

POPULATION DYNAMICS OF THE WILLOW PTARMIGAN IN THE NORTH OF YAMAL PENINSULA AND THE FACTORS AFFECTING THEM

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ABSTRACT.—Factors affecting the population dynamics of Willow Ptarmigan (*Lagopus lagopus*) were studied in the northern Yamal Peninsula in Russia, near the northern limit of the species' range. Self-regulatory mechanisms were apparently absent; that is, population increases did not promote the appearance of a population reserve, depress reproduction, or reduce the site fidelity index. Ptarmigan density did not reach the maximum level of the habitat capacity, and the main reason was that reproduction was low in the area and associated with high predation pressure. Hatching success was lower than that in more southern parts of the species range, and Arctic Fox (*Alopex lagopus*) predation was high because the arctic tundra is open, vegetation is low, and shelter is absent. Climatic conditions in the arctic tundra are also unfavorable for high ptarmigan fecundity because of the late onset of breeding, so that the hens must lay eggs during the spring molt rather than after it, as everywhere to the south. Clutch size is entirely determined by the timing of spring arrival, and this relationship is much stronger in the northern Yamal than in more southern latitudes. The degree of site fidelity among adults also is determined by the time of spring arrival. In years of late spring, up to one-half of the birds change their nesting area from that of the previous year, as distinct from temperate latitudes, where the ptarmigan is a territorially conservative species. Annual survival of birds over one year old varies only slightly from year to year. *Received 31 December 2010, accepted 1 August 2011.*

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ANALYZING MECHANISMS influencing annual fluctuations in numbers of ptarmigan (*Lagopus* sp.), Bergerud et al. (1985) put forward two hypotheses. According to the first, numbers of ptarmigan in the given year are limited by territorial spacing behavior which depends on population density. Those birds, not possessing territories, die. The second hypothesis main-

tains that the number of birds is defined by the level of reproductive success in the previous year, while density influences mortality to only a minor degree.

Population processes in Willow Ptarmigan (*L. lagopus*), as the most numerous game-bird species in the tundra, are rather well investi-

gated. Long-term studies on mechanisms of its population dynamics have been conducted in Scotland (Jenkins et al. 1963), Norway (Myrberget 1984), and Canada (Bergerud 1970, Hannon and Barry 1986). In Russia, such study areas have included the Bolshезemel'skaya tundra (Voronin 1978) and the lower reaches of Kolyma River (Andreev 1988). In most cases, researchers noted an influence of previous reproductive success on bird numbers, and that when density reached high values, self-regulatory mechanisms appeared, including increased territorial aggressiveness, decreases in clutch size, a higher frequency of unfertilized eggs, and other responses, all of which reduced the intensity of reproduction. Despite the great number of publications dealing with population dynamics of Willow Ptarmigan, however, the extreme northern areas of its range appear to have been neglected such that causal mechanisms remain unclear for those regions. In the present work, we present data obtained in the northern Yamal Peninsula near the northern limit of the species range.

STUDY AREA AND METHODS

Studies on population dynamics of Willow Ptarmigan were made during 1989–1995 at the Yaibari ornithological field station in the northeast of the Yamal Peninsula, (71°04' N, 72°20' E) located at the southern boundary of the arctic tundra subzone, in the lower reaches of Venuyeyouyaha River. Like the entire northern part of the peninsula, this area is a flat plain with elevations varying no more than 10–15 m. The slow-flowing rivers have wide floodplains with bogs and back-waters. Upland areas support moss-lichen and arctic tundra of various types, with streams, lakes and bogs. Vegetation consists mainly of mosses, lichens, herbaceous plants, and creeping willows (*Salix* sp.). A shrub layer (mainly *S. glauca*) up to 25–30 cm in height occurs only in some of the lowest places. The flat, undifferentiated territory provides for an even distribution of nesting ptarmigan.

The Yaibari Station is located near the limit of distribution of Willow Ptarmigan, which become rare to the north of 71° N and disappear at the latitude of Tambei settlement (71°30' N), about 50 km north of Yaibari Station (Danilov et al. 1984, Sosin et al. 1985). The floodplain willow thickets and nearby ridged tundra occurring along the large Venuyeyouyaha River on the east coast of the Yamal are, in fact, the most northern habitats of the Willow Ptarmigan, where its rather stable numbers still allow long-term ecological research.

