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Winter Adaptations in the Willow Ptarmigan

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ABSTRACT. The willow ptarmigan, *Lagopus lagopus*, dwells in a vast area with a variety of climatic and biotic conditions. Populations from northeast Asia must cope with extremely low temperatures along with progressive depletion of food resources throughout the winter. Being unable to roost in the snow at −40°C, a ptarmigan's daily life would cost 3.2-3.5 basal metabolic rate (BM), but by burrowing in snow for up to 21 hours per day, the bird saves at least 1.0 BM.

To meet daily energy demands on a midwinter day a ptarmigan needs about 60 g of food (dry weight), consisting mostly of willow buds and twigs. Early in winter the diet contains 12-15% protein and 20-25% fiber, declining later to 7-8% protein and increasing up to 35% fiber. Nitrogen concentration, crucial for food digestibility, declines by half (from 0.35 to 0.18%) during the six winter months. Nitrogen also causes increased food consumption in a feedback pattern. Nevertheless, many birds lose body weight constantly. To recover losses they need a more nutritious diet after the snow starts to melt.

Thus, the willow ptarmigan's adaptation to the polar winter appears as an individual balancing act within a few specific limits. Higher density of conspecific birds, colder winters and/or later springs may cause physiological damage to individuals, which eventually would lower the reproduction rate within the breeding population.

Key words: willow ptarmigan, winter ecology, metabolic rates, food quality, fiber digestion

RÉSUMÉ. Le lagopède des saules, *Lagopus lagopus*, habite un vaste territoire où prévaut une variété de conditions climatiques et biotiques. Les populations du Nord-Est asiatique doivent faire face à des températures extrêmement basses ainsi qu'à une diminution progressive des ressources alimentaires au cours de l'hiver. Comme le lagopède ne peut pas se percher sur la neige à -40 °C, sa survie quotidienne lui coûterait un taux de métabolisme basal compris entre 3,2 et 3,5 unités; mais en s'enterrant sous la neige jusqu'à 21 heures par jour, l'oiseau épargne au minimum 1,0 unité de métabolisme basal.

Pour répondre à sa demande quotidienne en énergie durant une journée du milieu de l'hiver, un lagopède a besoin d'environ 60 g de nourriture (poids sec), constituée principalement de bourgeons et brindilles de saule. Au début de l'hiver, son régime se compose de 12 à 15 % de protéines et de 20 à 25 % de fibres, quantités qui, au cours de l'hiver, diminuent jusqu'à 7 à 8 % pour les protéines, et augmentent jusqu'à 35 % pour les fibres. La concentration en azote, qui est cruciale pour la digestibilité alimentaire, baisse de moitié (de 0,35 à 0,18 %) au cours des six mois d'hiver. L'azote entraîne aussi une consommation alimentaire accrue selon un schéma de rétroaction. Beaucoup d'oiseaux cependant perdent constamment du poids. Pour récupérer ces pertes, ils ont besoin d'un régime plus nutritif dès que la neige commence à fondre.

L'adaptation du lagopède des saules apparaît donc comme un exercice d'équilibre individuel, à l'intérieur de certaines limites spécifiques. Une densité plus élevée d'oiseaux qui se nourrissent ensemble, des hivers plus froids et/ou des printemps tardifs peuvent causer des dommages physiologiques aux individus, dommages qui, à la longue, feraient baisser le taux de reproduction dans la population reproductrice.

Mots clés: lagopède des saules, écologie hivernale, taux de métabolisme, qualité alimentaire, digestion des fibres

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РЕЗЮМЕ. Белая куропатка, Lagopus lagopus, населяет обширный ареал с большим разнообразием климатических и биотических условий. На северо-востоке Азии ее популяции сталкиваются с наиболее низкими температурами при последовательном сокращении запаса пищи в течение зимы. В отсутствие возможности закапываться на ночь в снег свободное существование куропатки было бы эквивалентно 2.2 - 3.0 базальных метаболизмов (BM) при -40 С. Проводя около 21 ч/сутки в толще снега, куропатка выигрывает до 1.0 BM. Чтобы компенсировать суточные потребности в энергии, куропатке в середине зимы нужно около 60 г корма (сухой вес), который состоит из ивовых побегов и почек, содержащих в начале зимы 12-15% протеина и 20-25% клетчатки. Позднее, питание обедняется протеинами (7-8%) и обогащается клетчаткой (до 35%). Установлено, что концентрация протеинов в пище критически влияет на её переваримость (DC). Изменения в качестве питания сопровождаются падением коэффициента DC от 0.35 в декабре до 0.2 в апреле и вызывают необходимость употреблять всё возрастающий обьем корма. Птицы постепенно теряют в весе, и чтобы компенсировать истощение они должны перейти на более питательные корма после снеготаяния. Таким образом, адаптация белой куропатки к полярной зиме предстает как балансирование особей в рамках нескольких специфических ограничений. Более высокая численность зимующих птиц, более крепкие холода или запоздалая весна - любая из причин может ухудшить физиологическое состояние особей, что в конечном итоге проявляется в снижении репродуктивного успеха популяции в летний сезон.

