of Lidicker (1978) to explain population dynamics of voles. Although this attitude rightly provides a useful philosophical caution against simplistic generalizations, it is of little value for generating the specific hypotheses that are necessary for the field worker to test, and the amassing of more field observations without experiments is unlikely to be a satisfactory approach. In this section we discuss some specific, testable hypotheses which have been put forward to explain cycles, in order to see which ones fit the tetraonids.

Three points are important before doing this. First, a cycle may result from an extrinsic or intrinsic cyclic cause acting in a directly density-dependent way, or from an extrinsic or intrinsic cause acting in a delayed density-dependent way, and the cycle's pattern may depend on an interaction between extrinsic and intrinsic processes. Second, proximate causes should be distinguished from ultimate causes (Watson & Moss 1970). For example, if an animal starves because others

FIG. 1. Classification of processes which have been suggested to cause cycles in the abundance of animals.



Note. This is a classification of mechanisms and not of postulated adaptive reasons for the present situation having evolved. All proximate causes (except direct effects of weather) must have delayed density-dependent characteristics. Arrows point from cause to effect. We do not use arrows to connect ultimate causes, but this does not exclude interactions between them. A two-way arrow shows a possible two-way interaction. According to this scheme, spacing behaviour may therefore be ultimate or proximate in different circumstances. Causes are not necessarily exclusive: for example, a deterioration in food supply may increase the animal's susceptibility to disease or predation. Food supply can operate by a) catastrophic changes in climate and weather causing starvation, or b) overgrazing by the animals themselves, in which an inadequate quantity of food may cause starvation, or may be followed by a delayed recovery of the plants, or c) grazing at high density reduces food quality and the animals may respond by changing their spacing behaviour before direct starvation occurs.

exclude it from abundant food, starvation is the proximate and spacing behaviour the ultimate factor. Third, each population may cycle for different causes, or there may be some generalizations which we can make about all cycles in tetraonid numbers. We have already suggested some generalizations and shall continue to assume that all tetraonid cycles have something in common.

Intrinsic cycles in vegetation (Lauckhart 1957, Kimmins 1971) *and cycles in weather* (Lamb 1975) occur but have not been shown to correlate with tetraonid cycles. Moreover, the fluctuations of hares, or of individual species of grouse, or of other cycling species, are often not in phase with those of the same species in other countries or regions, and may have different periods (Mackenzie 1952, Keith 1963, Bergerud 1970). Although these points require further statistical study, the suggestions of Lauckhart and Kimmins seem to require the existence of a variety of vegetation and weather cycles in addition to those found hitherto by botanists and meteorologists.

Food shortage may result from fluctuations in food production or availability due to changes in weather. It may cause animals to starve to death,or may have more subtle effects on the population via reproduction and spacing behaviour. Severe damage to the food supply by desiccation can result in emaciation and death of breeding Red Grouse (Jenkins, Watson & Miller 1963), but this is unusual and not characteristic of most cyclic declines of Red Grouse. Watson & Moss (1972) summarized the evidence on Red Grouse that a qualitative deterioration in food supplies or nutrition due to weather (but without weather-induced damage to the plant) can be followed by maternally-induced poor breeding and increased aggression of young birds, in turn leading to population decline.

Even if food is unaffected by weather, animals might increase to such densities that they overgraze and deplete their food, as suggested for Brown Lemmings *Lemmus trimucronatus* by Thompson (1955). However, tetraonids remove only a small proportion of the food available (e.g. about 2 % in Red Grouse (Savory 1978)), if we define food as the total quantity of needles, catkins, buds or shoots that the tetraonids eat. An extension of the concept of overgrazing involves ideas of the sort put forward by Schultz (1964) and Haukioja & Hakala (1975). These invoke a deterioration in the plant's nutritive quality due to heavy grazing, either by a reduction in nutrient content or an increase in chemicals that make the plant more unpalatable or indigestible. Such heavy grazing by lemmings and voles might reduce numbers of Willow Grouse and Ptarmigan in Scandinavia, where these rodents do eat the heaths and shrubs that are preferred foods of the *Lagopus* species.