Results were obtained on a 3 km² study plot with a ratio of upland and floodplain habitats typical of surrounding tundra. The plot area was divided into 100 × 100-m squares by means of pegs with conspicuous labels (letters and figures) serving as the basic landmarks for bird observations. Annually, ptarmigan on the study plot were individually marked by colored bands and painted wing feathers (these conveniently remained white even in summer). Territorial males for marking were caught by use of an automatic snare on a dummy male as a decoy, using their aggressive reaction toward rivals. Females were caught on nests. In total, 138 birds (82 males and 56 females) were marked. Many of them nested on the study plot longer than one season, so in total during the studies, there were 201 individually-distinguishable birds.

Age of the captured birds was determined by pigmentation of the first two primary wing feathers (Bergerud et al. 1963) that allowed us to differentiate between yearlings and older birds. We defined the annual survival rate of adults (older one year) by their numerical proportion to the number breeding in the previous season. We started with the assumption that, if all birds began nesting in their first year of life and breed each year, adults lost over the winter were compensated by yearlings. If the number of birds was constant from year to year, the annual mortality rate of adult birds (older than one year) equaled the percentage of yearlings in the population. If the number of birds varied

from year to year, the number of surviving adult birds equaled the ratio of their number in the population to the total of last year's numbers. The error percentage of young birds (as well as the error percentage of the older birds, and the error percentage of the old birds that survived) was determined by the formula:

$$\mu = \sqrt{p(1-p) / n}$$

where p = the proportion of the yearlings, and n = the number of birds whose age was determined.

Such a simplified way of survival calculation is reasonable only in those populations where all individuals begin nesting in the first year of life and continue breeding annually. For ptarmigan nesting on the Yamal, an absence of "surplus" birds has been shown (Ryabitsev and Tarasov 1994); therefore such a way of calculating survival rate is quite applicable.

We tentatively calculated ptarmigan reproductive success as the survival rates of eggs and nestlings to the point at which fledged juveniles appeared (see Paevsky 1985). Thus, reproductive success derived from two measures: nesting success (the proportion of eggs that hatched) and the survival rate of nestlings to the point of fledging. The Mayfield method of estimating nesting success, as modified by V. A. Paevsky (1985), considered the probability of egg survival to the moment of hatching, whereas nesting productivity was defined as the number of chicks hatching per unit area, specifically the product of female density (nests), the average number of eggs in a clutch, and the calculated average nesting success.

We estimated variability in ptarmigan numbers as the average difference in nesting density between two consecutive years, expressed as a percentage. We avoided using a coefficient of variation (C_v), the usual expression of variability, because population density appreciably depended on density in a previous year. We expressed mean values arithmetically and with

a standard error (\pm SE). For the analysis of interrelation of two values, we used the Pearson's coefficient of correlation.

RESULTS AND DISCUSSION

The annual density of the nesting population of Willow Ptarmigan on the study plot varied from 7 to 17 individuals (from 4 to 9 mating pairs) per km^2 . The difference in numbers of nesting birds from one year to next year varied from 5% to 51% and averaged $27 \pm 7\%$ over 6 years. Figure 1 shows the dynamics of numbers of old and one-year-old (breeding for the first time) and their total numbers at Yaibari Station. The number of old birds was the most stable: the annual difference in their numbers varied from 1% to 47%, whereas yearlings varied from 45% to 1200%. Accordingly, the total number of ptarmigan was more strongly connected to the number of yearlings ($r = 0.79$, $p = 0.03$) than with the number of older ($r = 0.49$, $p = 0.27$) individuals.

Let's consider separately the reasons determining the numbers of young and old birds.

Number of Adults.—Evidently, two factors can influence the number of adults present: mortality and annual distribution over the range. The survival rate of birds older than one year varied slightly over the years (from 52 to 80%) averaging $68 \pm 6\%$. This means that mortality factors possibly changed little from year to year and essentially did not influence population dynamics (Tarasov 2005). It is remarkable that, in other parts of the range, reported survival rates of Willow Ptarmigan have been lower than in our study area: from 30–40% in Scotland (Jenkins et al. 1963) and Canada (Bergerud 1970, Hannon and Smith 1984) to 45–55% in Norway (Myrberget 1975, 1976).

