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Review

Tetraonid population studies – state of the art

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This review aims to compile the current knowledge of tetraonid population dynamics. As most of the grouse species in the world are game, long-term data often originate from hunting statistics. Many of these data sets show decreasing trend in population numbers. Environmental changes due to forestry and other human activities are the most obvious causes in this process. Some tetraonid species have populations which display both non-cyclic and cyclic dynamics of various length. Hence, cyclicity is not a species-specific property. However, most of the detailed population studies have been conducted in cyclic populations. No single factor has been found to explain the fluctuations. The possible effects of hunting on the dynamics are also explored. This is done by using logistic population growth model as a starting point and implementing various hunting strategies into it. The results show that, in most cases, the hunting pressure has to be high to change the original dynamical behavior of the population. It is concluded that better understanding of population fluctuations of tetraonids requires data of age-class specific mortality and fecundity, as well as of the direct and indirect effects of hunting.

1. Introduction

There are 17 grouse species in the world (Johnsgard 1983, for the genus *Tympanuchus,* see, however, the A.O.U. check-list 1982, Table 1). Taxonomically they belong to the subfamily Tetraoninae of the family Phasianidae (e.g., Hudson et al. 1966). According to the present view they are divided into six genera, *Centrocercus*, *Dendragapus*, *Lagopus*, *Tetrao*, *Bonasa* and *Tympanuchus*. All the species share several ecological properties. As a group the grouse can be characterized as chicken-like ground-dwelling birds, which inhabit mainly different forests of the Northern Hemisphere. Eight of the species belong to the North American fauna, seven have Palearctic distribution and two species are found over the whole Holarctic region (Table 1). The grouse feed on various seeds, leaves and berries, and the chicks eat insects.

From the population biological point of view tetraonids offer an unusual opportunity for studies of population dynamics. As gamebirds they have been managed long to secure sustainable yield. Hunting has also produced bag statistics for some of the longest time-series known in animal ecology. Third, their basic biology is well known (Rands et al. 1988). All this together makes many of the standard time-series analysis techniques feasible — and more importantly, this together with the knowledge of the grouse biology can produce valuable insight to the regulation of natural populations.

The aim of this review is to compile the knowledge of tetraonid population dynamics, and especially that of the common Finnish species, Capercaillie (*Tetrao urogallus*), Black Grouse (*T. tetrix*), Hazel Grouse (*Bonasa bonasia*) and Willow Grouse (*Lagopus lagopus*). Since the distribution of Rock Ptarmigan (*L. mutus*) in Finland is restricted to the most arctic areas of the northern part of country, the data are scarce, and will not be discussed among the other Finnish species.

Table 1. List of all the grouse species (in the genus Tympanuchus I have followed the practice of A.O.U. checklist 1982), body weight of both sexes (male above) and a short description of their main breeding areas (Johnsgard 1983 and references therein).

Species	Body weight (kg)	Distribution	Habitat
Sage Grouse	2.3 – 3.2	NW USA	Sagebrush
Centrocercus urophasianus	1.4 – 1.7		
Blue Grouse	1.2 – 1.3	Western North America from southern	Douglas fir forests
Dendragapus obscurus	0.8 – 0.9	Alaska to northern California	
Spruce Grouse	0.5 – 0.7	Northern parts of North America	Coniferous forests
Dendragapus canadensis	0.5 – 0.6	south of tree line	
Sharp-winged Grouse	0.6	The coast of southern Gulf of	Taiga forests
Dendragapus falcipennis	0.6	Okhotsk and Southern Yakutia	
Willow Grouse	0.5 – 0.7	Circumpolar tundra species	Tundra and
Lagopus lagopus	0.5 – 0.7		alpine forests
Rock Ptarmigan	0.5 – 0.7	Circumpolar tundra species	Treeless tundra
Lagopus mutus	0.4 – 0.7		
White-tailed Ptarmigan	0.3	Western coast of Alaska and	Alpine tundra
Lagopus leucurus	0.3	British Columbia	
Capercaillie	3.9 – 2.0	Northern Europe and Siberia	Coniferous forests
Tetrao urogallus	1.8 – 4.3		
Black-billed Capercaillie	3.1	Eastern Siberia	Taiga forests
Tetrao parvirostris	2.1		
Black Grouse	1.1 – 1.0	Northern Europe and Siberia	Various forests
Tetrao tetrix	0.9 – 1.3		and heathlands
Caucasian Black Grouse	0.9	Alpine zones of Caucasus	Timberline areas
Tetrao mlokosiewicki	0.8		and subalpine meadows
Ruffed Grouse	0.6 – 0.6	Northern parts of North	Aspen thickets,
Bonasa umbellus	0.5 – 0.7	America south of tree line	various forests
Hazel Grouse	0.4	Northern Europe and Siberia	Various forests
Bonasa bonasia	0.4		
Black-breasted Hazel Grouse	0.3	The mountains of southern Tsinghai	Coniferous forests
Bonasa sewerzowi	0.3	and central Kansu (China)	
Sharp-tailed Grouse	1.0	NW and central North America	Prairie, semidesert
Tympanuchus phasianellus	0.8		and forests
Greater Prairie Chicken	1.0	The prairie areas of SW USA	Prairie
Tympanuchus cupido	0.8		
Lesser Prairie Chicken	0.8	The prairie areas of SW USA	Prairie
Tympanuchus pallidinctus	0.7		