Ключевые слова: белая куропатка, зимняя экология, уровни метаболизма, качество кормов, переваримость клетчатки

INTRODUCTION

Among 19 species of the grouse family (*Tetraonidae*), the willow ptarmigan (*Lagopus lagopus*) is unique in several respects. It occupies a huge circumpolar area, the biggest in the family, extending from 48 to 76°N latitude and comprising a variety of climatic and biotic conditions. In addition to seasonal sexual dimorphism, the willow ptarmigan undergoes the most profound seasonal changes in morphology, physiology and behaviour. In many populations, seasonal migrations, as opposed to the residential habits of most other grouses, cover distances of several hundred kilometres. The willow ptarmigan, monogamous throughout the breeding season, produces up to 15 eggs per clutch, more than any other grouse species. In winter, the willow ptarmigan browses coarser foods, as compared with other grouse, and must meet

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more competitive pressure from the mountain hare (*Lepus timidus*) and, in some areas, the moose (*Alces alces*), both of which rely on the same willow thickets. All these features seem to be involved in creating the most remarkable character of the species — an ability to cycle with a wide geographical variety in cyclic periods and densities.

Low-shrub southern tundras criss-crossed with small rivers seem to be the optimal habitat for ptarmigan reproduction. But since these areas are covered by snow for about eight months a year, they are practically useless for these birds other than during the breeding season. Hence the birds wander southwards to larger valleys with denser and taller willow growth. In mountainous areas similar events may cause altitudinal movements.

Seasonal changes in habitat and cyclic changes in numbers both create a very specific pattern of tolerance and survival in the willow ptarmigan, which obviously prospers in the changing and severe polar environment.

The discussion here provides a framework for answering two questions: 1) what are the eco-physiological needs and constraints for an individual bird's survival in winter and 2) how do individuals cope with changing resources for the long-term survival of the species? This study is based on my own observations and experiments. The methods used and some principal results of this study have already been published (Andreev, 1981, 1982). A generalized summary of this material enhanced by further original data provides the basis for this paper. I hope it will add to the knowledge and understanding of the biology of this key arctic species established by my enthusiastic colleagues and predecessors (Semenov-Tian-Shanskii, 1960; Irving, 1960, 1980; Watson and Moss, 1980; Watson and Jenkins, 1964; West, 1968, 1972; Perfil'ev, 1975; Voronin, 1978; Hoglund, 1970, 1981; Brittas, 1984; Potapov, 1985; Hudson, 1986; Myrberget, 1975, 1987).

MATERIALS AND METHODS

Data for this study come from two localities in northeastern Asia: in 1979-82 in the Lower Kolyma area (69°N) and in 1979-88 on the Kolyma Upland (60-61°N), northwest of the city of Magadan, R.S.F.S.R. (Fig. 1).

Field respirometers to measure basal metabolic rates (closed system) were constructed by Dr. M.A. Vayn-Rib and myself and have been described in detail in Andreev (1986a). The system consists of two parts: the "cold" or "outside" plastic

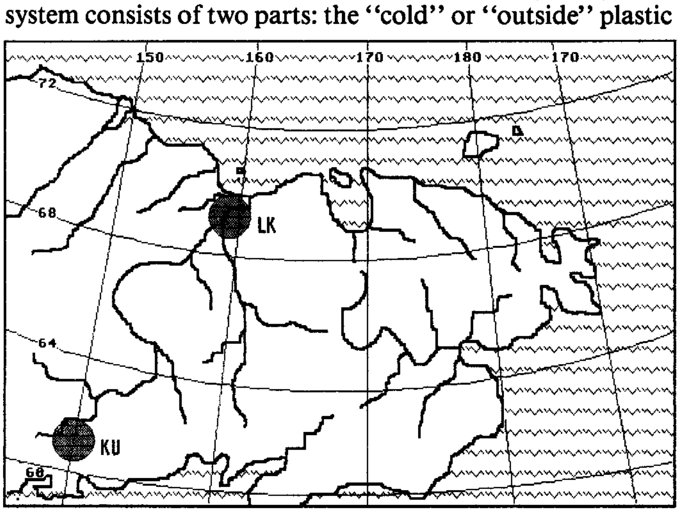

FIG. 1. Map of northeast Asia showing the study areas — LK, Lower Kolyma; KU, Kolyma Upland — and degrees of latitude and longitude.

chamber for placing a bird at ambient air temperature, and the "warm" box filled with oxygen (or air), which is gradually replaced by water drops falling with a frequency proportional to the intensity of energy metabolism. The second part is set in the laboratory under a constant temperature of +20°C along with the device counting and registering the number of drops through constant intervals. The chambers are connected to each other with a thin gum-elastic tube, and the carbon dioxide from the cold chamber is extracted by dry potassium alcali pellets, which work effectively down to −50°C.