Annual distribution of birds over a nesting area substantially depended on the strength of fidelity to their territories. The Willow Ptarmigan is known to be a territorially conservative species: adult birds occupy the previous year's

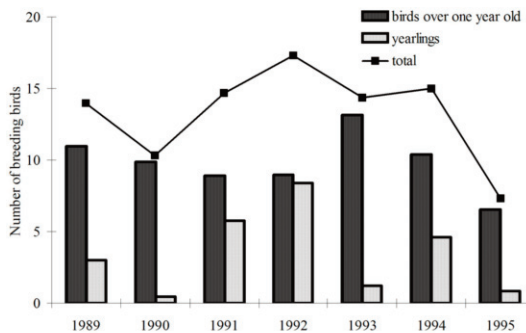


Figure 1. Dynamics of numbers of Willow Ptarmigan at Yaibari field station.

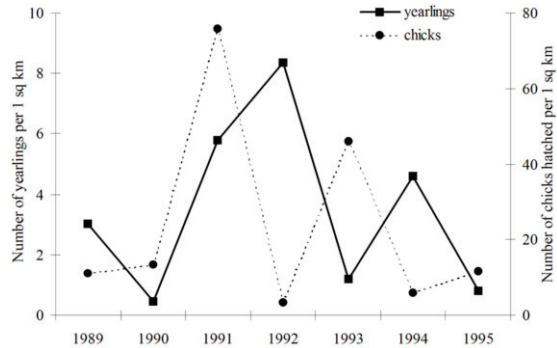


Figure 2. Nesting productivity of Willow Ptarmigan at Yaibari Station and numbers of breeding young birds.

territories for reproduction, as suggested by various studies at moderate latitudes (Jenkins et al. 1963, Voronin 1978, Schieck and Hannon 1989, and others). Adult populations, nesting from year to year on the same sites, form a basis of more or less stable density. It also offers the chance to consider, as principal causes of changes in numbers, the level of territorial aggressiveness and reproductive success (Bergerud et al. 1985).

However, in northern Yamal, an average of only $46 \pm 4\%$ of adults annually returned to the vicinities of previous nesting sites or even to the entire study plot, a much lower value than their annual survival rate. We (Tarasov 2005) previously found that the territorial fidelity of ptarmigan to the previous year's nesting area depends upon the time of spring arrival ($r = -0.92$, $p < 0.01$, $n = 6$ years). In years with a late spring, half of the males changed nesting areas. The proportion of the returned males in such years was significantly below their calculated level of survival. Possibly, the same tendency is characteristic of female Willow Ptarmigan nesting in the northern Yamal, but our data were insufficient to show it. Perhaps, in the northern range limit of Willow Ptarmigan, where long, cold springs often occur, some birds did not reach the study area, and remained to nest somewhere to the south, as suggested by similar data reported by

Pavlov (1974) for the Taimyr Peninsula. By his results, in years of late spring, the northern border of the Willow Ptarmigan range was displaced 1–1.5° latitude to the south.

Willow Ptarmigan near the northern border of their range seem to be polymorphic with respect to individual strategies of territorial behavior such that some birds easily change nesting areas when obstacles arise, while others return to former sites under any conditions. In the severe and unpredictable climate of the North, the conservative strategy is not always beneficial to birds. Such a strategy offers acquaintance with territory and neighbors, reducing time and energy expenditure for inspection of the nesting area and the establishment of territorial relations. The labile strategy allows birds to annually choose nesting areas with optimum living conditions within in a broadly unstable environment (see reviews: Sokolov 1991, Ryabitsev 1993).

Number of Yearlings.—The occurrence of ptarmigan in the northern Yamal can change depending on spring weather conditions which may influence the spring arrival and distribution of young birds in the same way adults are affected, and perhaps to an even higher degree. Range expansion in warm years occurs, apparently at the expense of young birds, as adults show higher fidelity to sites used in previous

years. As confirmation, for example, there were greater numbers of yearlings in early spring 1991, despite low nesting success in the previous season (Figure 2). We recorded the return of only one nestling among 109 marked in the previous year. In Canada, where the Willow Ptarmigan is a settled species, the philopatry index was estimated at 5% (Martin and Hannon 1987).