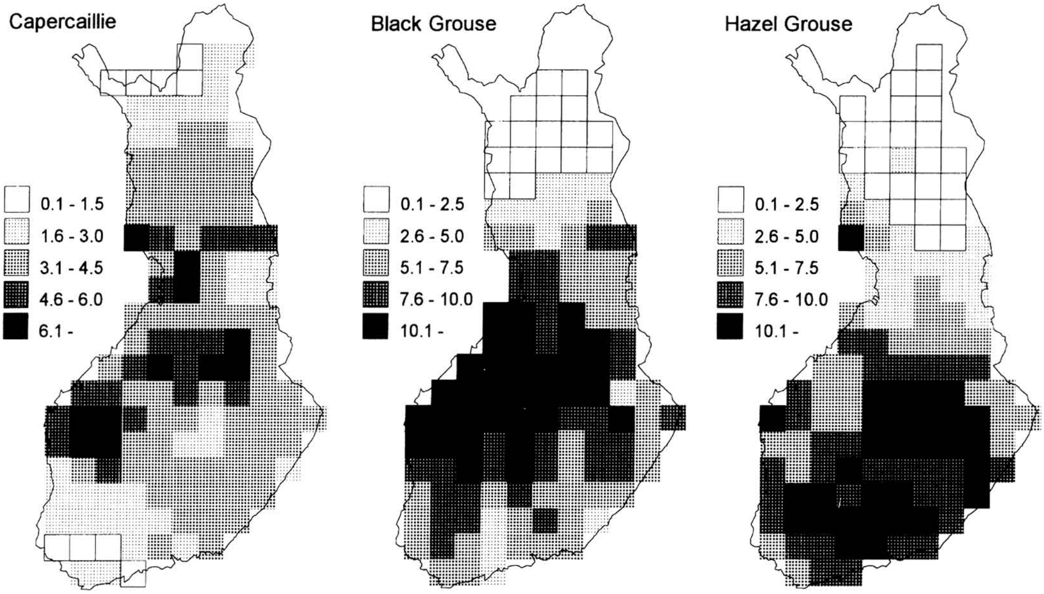

Fig. 1. The average population densities (ind. km^{-2}) of Capercaillie, Black Grouse and Hazel Grouse in 50 × 50 km squares in Finland 1988–1994 according to the wildlife triangle censuses (for the method, see Lindén et al. 1994). Note the different scaling for Capercaillie. The squares where the species has not been observed are excluded.

This review has its origin in the evaluation of the Finnish Game and Fisheries Research Institute project "Management of cyclic tetraonid populations", led by Harto Lindén. In the report (Anon. 1992) the evaluation group stressed the need to compile existing knowledge on population ecology of tetraonids, specifically the species breeding in Finland. Therefore, in the current report two themes — cyclicity and management — dominate the presentation. This work also serves as an onset of a larger research project launched for modeling and predicting long-term fluctuations of Finnish tetraonids.

2. Finnish species

As the five Finnish grouse species belong to four of the five genera in the Old World, they show a wide spectrum of grouse living habits and body size. Capercaillie is by far the largest grouse species of the world. The cock may weigh even 6 kg (Koskimies 1958), whereas the body size of Hazel Grouse is only about 0.4 kg (Table 1, Johnsgard 1983). Capercaillie is also the species most clearly associated with coniferous forests (e.g., Rolstad & Wegge 1987). Males prefer old, luxuriant forests whereas the female ranges are located more randomly. However, there are seasonal differences between and within sexes in the habitat selection (Rolstad 1988, Rolstad et al. 1988). As the male is about twice as heavy as the female (e.g., Koskimies 1958, Milonoff & Lindén 1989, Fig. 4), these differences may be a reflection of strong size dimorphism of the Capercaillie (Rolstad 1988, Gjerde 1991a). The distribution area of Capercaillie covers Finland excluding outer islands and the northern areas outside the range of pine (*Pinus sylvestris*) (Hyytiä et al. 1983, Fig. 1). Since the Capercaillie is a specialist pine needle herbivore during the winter time, the pine is an important factor in the living conditions of the species (Lindén 1984, 1988a, Gjerde 1991b). Outside the winter season Capercaillie eats berries, leaves of blueberries, herbaceous vegetation and caterpillars (Dementiev & Gladkov 1967, Klaus et al. 1989).

According to the data obtained from the wildlife triangle censuses organized by the Finnish Game and Fisheries Research Institute (Lindén et al. 1994, Fig. 1), the density of Capercaillie is on average at its highest in the Central Finland. The total population size of Capercaillie has decreased strongly during the last decades in Finland (Lindén & Rajala 1981, Järvinen & Väisänen 1984, Helle & Helle 1991).

Black Grouse is common in the whole country except in northern Lapland (Hyytiä et al. 1983, Fig. 1). It is also the most abundant grouse species of Finland. Unlike the Capercaillie, Black Grouse prefers young, 0–20 year old forest stands (e.g., Seiskari 1962, Swenson & Angelstam 1993). The food of Black Grouse consists mainly of catkins and buds of birch (*Betula pendula/pubescens*), berries (Seiskari 1962) and especially in winter also pine twigs and needles (Marjakangas 1986).

Hazel Grouse typically lives in 20–50 year old, dense Norway spruce (*Picea abies*) forests, mixed with alder (*Alnus glutinosa* and *A. incana*) and birch (Pynnönen 1954, Bergmann et al. 1982, Swenson 1993, Swenson & Angelstam 1993). In Finland the Hazel Grouse is the southernmost grouse species, although its distribution area reaches the southern and central parts of Lapland (Hyytiä et al. 1983, Fig. 1), where, according to the wildlife triangle censuses 1988–1994, are also the lowest densities of the species (Fig. 1). The Hazel Grouse eats berries, seeds, catkins and buds of alder and invertebrates (Seiskari 1962, Salo 1971).

Willow Grouse is the northernmost of the common grouse species of Finland. Typical Willow Grouse habitats in Finland are pine swamps in south and mountain birch forests in Lapland (Niemelä 1974). The shoots, buds and twigs of mountain birch (*Betula pubescens*) and willow (*Salix spp.*) comprise the main food resource of Willow Grouse (West & Meng 1966, Dementiev & Gladkov 1967).

3. Tetraonid population biology

In general, the data of densities of the grouse populations are scarce. Moreover, due to differences in the methods used to estimate the densities, all comparisons between areas and studies are largely hampered.

Both Capercaillie and Black Grouse are known to have survived over decades in very small isolated populations consisting of only 30–60 birds (Klaus 1994, Fig. 2E). This supports the general view of the strong reproductive potential of grouse. In Capercaillie it is also known from a Thuringian population that the possible inbreeding depression of a small population did not decrease the mean clutch size or hatching rate (Klaus 1994). These Central European data may serve as cue for the minimum viable population sizes.

3.1. Reproduction

All the grouse species produce one brood per year and the breeding occurs in the early summer. The incubation period ranges from 21 to 27 days, the shortest periods of 21–22 days being those of the Willow Grouse, Rock Ptarmigan and White-tailed Ptarmigan (Johnsgard 1983). The typical clutch size of tetraonids is 6–8 (Table 2) and the weight of the clutch represents 20–50% of the female weight (Johnsgard 1983). Female weight predicts well several variables in the breeding biology of the tetraonids, such as egg weight, incubation period and clutch mass, those being greater in large species. However, the clutch size varies independently of the female size (Sæther & Andersen 1988, Fig. 3). All the incubation and parental care is provided by females. This is so also in Hazel Grouse (Swenson & Boag 1993) and Willow Grouse (e.g., Hannon 1984) although they are the only commonly monogamous species among tetraonids. In the other species the sexes meet only during the prenesting period. True leks have been documented in eight species: Sage Grouse, Capercaillie, Black-billed Capercaillie, Black Grouse, Caucasian Black Grouse, Greater Prairie Chicken, Lesser Prairie Chicken and Sharp-tailed Grouse (Oring 1982, Johnsgard 1983). The young are precocial and usually able to fly, at least short distances, at the age of some days.