Three tame willow ptarmigan raised from eggs during the summer of 1985 were used for estimating temperature and heat flow in the snow burrow experiments conducted from December 1985 to January 1986 at the Aborigen research station in the Upper Kolyma. Thermistors and semiconductor heat flow discs, along with industrial automatic millivoltmeters, were used in these experiments (Andreev, 1986a). The method of placing a bird into snow and protecting it from predation are described in Andreev (1977). The idea of the experiments was to place a grouse into a transportable floorless cage, 3.0 × 3.0 × 1.5 m in size, made of wood and nylon seine net, and to set it at a fresh snow site. Thermocouples were connected with the laboratory by wire. It took at least two nights to acquaint the laboratory-raised ptarmigan with snow and train them to use snow as protection against frost.

To do this, I first prepared hand-made snow burrows with an open roof and tunnel. After placing the birds inside the burrow, the tunnel and the roof were gradually closed with pieces of packed snow. Later, when the birds started to construct burrows by themselves, I put the couples through small holes in the roof or tunnel and closed them by freezing and using thin wood sticks (Fig. 2).

FIG. 2. A willow ptarmigan being trained to roost in the snow. The wires connecting the couples with the ink recorder are seen on the snow surface as well.

For food preference and food digestibility experiments, these same birds were placed in separate cages, 0.5 × 0.5 × 0.5 m, under a constant temperature of −10°C. Food consumption, excretion of droppings and digestibility were measured at 72 h intervals. Routine agricultural analysis procedures were used to estimate the chemical composition of experimental and natural foods and excrements.

Energy contents of the food and droppings were estimated either with oxygen bomb calorimeters or by transforming data on chemical composition to energy content by standard energy equivalents of proteins (21.77 kj·g^{-1}), carbohydrates (18.84) and lipids (38.94).

To analyze natural foods, crops of shot birds were dried, and the percentage of different plant species and different parts of the same species were estimated by dry weight. For pieces of willow twigs, average diameter and weight were estimated on the basis of 100-150 samples. Before preparing crop samples for chemical analysis, food items were washed with warm water to neutralize the influence of crop enzymes on protein content. The amount of grit in the gizzards of shot birds and the average weight of a single grit stone was measured to determine seasonal changes in grit abundance.

The digestibility of natural foods was estimated by comparing the two statistical trends: crop weight of birds shot through the night and amount of droppings accumulated in the burrows of these same birds (Andreev, 1980).

Time activity budgets were described statistically by combining a few hundred observations from both localities. In addition, direct observations of foraging techniques and intensity of feeding birds were made at 20-60 min intervals.

RESULTS AND DISCUSSION

Basal Metabolic Rate

The survival of an individual in the polar winter is a complicated phenomenon involving a certain number of variables eventually integrated in a positive cost-benefit balance. Estimation of eco-energetic parameters might be a suitable way to measure the degrees of this fragile equilibrium and its limits. Consumption of willow food to gain energy and roosting in the snow to conserve energy are the two principal adaptations of the willow ptarmigan for withstanding periods of severe conditions. Other adaptations are the dense and thick mimicry plumage, snowshoe feet with a track pressure of 12-14 g·cm^{-2} (the lowest in the grouse family) (Andreev, 1980) and a beak strong enough to trim frozen willow twigs. Operating complementarily, these features are effective tools for dealing with prevailing frost, snow and tough shrubs. Generally speaking, feeding and roosting tactics depend on energy expenditures and food demands, which in turn depend on two principal measures of a homeotherm's homeostasis — the basal metabolic rate (BM, w) and the thermal coefficient (CdT, w·°C^{-1}). Derivative from these two is the standand metabolic rate (SM). (The terminology and symbols are from Kendeigh *et al.*, 1977.)

The following calculations are based on a mean of world data on the BM of willow ptarmigan (Table 1), 3.3 w (watts) as a reference level for a 600 g bird in winter. Accordingly, the thermal coefficient (C) is 0.084 w·°C^{-1}. Integrating these parameters, the lower critical temperature (tlc) would be +0°C.