The average clutch size of Willow Ptarmigan in the northern Yamal ($n = 108$, including second clutches) was 8.82 ± 0.23 eggs. It varied widely among years, however, from 5.50 ± 0.65 to 10.59 ± 0.78 eggs. Analysis of the factors influencing fecundity of Willow Ptarmigan in the northern Yamal has shown that clutch size is entirely determined by the timing of spring arrival ($r = -0.91$, $p < 0.01$, $n = 7$ years), and this relationship is expressed much more strongly than at more southern latitudes. The difference can be explained by feeding on poor quality food in winter, leading to considerable loss of mass, and the longer the winter, the higher the loss, meaning that fewer resources are available for egg production (Tarasov 1997a). An inverse relationship of clutch size to nesting density was not observed, nor was any relationship between clutch size and the age of nesting birds.

The second important population parameter is reproductive success. Nesting (incubating) success was averaged from 103 nests at $36 \pm 2\%$ (unweighted average for 7 years = $37 \pm 11\%$). It depended on the abundance of predators, mainly Arctic Foxes (*Alopex lagopus*), which were a major cause of nesting mortality and ruined nests, and almost irrespective of the numbers of rodents (Tarasov 1997b). In more southern areas, the relationship between the reproductive success of ptarmigan and the population dynamics of murine rodents is more direct (Voronin 1978, Myrberget 1984). Rather high nesting success of Willow Ptarmigan in the northern Yamal ($86 \pm 3\%$ and $69 \pm 3\%$) was noted only in 1991 and 1993 when Arctic Foxes were not abundant. In total, 257

of 363 lost eggs (71%) were attributed to Arctic Foxes. Other predators, mainly skuas of various species (*Stercorarius* sp.), destroyed 79 eggs (22%). Two clutches which remained without hens (caught by Snowy Owls, *Bubo scandiacus*) were included in these records of egg loss. A similarly high impact of predation on egg mortality (80%) was noted on the Taimyr Peninsula (Pavlov 1974). Embryonic mortality, according to our data, occurred in $5 \pm 1\%$ of eggs (27 of 518), and its relationship with ptarmigan density is unknown.

The annual survival rate of nestlings in the first two weeks after hatching also varied considerably between years. This period in the life of ptarmigan is considered the most sensitive. In Yamal, 30–50% of chicks die during this interval (Dunaeva and Kucheruk 1941, Piminov 1985, Tarasov 1997b). If sharp cold snaps occur in the first days of brood life, especially those with strong wind, and rain or snow, these can negatively influence the subsequent numbers of juveniles. Precisely this factor is known to be one of the main influences on the population dynamics of tetraonid birds in moderate latitudes.

The survival rate of nestlings can also be associated with predation pressure (Tarasov 1997b). So it was in 1989 when a sharp depression in the numbers of lemmings (*Lemmus sibiricus*) and adult ptarmigan in the north of Yamal appeared under a strong pressure of Snowy Owls, such that practically all nestlings were lost prior to fledging, even though owls did not catch them at all. That year, females with broods or hatching clutches were effectively caught by owls, whereas the males left their territories and escaped in flocks. We found the remains of two of five marked, brooding females eaten by owls, and an additional clutch on the study plot remained without a brood hen. Practically all marked ptarmigan (both males and females) disappeared from the study plot, having united in flocks and moved to floodplain willow thickets, except for a few females still occupied

with reproduction. Later they possibly all died. Thus, in 1989, all the broods of ptarmigan were lost. Even less favorable conditions for juvenile survival may be expected when the two negative factors coincide: bad weather and predation pressure. Yet despite the contribution of mortality and distribution over the range of dynamics in numbers of juveniles, the number of yearling breeders nevertheless most strongly depended on nesting productivity in the previous year ($r = 0.83$, $p = 0.04$, Figure 2).

So, the main factors influencing dynamics of numbers of Willow Ptarmigan in the northern Yamal should be considered as predation and time of spring arrival. The first factor determines reproductive success, and the second determines the distribution of birds within a nesting area and their fecundity. The mechanism of regulation of population size through territorial behavior in the northern Yamal is not apparent.

Numbers of Birds and Habitat Capacity.— According to one of two basic hypotheses explaining the reasons of annual fluctuations in ptarmigan numbers (Bergerud et al. 1985), the latter are limited by spatial behavior which depends on population density. The birds not possessing territories form a population reserve and experience lower survival rates resulting from predators (Watson 1965) and epizootics (Jenkins et al 1963).