3.2. Mortality

The mortality of any natural population is much harder to measure than fecundity. Therefore, the information of age-class specific survival is restricted to seven European and North American

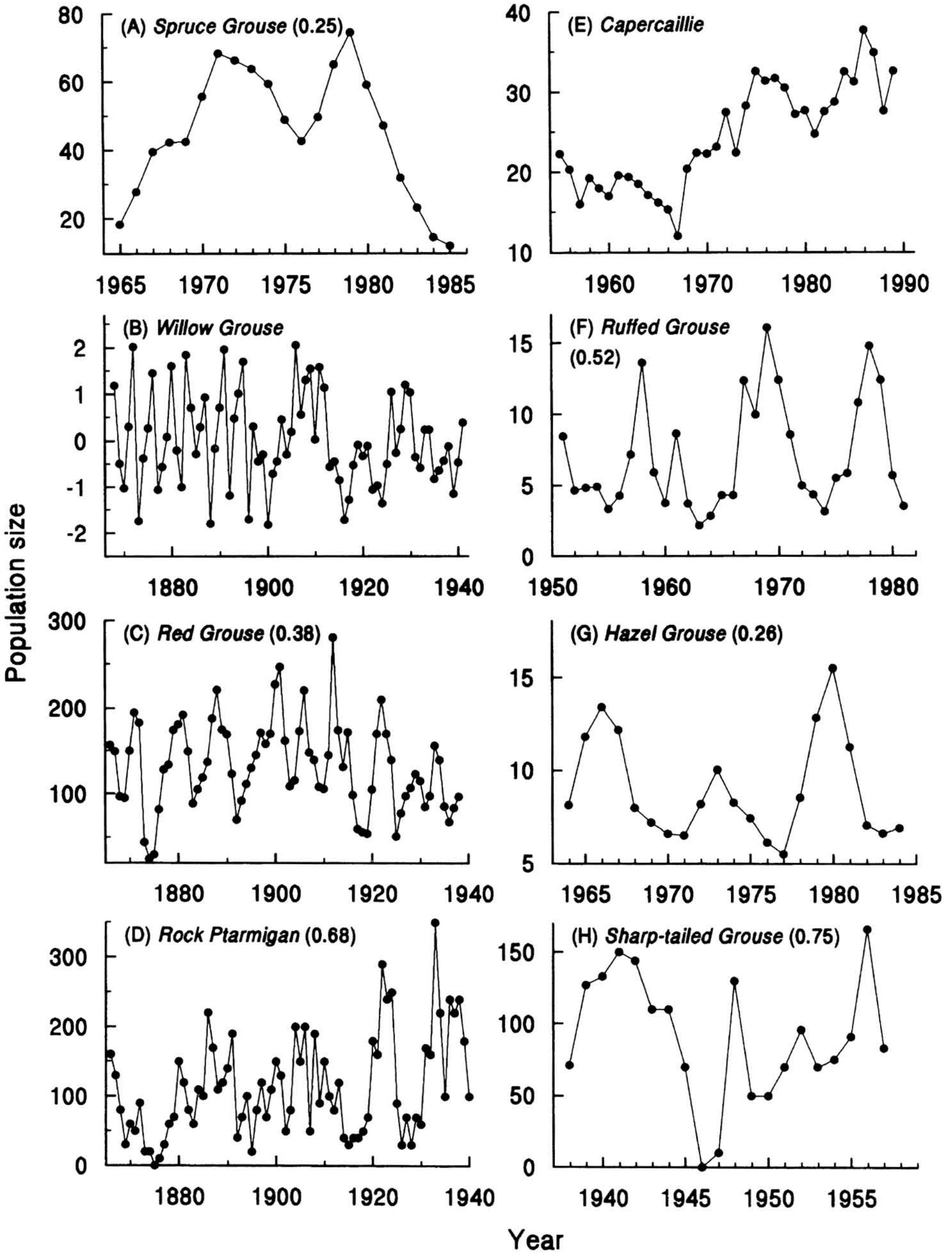

Fig. 2. Some representative time series of grouse population fluctuations. Note that the population sizes are indicated with different indices in the time series. (A) Spruce Grouse numbers in a 247 ha study area in southwestern Alberta 1965–1985 (Boag & Schroeder 1987). (B) Fluctuations of Willow Grouse in South Norway 1868–1941 (Hagen 1969). The data have been standardized to zero mean and unit variance as the original data are classified to "low", "mean" and "peak populations" in the local reports. (C) Annual bags of Red Grouse in Atholl estate 1866–1938 (Mackenzie 1952). (D) Annual bags of Rock Ptarmigan in central Scotland 1866–1947 (Mackenzie 1952). (E) Number of displaying cocks in the Fichtelgebirge, Germany 1955–1989 (Klaus 1994). (F) The bag record (× 1000) of Ruffed Grouse from Cache Creek Station, British Columbia 1951–1981 (Davies & Bergerud 1988). (G) Population density (ind. km^{-2}) in the province of Vaasa, Finland 1964–1983 (Lindén 1989). (H) Hunting-kill estimate of Sharp-tailed Grouse in North Dakota, USA 1938–1958 (Keith 1963). The number in parentheses after the species name is the *SD* of the R_t. This was not meaningful to calculate for time series B and E.

species, in which detailed population studies have been conducted. Because of the scarcity of information, it is difficult to assess, whether these figures are representative enough to allow us to form any general synthesis of the tetraonid mortality. However, the prevailing pattern in the age-specific mortality of tetraonids is — not surprisingly — that juvenile mortality rate is higher than that of adults (Table 2). Although the age-specific adult survival is rarely documented (see, however, Jenkins et al. 1963, Lewis & Zwickel 1982), it is most often assumed to be fairly constant. The bias in this assumption increases with the longevity of the species. However, probably the most pronounced difference in the grouse mortality schedules occurs between the juveniles and adults (Dobson et al. 1988). The first year mortality is high, the brood loss between June and August is typically 30–50% (Johnsgard

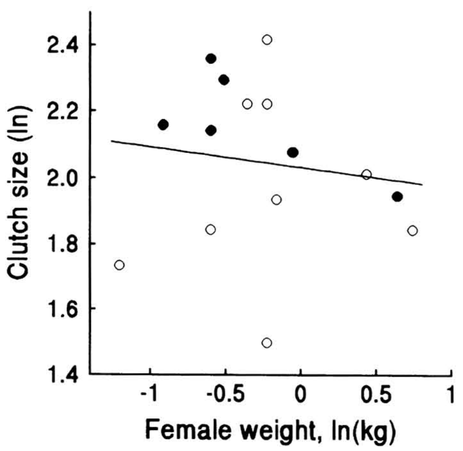

Fig. 3. The clutch size in relation to the (ln) female body weight ($y = 2.03–0.06x$, $R^2 = 0.02$, $P = 0.64$). The species having cyclic populations are indicated with filled circles.