It is noteworthy that a 600 g generalized grouse would have a basal metabolic rate of 3.6 w (Andreev, 1988a) and a generalized nonpasserine bird of the same weight would have a BM 1.2 times less than that of ptarmigan, i.e., 2.78 w (Kendeigh *et al.*, 1977).

From these estimates, I have calculated the standard metabolic rates (SM) for a ptarmigan roosting under a range of winter temperatures (SM = BM + C* [tlc − ta]) (Table 2).

As the birds spend most of the midwinter day roosting within snow burrows, their daily energy expenditures obviously depend on the temperature within the burrow. What are those temperatures?

A few correct measurements on temperatures in grouses' snow burrows (ts) have already been made to predict the level in the willow ptarmigan within 5–10° below thermoneutrality (Andreev, 1977; Marjakangas *et al.*, 1983; Korhonen, 1980). Thus, the standard metabolic rate of a roosting bird (NM = SM) might also be predicted to be about 1.1-1.2 BM.

Direct measurements of temperatures and heat flows in the roosting ptarmigan (Table 3) support these estimates. Measurements carried out through 94 h (7 nights) reveal the ts to be rather stable (from −16 to −12°C, −14° on average), whereas the ambient temperature (ta) changed twice as much (from −33 to −16°). This means the snow burrow temperature (ts) is effectively regulated by the bird.

The heat flow through the snow roof (qr) changed accordingly, being negatively correlated with ta (r = −0.86). As one can infer from the measurements of 24 December 1985 and 4 January 1986, the sideward heat flow (qs) is 1.46 times and the downward flow (qd) −1.6 times higher than the upward flow (qr). This implies an additional function of snowshow feathers to prevent the burrow's snow floor from melting under direct contact with the bird's body.

In these experiments the NM value, measured directly as the difference between energy consumed before sleeping and that excreted throughout the night, was found to be 3.9 w

TABLE 1. Data on basal metabolic rates of willow ptarmigan

Sources	Body weight (g)	BM, w	C, w·°C	tlc, °C
	SUMMER			
West, 1972	539	3.82	0.118	+ 7.7
Dolnik and Gavrilov, 1985	524	3.12	0.119	+12.0
Andreev, unpubl. data*	575	3.10	0.120	+14.0
SD	49	0.41		
AVERAGE	545	3.35	0.119	+12.0
	WINTER			
West, 1972	590	3.42	0.073	− 6.3
Auli, 1976	548	3.61	0.08	− 5.0
Mortensen and Blix, 1985	658	2.81	0.085	+ 7.1
Dolnik and Gavrilov, 1985	567	3.35	0.108	+ 9.0
Andreev, unpubl. data**	590	3.0	0.071	− 5.0
SD	21	0.40		
AVERAGE	590	3.24	0.083	0.0

*18 measurements at 0 to +20°C.
**15 measurements at 0 to −30°C.

TABLE 2. Temperatures and metabolic rates within snow burrows

t_a	0	−10	−20	−30	−40	−50
SM, w	3.3	4.1	5.0	5.8	6.6	7.5
SM/BM	1.0	1.2	1.5	1.8	2.0	2.3

TABLE 3. Experiments on heat environment in roosting *L. lagopus*

Date	Tn (h)	ta	ts1	ts2	qr	qd	qs	qb	NM (w)
		(°C)			(w·cm^{-2})				
23.12.85	15	−31	−17		1.5				3.5
SD			1.8		0.15				
23.12.85	15	−10						5.45	
24.12.85	10	−24		−15.6	2.4	3.55		4.66	5.3
SD				1.5	1.95	1.1		0.21	
25.12.85	13	−33			3.32				3.25
SD					0.35				
26.12.85	13	−18		−12.1			3.02	5.5	
SD				1.96			1.5	0.3	
27.12.85	13	−16		−12.9	2.4	5.7			2.91
SD				1.93	0.6	1.7			
4.01.86	15	−26	−11.0	−16.6	3.0		4.8		4.7
SD			0.4	0.3	1.0		0.72		
AVERAGE		−25		−14.3					3.9

Tn — longevity of the experiment.
ta — ambient temperature as measured 1.0 m above snow surface.
ts1 — burrow air temperature as measured between bird's back and the sealing.
ts2 — burrow temperature as measured on the upper surface of plumage.
qr — heat flow through the roof.
qd — heat flow downwards.
qs — heat flow sidewards.
qb — heat flow from the back skin surface through plumage.
NM — mean level of the night metabolism measured as the difference between energy consumption in the evening and energy excretion through night, corrected to Wb = 600 g.

in birds weighing about 600 g, or 1.2 BM. This is quite within the measured temperature range and the SM values predicted above. In the free-living birds, wintering at temperatures much lower than those of experimental birds (−40 to −45°C), the NM was found to be about 4.3 w, or 1.3 BM (Andreev, 1982). Additional energy requirements for warming up the burrow and heating frozen food in the voluminous crop might account for this difference.