According to our data, however, increased numbers did not produce a population reserve, nor did they result in decreased intensity of reproduction or a lower return of adults to former nesting areas. Absence of self-regulatory mechanisms is one of the most interesting features of the ecology of Willow Ptarmigan living in the northern Yamal, and strongly suggests that the numbers of ptarmigan within our study area do not reach the utmost level of habitat saturation.

Low reproduction (mainly reproductive success) of Willow Ptarmigan in the study area

with high predation pressure is a plausible explanation. In 5 of 7 years of observations, nesting productivity remained at a level of 3–13 nestlings per km². Only in two years, 1991 and 1993, when there were practically no Arctic Foxes, and lemmings served as a sufficient food reserve for birds of prey, the productivity reached 46 and 76 nestlings per km², respectively. The generally high level of clutch mortality can be explained by the openness of habitats in the arctic tundra, its low vegetation and consequently, the absence of shelter. Even though we have observed an inclination of ptarmigan to nest in floodplain willow thickets (though their height does not exceed 20–30 cm), nesting success did not appear higher, but rather lower, than in open tundra (Tarasov 1997b), probably because willow thickets occupy only about 4% of the area and are regularly checked by predators. Ptarmigan fecundity is also low in the arctic tundra of Yamal when late snowmelt causes large weight loss among females (Tarasov 1997a).

It appears that clutch size may be geared to the number of nestlings that parents can warm. Willow Ptarmigan nestlings possess a weak ability to thermoregulate (Aulie 1976) and demand periodic warming, meaning that overly large broods are less adaptive in the extremely cold summers of the Yamal tundra. It may be that the necessity of warming nestlings can be more important in maintaining monogamy than the male protection of females and broods. In Canada, the removal (shooting) of males did not decrease female survival or increase female weight loss at hatching (Martin 1984), and these observations have formed the basis for assuming that the protective behavior of males is useful only for preservation of the right of paternity in the case of repeated nesting.

Another source of reduced fecundity may be that the period of egg-laying in the northern Yamal (unlike more southern areas) partially coincides with the summer molt of females with its energetic cost. At Yaibari Station, 16

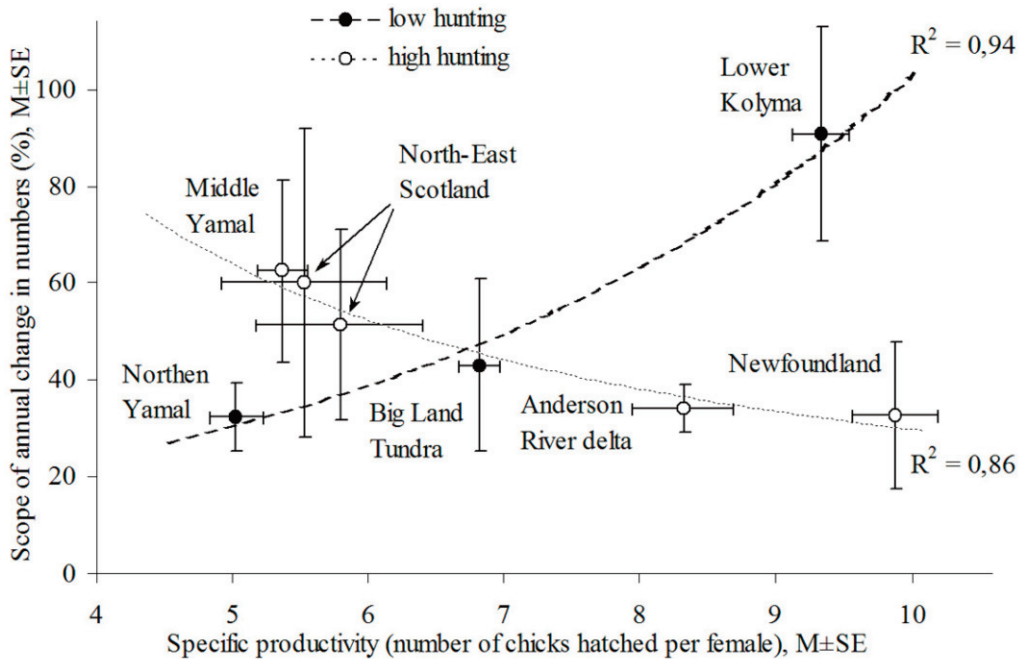


Figure 3. The relationship between the levels of variability of density and nesting productivity of Willow Ptarmigan in various parts of species range at different intensities of hunting.

marked females started laying when the molt had advanced an average of $63 \pm 8\%$ (on visual estimation). Egg-laying prior to molt completion is necessary because of the extremely short summer, but if the spring is cold and prolonged, egg dates are strongly shifted. Costs associated with both alternatives likely affected the fecundity of Willow Ptarmigan.