Table 2. Basic demographic parameters of grouse species. Note that the Red Grouse is included in the table although it is a subspecies of Willow Grouse. If the number of juveniles is not reported, it has been calculated from the given survival percentages whenever possible. For the exact criteria of determining the number of juveniles in August (juveniles are calculated either per adult female*, or only the adults with brood are taken into account$^{\Delta}$) and first winter mortality, see the original references. Unfortunately, for Sharp-winged Grouse and Black-breasted Hazel Grouse no information known to me was available.

Species	Clutch size	Juveniles in August	First winter mortality	Adult mortality
Sage Grouse	7–8^{1}	2.33$^{2\Delta}$	–	52–60%^{2}
Blue Grouse	6–8^{1}, 6–6.4^{3}	2.0–3.1$^{3\Delta}$	40–61%^{3}	25–31%^{3}
Spruce Grouse	5–8^{1}, 7.2–8.0^{4}	5.3–5.7$^{4\Delta}$	76–78%^{4}	50–74%^{4}, 51–56%^{5}
Willow Grouse	7–14^{6}, 7–10^{1}	6.4$^{7\Delta}$	75%^{8}	45%^{8}, 46%^{9}
Red Grouse	4–11^{10}	–	66.6%^{10}	71%^{10}
Rock Ptarmigan	7–11^{1}, 6.6^{11}	3.6$^{11\Delta}$	–	–
White-tailed Ptarmigan	5–6^{1}, 4–8^{12}	–	57–69%^{13}	29%^{13}
Capercaillie	6.2–7.9^{14}	2.1^{14*}	88%^{14}	45%^{15}
Black-billed Capercaillie	5–8^{16}	–	–	–
Black Grouse	7.1–9.0^{14}	2.5^{14*}	83%^{14}	44%^{17}
Caucasian Black Grouse	2–10^{16}	–	–	–
Ruffed Grouse	8–13^{1,} 7–16^{18}	–	45%^{19}	44%^{19}
Hazel Grouse	9–10^{6}, 7.5–9.7^{20}	2.3–5.2$^{20\Delta}$	–	64%^{21}
Sharp-tailed Grouse	5–17^{22}	–	–	–
Greater Prairie Chicken	8.2–12.9^{23}, 5–17^{22}	–	–	51–59%^{23}
Lesser Prairie Chicken	9–14^{1}	–	–	–

1. Bergerud (1988, and references therein), 2. Johnsgard (1983, and references therein), 3. Zwickel & Bendell (1972), 4. Ellison (1974), 5. Keppie (1987), 6. Haartman et al. (1963), 7. Bergerud (1970), 8. Myrberget (1975), 9. Myrberget (1984), 10. Jenkins et al. (1963), 11. Watson (1965), 12. Giesen et al. (1980), 13. Choate (1963), 14. Lindén (1981), 15. Moss (1987), 16. Dementiev & Gladkov (1967), 17. Angelstam (1984), 18. Cringan (1970), 19. Small et al. (1991), 20. Bergmann et al. (1982), 21. Jon Swenson, pers. comm., 22. Hamerstrom (1939), 23. Schroeder & Robb (1993)

1983), and the first winter mortality is 40–90% (Table 2). Since the grouse are ground nesting species the nest predation rate is commonly found high (e.g., Myrberget 1985, Storaas & Wegge 1984, 1987, Brittas & Willebrand 1991, Storch 1991). The first-yearlings are also probably easier prey than the adults for many avian and mammalian predators.

3.3. Long-term studies and environmental changes

Since the tetraonids are game species, part of the studies are based on hunting statistics, and also the ecological studies are often conducted to provide necessary information for game management. These dual objectives have markedly affected the research tradition and consequently the results obtained in different countries.

Unfortunately enough, there are not many long-term population studies and they are concentrated mainly on a few species. I collected the most comprehensive ones to Table 3. The list is not meant to be exhaustive by means of covering the whole field of population ecological literature of tetraonids. Rather, its aim is to give a general idea of the observed patterns in tetraonid population dynamics. To further this aim, I also selected some of the studies for Fig. 2. As one can see, the fluctuations can be strong and more or less regular. The reproductive rate is defined here as $R_t = X_{t+1} - X_t$, where X_t denotes (ln)population size at time *t*. Large values of standard deviation of R_t indicate prominent variation in the change of population numbers of consecutive years (Fig. 2). The variability in R_t of Hazel Grouse from the province of Vaasa (*SD* = 0.26) is rather small compared to the other populations in Fig. 2.

Modern forestry has created prominent changes in the tetraonid habitats in Fennoscandian countries. The strongest effects of forestry on the landscape are the change in the forest age structure towards younger age classes and the fragmentation of formerly uniform forest areas (e.g., Rolstad & Wegge 1989a). Understanding the effects of this development on tetraonid population dynamics has been an obvious challenge to game management. The decreasing trend of tetraonid populations in Finland has been well documented with various methods (Sammalisto 1977, Lindén & Rajala 1981, Järvinen & Väisänen 1984). The simultaneous decrease of Capercaillie, Black Grouse and Hazel Grouse indicates — at least partly — a common reason behind the decline (Helle et al. 1987).

Capercaillie, Black Grouse and Hazel Grouse differ in their habitat selection, and the dominant tetraonid species changes during forest succession. Why, then, the forestry seems to have adverse effects on the populations of all the three species? At least one would expect the Black Grouse to benefit from the increase of younger forest age-classes. However, this is probably an oversimplification: despite the increase of young age-classes in forests the amount of potential grouse habitats has decreased. This is due to large scale changes in the structure of forest mosaic and change in the relative abundances of tree species (Helle et al. 1987). For Capercaillie the harmful mechanism is the disappearance of suitable lekking sites due to fragmentation of old forests, not only the decrease of the total area of old forests (Seiskari 1962, Helle & Järvinen 1986, Lindén & Pasanen 1987, Rolstad & Wegge 1987, 1989b,c, Rolstad 1989, Valkeajärvi & Ijäs 1991). However, the mechanism behind the decrease of Black Grouse and Hazel Grouse is less well documented and understood. Although both species require deciduous trees, especially birch and alder in their feeding and breeding habitats (Helle et al. 1987, Swenson 1993), their population trends cannot be explained solely by the proportion of deciduous trees in forests (Helle & Helle 1991, see, however Järvinen & Väisänen 1984). To some extent, the detrimental effect of forestry on tetraonids may be locally connected to increased nest predation pressure in fragmented habitats (Andrén et al. 1985, Andrén & Angelstam 1988).