Thus, by roosting in the snow, a ptarmigan would save up to 1.0 BM under −45°C. Being forced to come out of the snow in the morning to feed, the bird must increase its energy losses to compensate for thermoregulation and such movements as flight, walking and browsing. Along with night losses, these needs determine the level of daily energy expenditures (DEE). Clearly, the baseline for estimating DEE would be the NM value, corrected by activity and thermoregulatory expenditures.

Time Activity Budgets

The willow ptarmigan commonly has two peaks of feeding activity a day (Tam, morning; Tae, evening), separated by a resting period (Tr). Of the three variables, Tr is most stable, being about 2.5 h·day^{-1} (Andreev, 1982). In December a willow ptarmigan spends about 2 h feeding in the morning and about the same in the evening. As days become longer the feeding activity also increases (Fig. 3).

These birds that winter in the mountainous areas frequently visit rare snow-free places to collect grit. In the Lower Kolyma no stones occur in the soil (Fig. 4). This obviously leads to a specific constraint in the bird's digestive ability.

Ptarmigan usually feed in flocks whose size is clearly related to the abundance of food. They follow two polar patterns of eating — a "slow" and a "fast" one. In the slow pattern, a morning routine, they eat 6.8-12.8 g·h^{-1} (dry wt) of food as they walk along the shrub willows (*Salix pulchra, S. krylovii*) or dwarf birch (*Betula middendorfii, B. exilis*) carefully selecting twigs and buds. The fast pattern, when they eat up to 30 g·h^{-1} is followed during extreme frosts and as they are pressed by time shortage in evenings; this greater food intake is achieved by browsing in the crowns of bigger willow species (*S. lanata, S. schwerini, Chosenia arbutifolia*) but is less nutritious. In this case a ptarmigan can cut as many as 120 twigs a minute. Thus, by combining the preferable ground feeding ("slow") with the more accessible but, in some respects, less advantageous feeding in the crowns ("fast"), a ptarmigan achieves the most appropriate balance between gains and losses (Fig. 5).

Daily Energy Expenditures: Predictions and Measurements

The above data establish principal relations within an individual's energetics and enable us to determine quantitative limits for DEE in free-living birds. I simulated it for the two geographical localities, taking into consideration the data on day length, snow thickness and ambient temperatures (Table 4). According to the calculations (Fig. 6), the predicted DEE level changes between 1.3 and 1.8 BM (1.4 on average), with the peak in early winter (December) for birds dwelling in continental localities (the Kolyma Upland). The peak is obviously caused by a shortage of snow cover during the cold of October and November. The simulated DEE is lowest in midwinter and increases toward spring, along with day length and the Ta value. According to these estimates, additional energy expenditures while out of the snow during the day are equal to 0.1-0.6 BM. This suggests that if the habitat lacks snow, living outside under the extreme cold conditions of NE Asia (−45 to −55°C) would cost a ptarmigan 2.2-3.0 BM.

In the free-living birds the daily metabolizable energy (ME) might be a suitable basis for estimating DEE values. Assuming body mass is constant, then DEE = ME.