The question whether grazing by tetraonids themselves can deplete their food supplies sufficiently for their own numbers to be affected is not clear, however. The key point here is that tetraonids are very selective feeders. For example, Capercaillie and Ruffed Grouse have certain preferred feeding trees which become obviously grazed (Seiskari 1962, Gullion 1970b), even though many trees nearby remain virtually untouched. Similarly, relatively heavy grazing at preferred sites has been noted in Ptarmigan (Gardarsson & Moss 1970) and White-tailed Ptarmigan (Moss 1972). If it is postulated that only these sites provide food of adequate quality for survival, then overgrazing of this small number of preferred sites could be important. The insulation qualities of the snow for roosting (Gullion 1970a) at such sites may also be important, because the birds' energy balance depends on an interaction between input of food and losses of heat. Similarly the birds' choice of such sites may be influenced by the topography or structure of the site or tree, because of their other needs such as shelter and avoidance of predators. Hence, at high densities such sites may be overgrazed, and birds may starve there, or competition for these sites may drive subordinate individuals to areas that are inferior for food or snow, where they also may in turn starve or become more vulnerable to other proximate factors such as predation (Gullion 1970a). Theoretically, heavy grazing at such sites might affect the plant so that food quality is reduced for a year or two, thus adding to the delayed density-dependent effect on the animal population, but there is no evidence for this. In general, however, high densities of tetraonids at such sites may lead to a reduction in their plane of nutrition or energy balance. Even although this may not be enough to cause starvation or poor breeding, it may provide a trigger for the onset of physiological or behavioural processes which themselves cause the decline (see below).

Predation may cause cycles in Ruffed Grouse as a secondary effect of cycles in Snowshoe Hares (Grange 1949, Lack 1954). Keith et al. (1977) suggested that, as hares increase, so do their predators. At high densities the hares overgraze their food and so decline in numbers, the ratio of predators to hares increases, and predation then lengthens the duration of the decline and deepens the trough (Keith 1974, Keith et al. 1977). As hares decline, the predators switch to eat more grouse and so the grouse decrease. When hares and grouse become scarce, the predators also decline. Rusch & Keith (1971) studied Ruffed Grouse in Alberta for two years. Spring numbers were said to increase over three springs, due to an increase in juvenile survival over the second winter. They attributed this increase to Great Horned Owls *Bubo virginianus* switching from grouse to hares. However, their data show that the Lynx was a more important predator than the Great Horned Owl, and Lynx predation actually increased in the second winter by more than enough to compensate for the reduced owl predation. The estimated number of grouse killed overwinter by all predators was almost the same in both winters, and indeed the estimated proportion that was killed increased in the second winter. In our view, the data therefore go against the authors' conclusion. Later, Keith et al. (1977) showed that the May-July predation rate on adult Ruffed Grouse by avian predators varied in a delayed density-dependent way with April density of hares (i.e. further evidence of the switch in predation). But it showed no relationship with grouse density, and so is unlikely to be the cause of cycles in breeding stocks of grouse. In any case, winter loss, not summer loss of adults, is the proximate process determining spring density of Ruffed Grouse, but Keith et al. give no further data on winter loss.

Myrberget (1972) wrote that Stoats *Mustela erminea* switching their predation from lemmings and voles to grouse not only caused the cycle of Willow Grouse in Norway, but determined its short duration (3—4 years, like that of the small rodents). However, even if a switch in predation from mammal prey is shown to be sufficient to account for some grouse cycles, it is not necessary. Myrberget (1970, 1972) gave examples of declining Willow Grouse populations where egg predation was low because Stoats happened to be absent. In Iceland, Ptarmigan show clear, regular cycles (Gudmundsson 1960), although no small rodents abound in the Ptarmigan habitat. Also, Gudmundsson (1970) wrote that, despite heavy predation in summer on his study area by Gyr Falcons, the cycles could not be attributed to predator-prey oscillations.

Even if the number of birds killed by predators is the same as that lost from the population, it does not necessarily follow that predation causes the decline in numbers. Errington (1943, 1945) gave anecdotal evidence that Muskrats *Ondatra zibethica* and Bob-white Quail *Colinus virginianus* of low social status may form a doomed surplus which would die anyway, whether killed by predators or not. This, rather than which proximate mortality factors happen to be present or absent at the time and so remove the surplus, may be the important process.

Parasites or other disease may reduce populations in a way like predators, that is, occurring more frequently at high density but with a lag of a year or two. The incidence of a nematode parasite was associated with density in Ruffed Grouse (Dorney & Kabat 1960), with a one-year lag in the later part of a grouse decline. However, although a high incidence of parasites, along with emaciation and death of many breeding grouse, occurred during one decline of Red Grouse (Jenkins, Watson & Miller 1963), other declines are not accompanied by these features. One may also ask whether stress resulting from social behaviour pre-disposes certain social classes to suffer more from such parasites, rather than the parasites simply increasing in relation to host density.