4. Factors affecting the fluctuations of tetraonids

That a population of a given species is somehow regulated is of vital importance to its long term persistence (see e.g., Royama 1992). Therefore, to gain a proper understanding of the fluctua-

Table 3. Representative grouse population studies. If there are more than one publication of a given population, the most thorough one is used. Very fragmentary sources have been avoided. Trend in population numbers is divided to three classes: + = increased, – = decreased and ± = no change during the study period, X means that the data have been transformed to eliminate the trend.

Species	Study period	Study site	Pattern	Trend	Authors
Sage Grouse	1974–1983 (10)	Colorado, USA			Braun 1984
Sage Grouse	1941–1983 (43)	Oregon, USA			Crawford & Lutz 1985
Blue Grouse	1950–1969 (20)	Vancouver Island, Canada		–	Zwickel & Bendell 1972
Blue Grouse	1979–1984 (6)	Hardwicke Isl., Br. Columbia			Zwickel et al. 1988
Spruce Grouse	1965–1985 (21)	Alberta, Canada	Cyclic (9)		Boag & Schroeder 1987
Spruce Grouse	1965–1970 (6)	Kenai Peninsula, USA		–	Ellison 1974
Willow Grouse	1955–1965 (11)	Newfoundland	Cyclic (10)	±	Bergerud 1970
Willow Grouse	1867–1943 (77)	South Norway	Cyclic (3–4)	±	Hagen 1969
Willow Grouse	1963–1975 (13)	Västerbotten, Sweden	Cyclic (3–4)	±	Hörnfeldt 1978
Capercaillie	1963–1975 (13)	Västerbotten, Sweden	Cyclic (3–4)	±	Hörnfeldt 1978
Black Grouse	1963–1975 (13)	Västerbotten, Sweden	Cyclic (3–4)	±	Hörnfeldt 1978
Hazel Grouse	1963–1975 (13)	Västerbotten, Sweden	Cyclic (3–4)	±	Hörnfeldt 1978
Willow Grouse	1964–1983 (20)	Finland, whole country	Cyclic (6–7)*	–	Lindén 1989
Capercaillie	1964–1983 (20)	Finland, whole country	Cyclic (6–7)*	–	Lindén 1989
Black Grouse	1964–1983 (20)	Finland, whole country	Cyclic (6–7)*	–	Lindén 1989
Hazel Grouse	1964–1983 (20)	Finland, whole country	Cyclic (6–7)*	–	Lindén 1989
Willow Grouse	1976–1984 (9)	N Gulf of Bothnia, Sweden			Marcström et al. 1988
Capercaillie	1976–1984 (9)	N Gulf of Bothnia, Sweden			Marcström et al. 1988
Black Grouse	1976–1984 (9)	N Gulf of Bothnia, Sweden			Marcström et al. 1988
Hazel Grouse	1976–1984 (9)	N Gulf of Bothnia, Sweden			Marcström et al. 1988
Willow Grouse	1890–1967 (78)	Trollheim, Norway	Cyclic (4–5)	±	Moksnes 1972
Willow Grouse	1960–1980 (21)	Tranøy, Norway	Cyclic (3–4)	±	Myrberget 1972, 1984
Willow Grouse	1911–1951 (41)	Finland, whole country	Cyclic (x–x)		Siivonen 1952
Capercaillie	1911–1951 (41)	Finland, whole country	Cyclic (x–x)		Siivonen 1952
Black Grouse	1911–1951 (41)	Finland, whole country	Cyclic (x–x)		Siivonen 1952
Hazel Grouse	1911–1951 (41)	Finland, whole country	Cyclic (x–x)		Siivonen 1952
Willow Grouse	1963–1982 (20)	Tranøy, Norway	Cyclic (3–4)		Steen et al. 1988
Willow Grouse	1965–1983 (19)	Lövhögen, Sweden	Cyclic (3–4)		
Red Grouse	1875–1983 (109)	Scotland	Cyclic (4–6)	–	Barnes 1987
Red Grouse	1977–1991 (15)	Yorkshire, England	Cyclic (4–5)	±	Hudson et al. 1992a
Red Grouse	1956–1961 (6)	Glen Esk, Scotland	Cyclic (4–5)		Jenkins et al. 1963
Red Grouse	1865–1944 (80)	British Isles	Cyclic (6–7)		Mackenzie 1952
Black Grouse	1850–1949 (100)	Scotland			
Red Grouse	1848–1909 (62)	Northern England, Scotland	Cyclic (6–7)	±	Middleton 1934
Black Grouse	1897–1924 (28)				
Red Grouse	1870–1977 (108)	North England	Cyclic (4–5)	X	Potts et al. 1984
Red Grouse	1962–1978 (17)	Kerloch, Scotland	Cyclic (5–8)		Watson et al. 1984b
Red Grouse	1979–1989 (11)	Rickarton, Scotland	Cyclic (5–8)		Watson et al. 1988
Rock Ptarmigan	1977–1987 (11)	Cervières, France			Ellison et al. 1988
Rock Ptarmigan	1864–1942 (79)	Island	Cyclic (10)		Gudmundsson 1960
Rock Ptarmigan	1886–1938 (53)	Scotland			Moran 1952
Capercaillie	1886–1938 (53)	Scotland			Moran 1952
Black Grouse	1886–1938 (53)	Scotland			Moran 1952
Rock Ptarmigan	1951–1964 (14)	Cairngorns, Scotland			Watson 1965
Rock Ptarmigan	1960–1969 (10)	Alaska, USA			Weeden & Theberge 1972
White-tailed Ptarmigan	1959–1962 (4)	Montana, USA		–	Choate 1963
Capercaillie	1971–1983 (13)	Thuringia, Germany		–	Klaus 1984
Capercaillie	1975–1984 (10)	Glen Tanar, Scotland		±	Moss 1986
Capercaillie	1953–1962 (10) 1967–1976 (10)	Sørlandet, Norway		–	Wegge & Grasaas 1977
Black Grouse	1973–1982 (10)	Grimsö, Sweden	Cyclic (3–4)	±	Angelstam et al. 1985
Greater Prairie Chicken	1936–1963 (28)	Illinois, USA		–	Yeatter 1963
Lesser Prairie Chicken	1962–1970 (8)	New Mexico, USA		–	Campbell 1972
Ruffed Grouse	1951–1981 (30)	British Columbia, USA	Cyclic (10)	±	Davies & Bergerud 1988
Ruffed Grouse	1966–1972 (6)	Alberta, Canada		–	Fischer & Keith 1974
Ruffed Grouse	1932–1966 (34)	Minnesota	Cyclic (10)	–	Gullion 1969
Ruffed Grouse	1962–1975 (13)	North America	Cyclic (10)	±	Keith & Rusch 1986
Ruffed Grouse	1950–1984 (34)	Minnesota	Cyclic (10)	±	

* except Lapland.

tions of any population, one has to seek for the regulating mechanisms. There are three main categories of suggested factors affecting the population fluctuations in tetraonids: predation, parasites and inherent regulatory mechanisms. It is hard to say, whether the preoccupation with cyclicity in animal ecology has emphasized studies of cyclic tetraonid populations, or whether the findings of cyclically fluctuating grouse populations have helped to maintain interest in cyclicity. Whatever the truth is, most of the studies have been conducted in cyclic (or sometimes quasi-cyclic sensu Nisbet & Gurney 1982) populations.