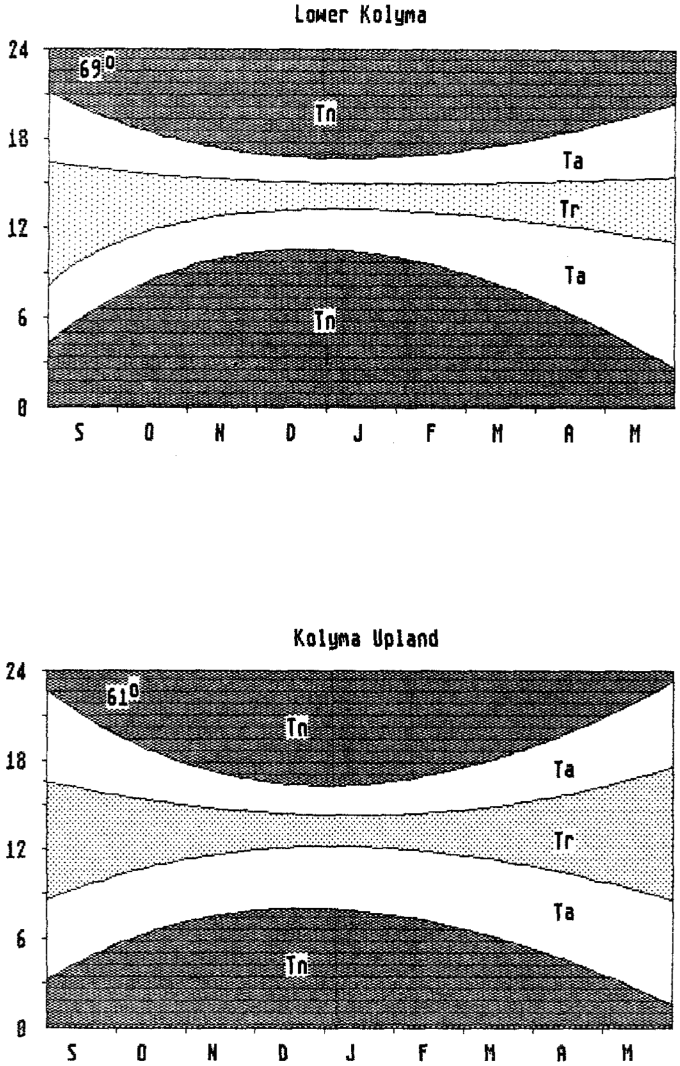

FIG. 3. Change of time activity patterns of willow ptarmigan through the winter in the two localities. Transitional lines between the night roosting period (Tn), the feeding period (Ta) and the day resting period (Tr) are averaged based on the activity statistics and observations and corrected to the local time (vertical scale, in h). Months are indicated along the horizontal scale.

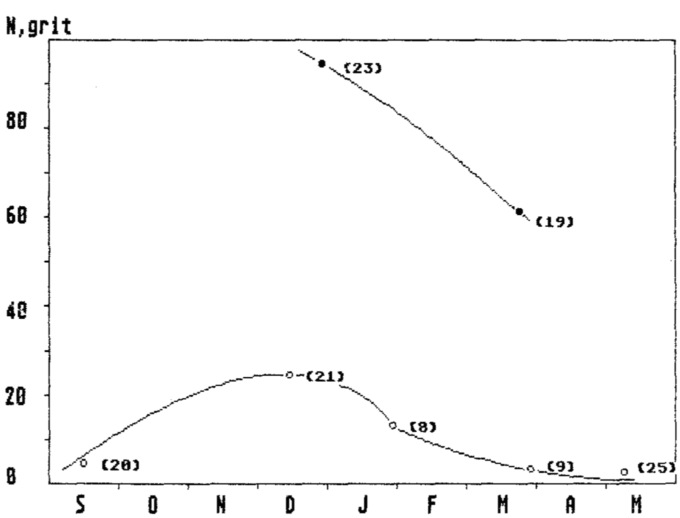

FIG. 4. Seasonal changes in average grit number (N) in the willow ptarmigan gizzards in the Lower Kolyma (open circles, lower curve) and in the Kolyma Upland (black circles, upper curve). Sample size is given in parentheses.

To measure actual values for ME one needs to know the amount of daily food intake (Mf, g·day^{-1} and the quantity of droppings (Md) and caecal excrements (Mc, g dry weight per 24 h), along with data on energy contents of food and droppings. All these parameters are taken from my studies published elsewhere and used for calculations here (Andreev, 1982; Fig. 6).

All measured ME points appear more or less below the predicted lower DEE level and are based on large sample sizes. The difference is most prominent in the spring, implying that the birds must lose body weight to meet DEE demands. Indirectly, this conclusion is supported by the body weight statistics (Fig. 7).

The rates of energy excretion were found to increase in parallel through winter in both study areas (Fig. 8), reflecting changes in the food quality and birds' digestive ability. The digestibility (DC) was also found to decrease to half in the course of winter: from 0.35-0.40 in December to 0.18-0.22 in April (Andreev, 1982, 1986b). So assuming DC changes gradually and DEE = 425 kj·bird^{-1}·day^{-1}, energy content of the diet (20.5 kj·g^{-1} and DC ≃ MEC), the rate of daily food consumption would increase from 56 g·day^{-1} in mid-winter to 104 g·day^{-1} in spring. The calculations on the basis of the amount of droppings — Mf = (Md + Mc) / (1-DC) (Fig. 8) — will provide us with a similar result.