Stress caused by spacing behaviour at high densities was proposed by Christian (1975) as a mechanism which upsets endocrine functions in mammals at high density, causing consequent reproductive failure and population decline. Although there is good evidence of this with mammals at artificially high density in the laboratory, the demonstration of it in field populations is absent or unconvincing. Höhn (1967) suggested that endocrine failure explained the flocks of supposedly non-breeding Willow Grouse that he saw in summer. But his observations were anecdotal, and there is a simpler explanation. This is that they consisted of unmated cocks and failed breeders, which are known to be common enough in several detailed studies of this species.

Changes in spacing behaviour at high densities are the basis of Chitty's (1967) genetic hypothesis. He suggested that genetically more aggressive animals are at an advantage in crowded populations and are selected for at high densities. Such aggressive animals cause great mutual interference, and so a decline occurs and the declining population comes to contain a high proportion of aggressive animals. A low density ensues. There is then no longer any advantage in being aggressive, and so the population increases again.

A recent big decline of Red Grouse continued despite our increasing the food's nutritive value by applying fertilizer (unpublished). Hence, although a deterioration in food supplies is sufficient to cause some declines (Watson & Moss 1972), it is not necessary. At high density, a higher proportion of birds emigrated, the spring sex ratio favoured males, and competition for territory increased. These features became more marked during the decline. Whether such grouse are responding to high density, or to shortage of space or mates, or to less food per bird, can be decided only by future experiments. In relation to Chitty's hypothesis, one may ask whether genotypic changes follow population changes (i.e. effect) rather than precede them (i.e. cause). Henderson's (1977) study in Red Grouse indicated the former. In any case, the important point is that the observed changes in spacing behaviour caused the decline. Genetic or physiological correlates are unimportant for population limitation unless they cause the relevant changes in spacing behaviour and are not merely associated with them.

Conclusion

We suggest the following testable hypothesis as a general explanation for cycles in tetraonids: a) spacing behaviour is different in the decline phase from the increase phase, b) changes in spacing behaviour which start at high density and continue after it cause increases in overwinter mortality and summer dispersal, and c) if other factors such as predation or food shortage cause large losses of eggs and chicks before the winter, the above mechanism may not come into operation.

The evidence indicates that extrinsic mortality factors are no more than sufficient to cause declines. Nevertheless this is still uncertain, as so few experiments have been done. Hypotheses that are rejected offer more reliable understanding than those that are confirmed. It would therefore seem wise for more work to be done in attempts to alter food supplies or remove predators, so that the basis for rejecting or accepting the generality of such factors is improved.

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Selostus: **Metsäkanojen jaksottainen kannanvaihtelu**

Watson tutkimusryhmineen on maailmankuulu Skotlannin nummiriekkoa koskevista tutkimuksistaan. Tässä kirjoituksessa tekijät luovat katsauksen nykyiseen tietämykseen metsäkanojen jaksottaisesta kannanvaihtelusta ja sen syistä sekä esittävät oman selityshypoteesinsa. Jaksottaisella kannanvaihtelulla tarkoitetaan sitä, että korkeat ja alhaiset tiheydet toistuvat säännöllisemmin kuin sattumanvaraisessa kannanvaihtelussa. Esim. riekon tiheyden on todettu vaihtelevan sen levinneisyysalueen eri osissa 3—4, 6 ja 10 vuoden jaksoissa sekä myös jatksottomasti.Ongelmana on selittää, mistä jaksottainen vaihtelu tietyllä alueella johtuu.

Aluksi tarkastellaan, onko jaksottaisilla populaatioilla yhteisiä ominaisuuksia, ja kiinnitetään erityistä huomiota siihen, tapahtuuko jälkeläisten kuolevuus, aikuisten kuolevuus ja siirtyminen muualle (dispersal) juuri tiettynä vuodenaikana. Suurta vaihtelua esiintyy, mutta talvikuolevuus näyttää olevan vain edeltänyttä kesäkuolevuutta tasaava; jos kesäkuolevuus on ollut alhainen, talvikuolevuus on suuri, ja päinvastoin. Esim. nummiriekon syksyllä reviireihin asettuneet koiraat säilyvät hengissä, mutta reviirittömät kuolevat talvella olipa niitä paljon tai vähän. Kaikki tetraonidit eivät ole territoriaalisia. Myös muu ryhmänsisäinen kilpailu kuin reviirikäyttäytyminen voi talvella rajoittaa tiheyttä. Jos kilpailu määrää talvikuolevuuden, kannanvaihtelun jaksottaisuus voi johtua kilpailun jaksottaisuudesta tai (jos talvikuolevuus on tasainen) kesäkuolevuuden jaksottaisuudesta.