4.1. Predation

The regulatory power of predation on any population is dependent on the timing of the predation event (Crawley 1992). When predation occurs before the other density dependent mechanisms, its effect may be partly compensated by decreasing the competition. On the other hand, predation occurring after the density dependent mechanisms decreases the net growth rate of the prey population. This is, of course, a somewhat simplistic view since many of the predators utilize the same prey species all year round. Also the characteristics of the predators in the generalist — specialist continuum affect the regulatory possibilities of the predator population.

As ground nesting birds, grouse are relatively vulnerable to nest predation by mammals and corvids (Klaus 1984, Parker 1984, Lindström et al. 1987). The adults are preyed upon by mammals, hawks and owls (e.g., Rusch & Keith 1971, Lindén & Wikman 1983, Klaus 1984, Keith & Rusch 1986, Tornberg & Sulkava 1991). Hence, the known predators of tetraonids are generalists with the exception of parasites of Red Grouse (discussed below), and no actual coupled predator-prey systems are known. That is, there are no known predators whose density would be mainly determined by the density of grouse, and which could in that way regulate the grouse population. Theoretically, density dependent predation with sigmoidal functional response is capable of producing cyclic prey dynamics (e.g., Crawley 1992). In nature this mechanism could be achieved, e.g., by predator switching the prey species that is abundant at a given moment or by aggregating in areas of high prey density.

This theoretical presupposition has deserved some evidence in the form of the alternative prey hypothesis (Hagen 1952, Lack 1954, Angelstam et al. 1984, 1985). The hypothesis states that when vole populations crash, predators shift their diet to grouse. Thus, predators may connect the vole and grouse dynamics. Lindström et al. (1994) have emphasized the role of red fox (*Vulpes vulpes*) in this predator-prey complex. The same basic idea of predators' diet shift causing the fluctuations have been utilized in explaining the ten year cycle of some North American grouse species (e.g., Royama 1992). It is worth noting, however, that the implicit assumption of matching cycle lengths of voles, predators and grouse are not always found. The cycle length of Finnish tetraonids is 6–7 year (Lindén 1988b). Lapland is an exception with its somewhat shorter, and less distinct, cycles closer the 4 year cyclicity observed in voles (Lindén 1988b). This indicates that the effect of predation on grouse populations may be influenced by some other factors besides diet shift of predators. The question of the grouse population regulation by predation is further complicated by the lack of knowledge of the other density dependent mechanisms regulating the grouse population. In some cases, however, it seems evident that predators may regulate grouse populations at least locally. Marcström et al. (1988) removed predators experimentally from two islands in the northern Baltic. After predator removal they observed higher average brood size and proportion of females with brood in August. This resulted in higher overall autumn population density in the areas where the predators had been removed compared to control areas.

4.2. Parasites

The body of knowledge concerning the grouse parasites is rather thin. So far several types of endoparasites, such as Nematodes, Cestodes, Coccidia and some protozoans have been scored from a number of grouse species (Oliger 1940, Lund 1954, Hudson et al. 1985, Allan & Mahrt 1987, Gibson 1990, Watson & Shaw 1991, Wilson 1983, Höglund et al. 1992, Forbes et al. 1994, Holstad et al. 1994). However, the regulation of grouse populations by parasites have not been reported with the exception of Red Grouse (Hudson et al. 1985, 1992a, Hudson & Dobson 1989, Dobson & Hudson 1992).

Anderson and May (1978, 1979), and May & Anderson (1978, 1979) have shown theoretically some of the critical preconditions of the coupled parasite-host relationships in which the species regulate each others density. There are three critical properties of the parasite governing the resulting dynamics in the case of a simple one host, direct life cycle system. These are mortality of the free-living stage, pathogenicity and the frequency distribution of the parasite in the host population. The dynamics of the parasite and the host populations will tend to oscillate if the mortality of the free-living stage of the parasite is low, the pathogenicity of the parasite is lower than the reduction in host fecundity, and the parasite is not highly aggregated.

The Red Grouse have a specialist parasitic nematode, *Trichostrongylus tenuis*, and become infected most probably directly by eating heather, *Calluna vulgaris* (Hudson et al. 1992a). As the Red Grouse display both cyclic and non-cyclic fluctuations it is interesting that the worm burden has been shown to be higher in cyclic than in non-cyclic and intermediate populations (Hudson et al. 1985). The Red Grouse — *T. tenuis* system also meet the three theoretical preconditions of the Anderson-May model (Anderson & May 1978, 1979, May & Anderson 1978, 1979, Hudson, et al. 1992a, Dobson & Hudson 1992). The parasite also increases the predation risk of Red Grouse, which reduces the delayed density-dependent effects of parasite on host survival and breeding, and thus diminishes the tendency to oscillation (Hudson et al. 1992b). This is also in accord with the theoretical explorations of this type (May & Anderson 1978, Dobson & Hudson 1992). However, despite having a solid theoretical background and empirical evidence of population regulation by nematodes in Red Grouse, parasitism is not likely to be an universal explanation for grouse population regulation. Since the Red Grouse is an intensively managed species, its density is much higher than it would be without predator control and habitat management. Without predator control, the density would obviously be so low that regulation by parasites would not be manifested (Hudson & Dobson 1991).