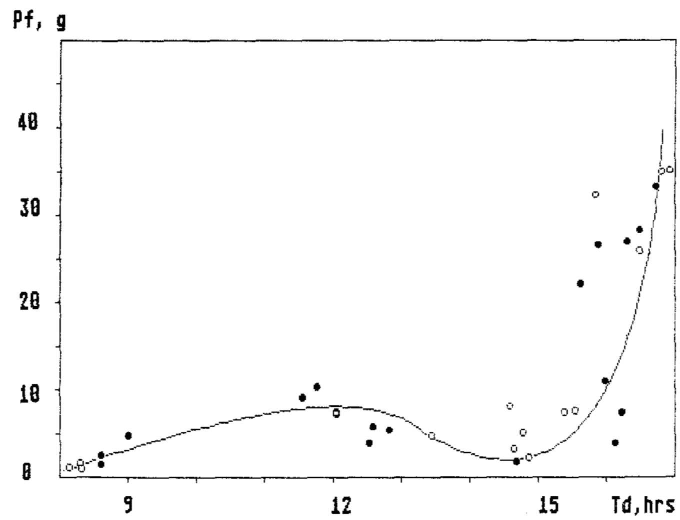

FIG. 5. Dry weight of crop's content (Pf) indicates "slow" (8-12 h) and "fast" (15-18 h) patterns of feeding behaviour in Lower Kolyma (open circles) and Kolyma Upland (black circles). For both localities data were collected in February 1980. Horizontal scale (Td), time of day (hrs).

TABLE 4. Winter environment parameters for two localities in northeast Asia

	Average daytime temperatures (°C)		Average day-length periods (h)		Average snow-cover depth (cm)	
Month	LK[1]	UPL[2]	LK	UPL	LK	UPL
O	−11	−14	11.4	11.2	15	10
N	−22	−26	7.0	9.0	30	22
D	−29	−34	5.2	7.2	35	32
J	−33	−37	5.6	8.4	45	40
F	−34	−35	9.8	11.2	50	48
M	−25	−28	13.0	13.4	55	50
A	−18	−15	17.2	16.0	45	45

[1]Data for Lower Kolyma.
[2]Data for the Kolyma Upland.

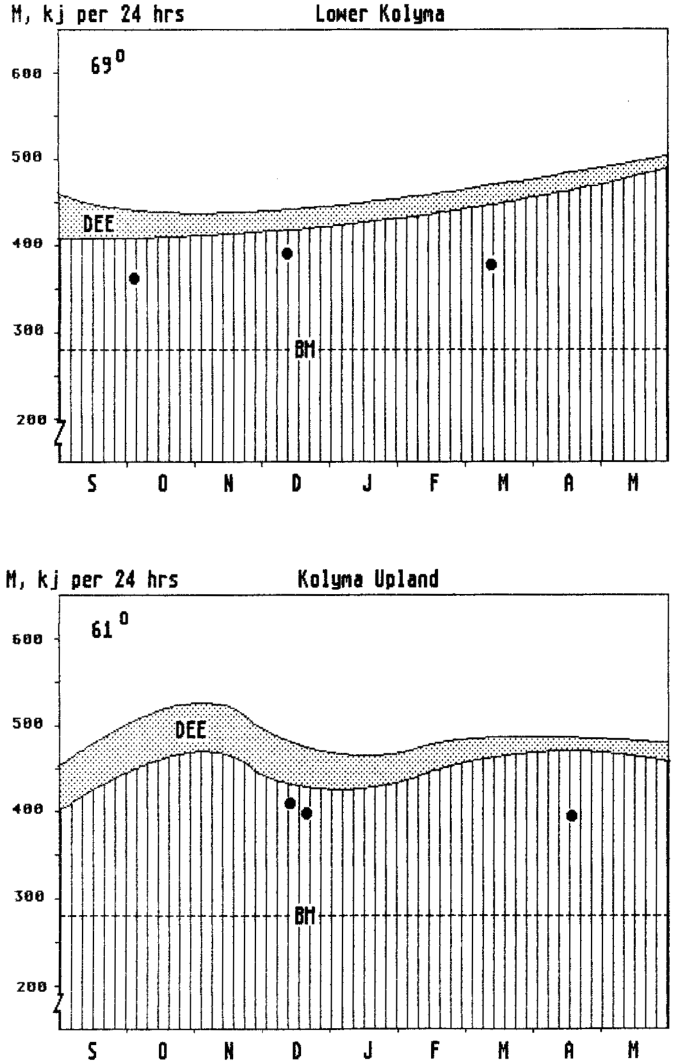

FIG. 6. Predicted (curves) and measured (points) values for DEE for the two localities. Dotted horizontal line shows the level of the basal metabolic rate. Staying inside or outside the snow burrow in the daytime accounts for the two limits of DEE. The vertical scale (M) shows the metabolic rate of a 600 g willow ptarmigan in kilojoules per day; the horizontal scale indicates months.