Kesänjälkeinen kannan vaihtelu voi johtua mm. munamäärästä, pesätuhoista, poikasten kuolevuudesta huonolla säällä, riittämättömästä ravinnosta ja saalistuksesta. Ulkaiset syyt voivat aikaansaada kannanvaihtelua, mutta kirjoittajien mielestä ulkoisia syitä on korostettu yksipuolisesti, koska useimmat tutkijat ovat keskittyneet vain niihin. Myös populaationsisäiset syyt tulisi ottaa huomioon.

Havaitut talvikuolevuudet voivat olla virheellisiä siksi, että syksyiset vertailukannat arvioidaan usein edeltävän kevään tiheyden ja loppukesän emo-poikaslukusuhteen perusteella. Oletetaan kaikkien kevätlintujen pesivän ja pesineiden sekä poikasten pysyvän paikallaan, vaikka osa voi jäädä pesimättä ja osa siirtyä kesällä alueelta toiselle. Siirtymisiin alueelta toiselle on tulevaisuudessa kiinnitettävä enemmän huomiota.

Jaksottaisten kannanvaihtelujen syitä on selitetty monilla tavoilla. Kolme tärkeätä

Appendix. Classification of parameters associated with population changes in three cyclic species of Tetraonidae.

Species	Study	Reduction in clutch size below its maximum value[b]	Nest loss or egg loss	Chick loss	Combined "production" loss[c]	Winter loss[c]			Typical period of cycle (years)[de]
						Total	Adult	Juvenile	
Lagopus lagopus	Jenkins, Watson & Miller	+	+	+	+	+			6[f]
	Bergerud	g	probably +	probably +	+	h			10
	Myrberget	+x[i]	+x[i]	+	+[j]	+	+	+	3—4
	Watson & O'Hare				x	x			apparently no cycle
Lagopus mutus	Watson	+		probably +	+	+			6[fk]
	Weeden & Theberge	+	+	—	+	+	+	+	10
	Gudmundsson (1971, 1972), and pers. commun.*	x[l]		+x[m]				+	10
Bonasa umbellus	Bump *et al.**		+[n]	+[o]	+[p]	+[q]			10[r]
	Dorney & Kabat*			+[s]					10[r]
	Allison*				+[t]				10[r]
	Gullion*				u	+[v]	+[v]	+[v]	10[r]
	Graham & Hunt, Ammann (1972)								no cycle