The factors listed above help to explain the rather low productivity of Willow Ptarmigan in the northern Yamal. Our calculation of average long-term productivity, taking into account our data on nestling survival, yields about three fledglings per pair of adults. In Norway, for example, the same ratio of young and adult birds was observed at the end of September (Myrberget 1974), 2.5 to 3 months after fledging.

Stability in Numbers.—It would be logical to assume that nesting productivity not only largely determines population numbers, but also the degree of their variability. For compar-

ison, we took eight geographical areas where long-term population studies of Willow Ptarmigan have been made: northern Yamal Peninsula (Russia, 1989–1995, our data), middle Yamal (Russia, 1982–1993, Ryabitsev 1993), Bolshezemel'skaya tundra (Republic Komi, Russia, 1970–1975, Voronin 1978, 1991), the Kolyma River (northeastern Russia, 1978–1987, Andreev 1988), two areas in Scotland (a highland and a lowland, 1957–1961, Jenkins et al. 1963), and two areas in Canada (Anderson River, Northwest territories, 1958–1986, Hannon and Barry 1986; and a Newfoundland Island, 1955–1965, Bergerud 1970).

It appears that the intensity of hunting can influence these relationships (see Figure 3). When the influence of hunting is insignificant, but an increase in ptarmigan number is effectively checked by predators (as, for example, in the northern Yamal and in Bolshezemel'skaya tundra), numerical fluctuations are insignificant. It is also possible to

observe 3–4-year cycles, with the peaks coinciding with peak lemming years or following these years.

In Bolshezemel'skaya tundra, where nesting productivity of Willow Ptarmigan is significantly higher than in the northern Yamal, there appears to be higher variability in numbers. But the widest scope of annual fluctuations (more than 90%) has been noted at the Kolyma River where practically all predator pressure is absent, and number of ptarmigan is determined mainly by food conditions (Andreev 1988). In the process of numerical increase, ptarmigan destroy the annual sprouts of the willows, the basic source of winter food, and then there follows a sharp decline in ptarmigan number, followed by gradual increase with the process of resource restoration. Large year-to-year changes in numbers of ptarmigan are accompanied by high productivity, whereas low productivity promotes the maintenance of relatively stable numbers. It also appears that, in the absence of such factors as predation and hunting, population self-regulatory mechanisms are insufficient to effectively restrain population growth.

Another picture emerges in conditions of intensive hunting. Effect of hunting in the middle Yamal Peninsula is stronger than in the northern Yamal, and fluctuations in numbers are higher, although nesting productivity is not much greater. Perhaps the relatively stable numbers at the limit of the range are due to undersaturation of habitat, although (it would seem) it should be more volatile in this area. In Scotland and Canada, where from 15 to 40% of populations are annually withdrawn, with sufficient levels of productivity, the average difference in nesting density between years is low, on the order of 30–50%. Those conducting studies in these areas (Jenkins et al. 1963, Bergerud 1970, Hannon and Barry 1986) often mention that hunting has little influence on the dynamics of those populations because the losses compensate for other forms of mortality. Apparently, however, this is not always true.

First, when hunting is well organized, it tends to remove the maximum number of birds. It is also possible that population size is supported at the level corresponding to the greatest numerical growth rate. Secondly, Lack (1965) showed that, in those places where the removal of birds is lengthy and intensive, food resources and nesting habitats, as a rule, are artificially improved, and the number of predators ruining nests is actively regulated. Voronin (1978), analyzing clutch sizes of ptarmigan in Bolshezemel'skaya and Timansky tundra, concluded that high selective elimination — and hunting is exactly like this (Schwarz 1969) — has led to selection in the Timansky population of Willow Ptarmigan for increased fecundity. These data suggest that hunting, on the one hand, can promote increases in reproduction, and on the other hand, the maintenance of more or less stable population size. More stable densities may therefore be expected in conditions of high predation pressure or intensive hunting. When such factors are relaxed, ptarmigan numbers become more variable.

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