4.3. Tetraonid cycles

The cyclic population dynamics has gained persistent attention in the ecological literature. Therefore, since several grouse species are known — or argued for (Table 3) — to display cyclic dynamics, it will be discussed separately here. I do not define cyclicity rigorously here, instead I call the observed pattern cyclic in Table 3 if that is the interpretation of the authors. Cyclicity in grouse is a phenomenon of northern populations as is the case with other cyclic vertebrates as well (Keith 1963, for a recent review of cyclic mammal populations, see Akçakaya 1992). It is important to notice that the cyclicity of grouse populations is not a species-specific property; there are both cyclic and non-cyclic populations as well as various cycle lengths in the same species (Table 3). This is also known of cyclic mammals (Hansson & Henttonen 1985, Hanski 1987). The best known cycle among tetraonids is that of Red Grouse. The length of the Red Grouse cycle is 4–6 years depending on the site (e.g., Middleton 1934, Hudson 1992). The cycle length of the Finnish populations of Capercaillie, Black Grouse and Hazel Grouse is somewhat longer, generally 6–7 years, but shorter in Lapland (Lindén 1988b, 1989). The longest cycles are typically found in North America, where several populations of Willow Grouse and Ruffed Grouse display 10 year cyclicity (e.g., Bergerud 1970, Davies & Bergerud 1988).

A number of different hypotheses explaining the cyclic behavior of some grouse populations has been presented. As the regulatory power of predation and parasites has been discussed earlier, I concentrate here on the remaining aspects concerning particularly cyclicity. Plant-herbivore interaction is one possibility causing the cycles (e.g., Andreev 1988). However, although the Red Grouse is clearly associated with heather, food enrichment experiments have shown that the population decline cannot be prevented by fertilizing heather (e.g., Watson et al. 1984a). Plant-herbivore interaction has not been shown to cause regular population fluctuations in any other grouse species either. Some weather variable could also be possible factor behind cyclicity. However, as it has been shown theoretically that any weather-derived population regulation mechanism is necessarily fragile (Royama 1992), and there is no convincing empirical evidence either, I refrain from discussing more such a hypothetical alternative.

Chitty (1967) presented the so-called polymorphic behavioral hypothesis to explain cyclic population fluctuations. Page & Bergerud (1984) found the original formulation of the theory insufficiently precise and elucidated it to attain a better testable model. The core of the model is the Mendelian inheritance of aggressive behavior (two alleles at one locus), with recruitment being inversely related to female aggressiveness (i.e., female genotype). The aggressive individuals are also considered to be always more successful in space competition than the non-aggressive ones. To test the model assumptions, Page & Bergerud (1984) utilized data from a Willow Grouse population which was known to display ten-year cyclicity (Bergerud 1970). However, as the model suggests a difference between the breeding performance of aggressive and non-aggressive individuals, all parameters could not be readily extracted from the real population data. A stochastic element was incorporated in the model to represent the weather. This was done by randomly varying the August brood size around the mean of the particular genotype, with variation increasing with aggressiveness (10–60%). The stochastic element increased the amplitude of the cycles. By letting the territory size of the aggressive birds be six times larger than the territory of the non-aggressive individuals, and by using the population parameters of Willow Grouse, a stable ten-year cycle was achieved. Interestingly, by altering the demographic parameters to better match to those of some other grouse species, e.g., Blue Grouse, the model dynamics closely resembled that perceived in nature. However, despite the striking similarity in the time series of natural grouse populations and model results, the basic assumptions of the model are hard to justify. The inheritance of aggressiveness could be due to androgen levels, but the hormone interactions are complex and therefore hardly likely to operate via simple Mendelian inheritance. Also the assumption of aggressive females being poorer mothers than non-aggressive females, is dubious.

The latest genetic hypothesis (Watson et al. 1994) concerning the Red Grouse cycles refer to the possibility of kin-selection. This requires territoriality as the mechanism causing population fluctuation. However, territoriality is not known to exist in all the cyclic grouse populations. Therefore, I suggest that there is not an universal explanation for grouse cycles, but a number of population properties, e.g., relatively high productivity and mortality rates, which together with biotic interactions can yield regular fluctuations. This is indicated by Fig. 3: the species which have cyclic populations tend to have larger clutch size in relation to (ln) female body size than the species with different dynamics. The body size, or the size dimorphism give no cue of the probability of cyclicity (Fig. 4). Here the size dimorphism is assessed by using the residuals of the regression model where (ln) male body size is the dependent variable and the (ln) female body size is the independent variable. This method avoids the typical fallacies related to simple body size ratios (Ranta et al. 1994).

5. Tetraonids as game birds

Tetraonids are a notable natural resource in many areas. Although the grouse are a significant food source for only a few people today, they are still hunted intensively. In some cases, e.g. the Red Grouse (Krebs & May 1990), they also have marked financial value. The grouse are hunted in autumn in most areas (Baines & Lindén 1991). This is preferable since it is the most productive way of hunting in long term (e.g., Doubleday 1975) and facilitates the sustainable management (Baines & Lindén 1991).

5.1. Hunting — Man as a predator

There are certain distinguished characteristics when considering man as a predator of grouse populations. The numerical response of man to the prey density is restricted to concentrating the hunting effort to high density areas. It is also

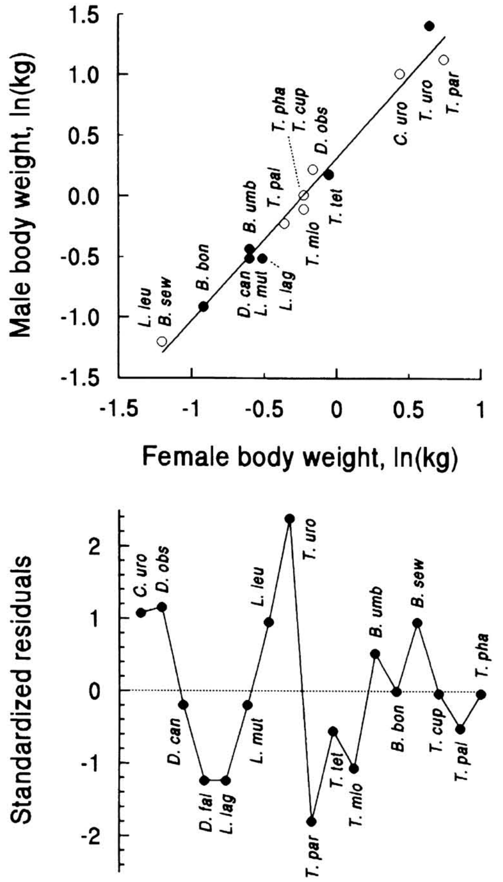

Fig. 4. Size dimorphism in the grouse species. In the upper panel is the (ln) male body weight plotted against the (ln) female body weight, and the species having cyclic populations are indicated with filled circles. The regression model is: $y = 0.31 + 1.34x$ ($R^2 = 0.98$, $P < 0.001$). The lower panel presents the standardized residuals of the regression model above. As the residuals have been standardized, the y-axis is in *SD* units.

noteworthy that there is not necessarily a time lag in the human response, although it is possible (e.g., Berryman 1991, Fryxell et al. 1991). The functional response curve of man has been interpreted as concave in Finland — however, if the tetraonids were more abundant, the curve would probably follow the convex or sigmoidal functional response (Lindén 1991). Moreover, the closed hunting seasons in some areas of low grouse density can be seen as refugia. Strictly speaking, these refugia are fixed number refugia if there exists some agreement of the lower critical population density (Crawley 1992).