Note. A blank space means no published data.
+ Higher in declines than in increases, though the difference is not necessarily statistically significant (see *)
— Not higher in declines than in increases
x Directly density-dependent
* The statistical analyses were done by us in these cases, as the data are not easily accessible to readers; with the other studies, readers can work out their own analyses if necessary
a Black grouse and capercaillie are mentioned in the text but we omit them from this table because detailed population data comparable with the other species are lacking. A separate point is that, although there is evidence that black grouse and capercaillie fluctuate in parallel with willow grouse and red grouse, the suggestion that they cycle has not been formally demonstrated
b For ease of comparison we use a "loss" here instead of mean clutch size, as all the other columns involve losses
c Assuming no summer movement
d Suggestions of cycle periods longer than those given here have been made for southern Fenno-scandia (Siivonen 1948). However, neither these suggestions nor the 3—4 year cycles in Fenno-scandia have been analysed statistically
e The quoted cycle periods are based on bag figures from the countries concerned, and therefore presumably reflect autumn densities, whereas the population studies include data on the density of the breeding stock in spring or summer, and tend to emphasise breeding density. As the population studies have been done over a much shorter number of years than the long runs of bag figures, each study can be no more than consistent with the quoted cycle period typical for that country and cannot demonstrate it
f Based on Mackenzie's (1952) long runs of bag figures for red grouse and ptarmigan, and on Williams' (1974) statistical analysis of the red grouse bags in Middleton (1934) and Mackenzie (1952). Out of 14 series that she analysed from various regions of Scotland, England, Wales and Ireland, six showed strong evidence of a 6-year cycle. The other eight were doubtful, possibly because Mackenzie had lumped the figures from different moors, a practice likely to smooth out peaks and troughs. Even so, only two series showed no evidence of cycling. The remaining six fluctuated non-randomly, with inconclusive evidence for different periods of 4, 5 and 10 years
g Clutch size possibly lower in the decline than in the increase, but data insufficient
h "Relatively constant", but few data; also, November-May loss varied from 57—77 % over four years of decline
i Due largely to one year
j Loss said to be fairly constant, but in fact slightly higher in declines than in increases
k In this case the data from the population study are consistent with a 10-year cycle rather than the 6-year one suggested by Mackenzie's (1952) bag figures
l Clutch size was correlated with spring density ($r_6 = -0.82$, two-tailed $P<0.02$)
m A suggestion of inverse density-dependence is due to only one point, in the peak year. Both years of major decline had chick losses higher than usual, one (in the peak year) with very bad weather in the chick period, but the other (after the first spring of much lower numbers) without bad weather
n Higher at Connecticut Hill in declines than in increases (Mann-Whitney $U=0$, $N=4$ & 8, two-tailed $P=0.004$)
o Said to be low, but varied from 51—81 % between years, and higher in declines than in increases (ns)
p Higher in declines than in increases $U=2$, $N=4$ & 8, two-tailed $P=0.016$)
q Variations in juvenile autumn numbers closely paralleled variations in total losses from that autumn to the next, whereas adult numbers in autumn did not; hence, juvenile loss contributed largely to changes in numbers between years
r The 10-year cycle in North American mammals has been statistically analysed (Bulmer 1974), but the data on ruffed grouse have gaps and are therefore not good enough for statistical analysis. Nevertheless, there is quite strong evidence of a 10-year cycle in ruffed grouse (Lack 1954; Keith 1963)
s Higher in declines than in increases, but data or statistical analyses were not given
t Number of young reared per hen was smaller in declines than in increases $U=1$, $N=$ 10 & 4, two-tailed $P<0.02$)
u Breeding success was poorer in some years (in some declines), said to be due to variations

in the proportion of hens that fail to lay and/or a high proportion of nest losses, and/or chicks having poor stamina, but data on these aspects were not published

v Said to be roughly constant each winter, but in fact overwinter survival of adult males was poorer in declines than in increases ($U=0$, $N=5$ & 2, 2-tailed $P=0.094$). The worst overwinter survival of juvenile males and of adult males was in the main year of decline, and the best in the first year of increase. Survival after three years of age was worst for the male cohorts from the peak and first year of decline, good for the cohort from the second year of decline (which by three years on would be into the first year of the next increase), and good for the cohort from the last year of increase before the peak.

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seikkaa on huomattava. Ensinnäkin, jaksottaisuus voi johtua ulkoisesta tai sisäisestä syystä, joka vaikuttaa joko suoraan kannan tiheydestä riippuen tai aikaviiveen jälkeen vasta myöhemmin edeltäneestä tiheydestä riippuen. Toiseksi tulee erottaa lähimmät, viime käden (proksimaattiset) syyt ja perimmäiset (ultimaattiset) syyt. Jos eläin kuolee nälkään siksi että toiset eivät anna sen syödä, nälkiintyminen on proksimaattinen ja lajinsisäinen kilpailu ultimaattinen syy. Jaksottaisten kannanvaihtelujen syiksi mainitaan kirjallisuudessa mm. kasvillisuuden ja sään jaksottaisuus, kasvien ja niitä syövien herbivorien vuorovaikutus, saalistus, loiset ja taudit, kilpailusta johtuva stressi ja hajaantumiskäyttäytymisen (spacing behaviour) muuttuminen suurissa tiheyksissä.

Tekijöiden mukaan lupaavin yleinen selitys jaksottaisuudelle on hajaantumiskäyttäytymisen muuttuminen. Se on erilaista tiheyden lasku- ja nousuvaiheissa. Korkean tiheyden aikana alkava ja sen jälkeen jatkuva hajaantuminen lisää talvikuolevuutta ja kesäaikaista siirtymistä muualle. Jos muut syyt, kuten saalistus tai ravintopula, karsivat suuresti munia tai poikasia ennen talvea, hajaantumiskäyttäytymisen merkitys on vähäisempi. Ulkoisten syiden osuus jaksottaisuuden syntymisessä ei ole täysin selvillä. Tarvitaan erityisesti ravinnon ja saalistajien määrän muuttamista kokeellisesti, jotta niiden yleinen merkitys paljastuisi.

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