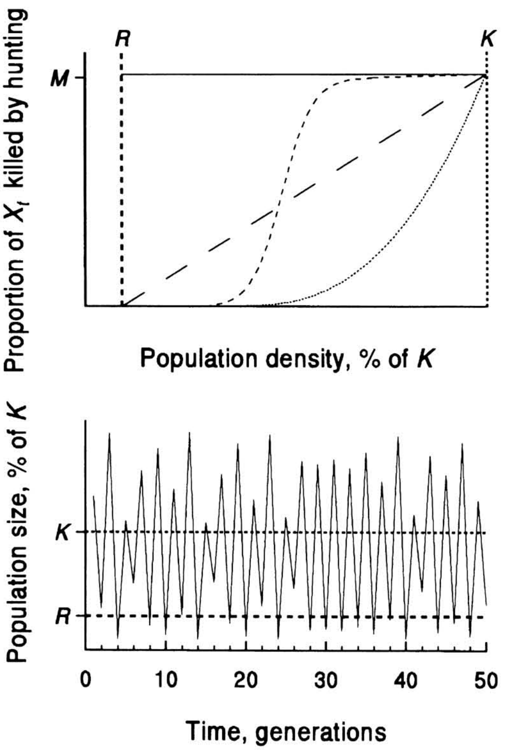

Fig. 5. Graphical presentation of the hunting model (eq. 1). Population density (% of *K*), and proportion of the population killed by hunting are indicated in the upper panel. *M* denotes the maximum hunting mortality, *R* is the critical population density under which no hunting is allowed and *K* is the carrying capacity. The four different hunting schemes are sigmoidal (dashed line), linear (long dashes), concave (dotted line), and constant proportion hunting (solid line). The lower panel shows one realization of chaotic ($r = 2.75$) population dynamics (transition phase has been omitted). Population numbers under the critical population density, *R*, are closed seasons in terms of the hunting strategy.

In order to demonstrate the possible effects of hunting on the dynamical behavior of a given population, I used a simple logistic population growth model with varying hunting schemes (Fig. 5). The population grows according to:

$$X_{t+1} = X_t \exp\left[r\left(1 - \frac{X_t}{K}\right)\right] - (h_t X_t). \quad (1)$$

Here t denotes time, r is the population growth rate, K is the carrying capacity, and h_t represents the proportion of the population killed by hunting. As it is well known that the dynamics of the eq. (1), without hunting of course, can be changed from stable to limit cycles and chaos by increasing the r value (e.g., May 1976). I chose three different values for r. These are 1.0, 2.5 and 2.75 producing stable dynamics, two-point limit cycle and chaos, respectively. Thus, the population growth is density-dependent and the hunting mortality is additive. The hunting scheme had four different alternatives (1) sigmoidal response (i.e., Holling's type III response; Holling 1959), (2) linear response, (3) concave response, and (4) constant proportion hunting (Fig. 5). Before the population was subjected to hunting the population size, X_t, had to exceed a critical limit, R, which is a proportion of K. This limit was constructed to represent a situation where the population numbers are so low that the hunting season has to be closed totally. The value of R was set zero or to 20% of K. The results are presented in Table 4. The most prominent result is that the hunting pressure has to be generally high in order to change the dynamical behavior of the population. It is rare that the hunting pressure is over 20% in any controlled management strategy (see e.g., Lindén & Sorvoja 1992), but it is possible in some cases (e.g., Palmer & Bennett 1963, DeStefano & Rusch 1986). Therefore, although most of the results require rather high hunting pressure, they are not of theoretical interest only. The most sensitive type of the original dynamics is chaos, which is readily stabilized to limit cycle with hunting pressure being less than 10% in every hunting scheme (Table 4).

Table 4. The simulation results of the hunting model. The values represent the hunting pressure needed to yield either stable dynamics, limit cycle or chaos from the original dynamics. The size of the refuge, R, is either zero or 20% of the carrying capacity, K. When R = 20% the maximum hunting pressure is calculated so that the proportion of the closed seasons (in parentheses) is less than 100%. The reported proportion of the closed seasons is the maximum achieved in the given range of hunting pressures. Note that extinction is not allowed in any case.

Original dynamics	Refuge % of K	Dynamical behaviour after hunting			
			Stable		
		Sigmoidal	Linear	Concave	Constant
Stable,	0	≤ 73	≤ 99	≤ 99	≤ 62
r=1	20	≤ 55	≤ 99	≤ 99	≤ 55
2-point cycle,	0	≥ 42	18–48	11–25	42–91
r=2.5	20	42–86	18–48	11–25	42–86
Chaos,	0	53–94	21–41	13–22	54–93
r=2.75	20	53–88	21–41	13–22	54–88
			Limit cycle		
		Sigmoidal	Linear	Concave	Constant
Stable,	0	75–96	–	–	–
r=1	20	–(100)	–	–	–
2-point cycle,	0	≤ 41	≤ 17	≤ 10, 26	≤ 41
r=2.5	20	≤ 41	≤ 17	≤ 10, 26	≤ 41
Chaos,	0	6–52	2–20, 42–45	1–12	6–53
r=2.75	20	6–52	2–20, 42–45 (29)	1–12 (26)	6–53 (26)
			Chaos		
		Sigmoidal	Linear	Concave	Constant
Stable,	0	97–99	–	–	–
r=1	20	–(100)	–	–	–
2-point cycle,	0	–	49–54	27–31	–
r=2.5	20	–	49–54 (50)	27–31 (41)	–
Chaos,	0	1–5	1	–	1–5
r=2.75	20	1–5 (51)	1 (26)	–	1–5 (26)

6. Prospects

Knowing age-class specific mortality and fecundity parameters would improve the current understanding of tetraonid population dynamics. Better knowledge of these parameters could also render the improvement of different harvesting strategies. There are some gaps in the basic knowledge of the effects of hunting as well. As Baines and Lindén (1991) suggest, attention should be given to the birds that survive from hunting; although they are not killed, hunting may cause physiological stress, change their behavior, or make them more vulnerable to natural predation.

To conclude, the long-term dynamics and large-scale phenomena in Finnish tetraonids can be discerned from the current data basis. However, more detailed studies focusing on the age-class specific performance of the individuals would be of value.

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