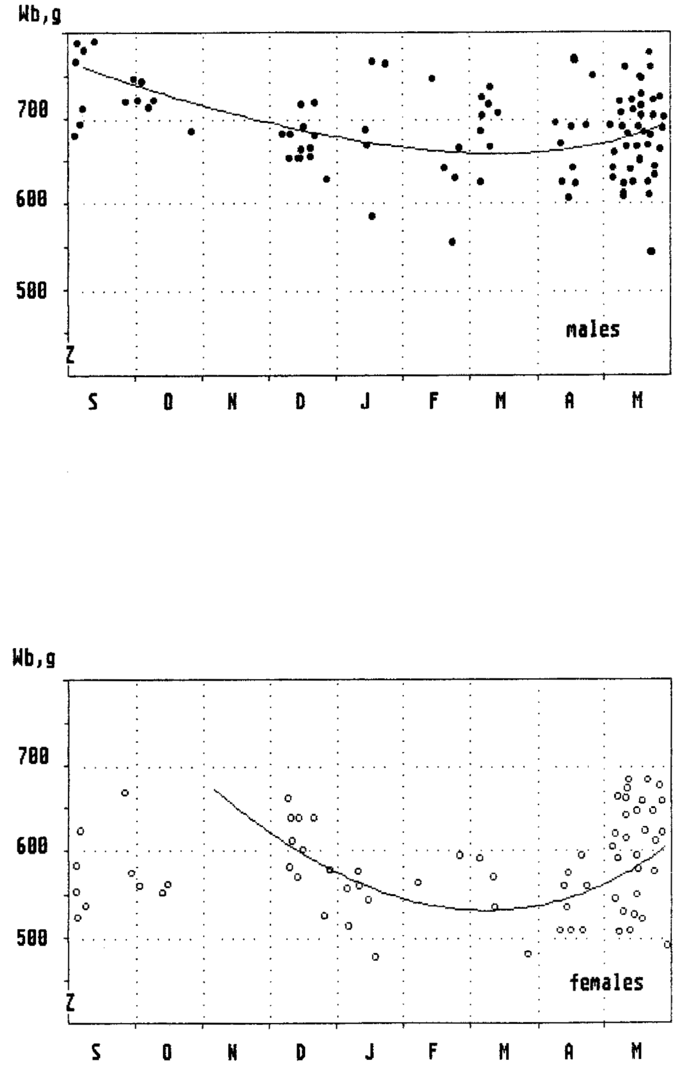

FIG. 7. Body weight (Wb, in grams) statistics for the willow ptarmigan males (upper plot) and females (lower plot) from Lower Kolyma. In both sexes it decreases from October to April (horizontal scale), then starts to increase. Data for a range of years (1979-83) are combined.

Changes in Food Quality through the Winter

If birds lack energy and consume more food to meet the demands, why then can they not browse even more to keep the body mass stable?

When able to select from a variety of food items, the willow ptarmigan prefers a diet containing 13-18% protein, 10-20% fiber, 5-10% lipids and up to 50% carbohydrates (Moss and Hanssen, 1980; Andreev, 1986b). Thus, carbohydrates may cover up to 75% of a bird's metabolic requirements. Proteins and lipids together will constitute 20-23% ME, the remaining 2-5% being provided by fiber. Most natural winter foods (willow buds and twigs) contain less protein (7-11%) and more fiber (25-32%) than ptarmigan prefer, so the fiber digestion is needed to generate additional energy.

Several important and intriguing features emerged from the experiments on willow ptarmigan nutrition (Andreev, 1986b). First, the more fiber a diet includes, the more energy (up to 30% ME) the fiber will produce. Second, the digestibility of food and that of fiber crucially depends on the bird's nitrogen balance (Fig. 9). This implies that small variations in protein concentration in natural diets may cause comprehensive changes in individual metabolism. Therefore feeding for more nitrogen becomes an important priority for the free-living birds.

Visible abundance of willow shrubs in winter habitats of willow ptarmigan does not reflect the quality of a bird's nutrition, since the thickness and density of snow alter foraging conditions unpredictably. Changes of any sort have a negative effect during the course of winter, the differences being quantitative as well as qualitative.

For example, in autumn ptarmigan in the Lower Kolyma ate willow twigs 0.8-1.5 mm in diameter and dwarf birch buds. By December, when snow cover was deeper, the diet included willow twigs and flower buds. The buds found in crops usually disappeared by March, while twigs became thicker and heavier (Fig. 10). Finally, when twigs became too thick for the birds to cut, they were replaced by willow bark (Fig. 11). The bark itself is a fairly nutritious food, but it requires too much time for a bird to obtain a sufficient amount. This shift in crop contents was most obvious in years of deep snow and high density of ptarmigan and hares.

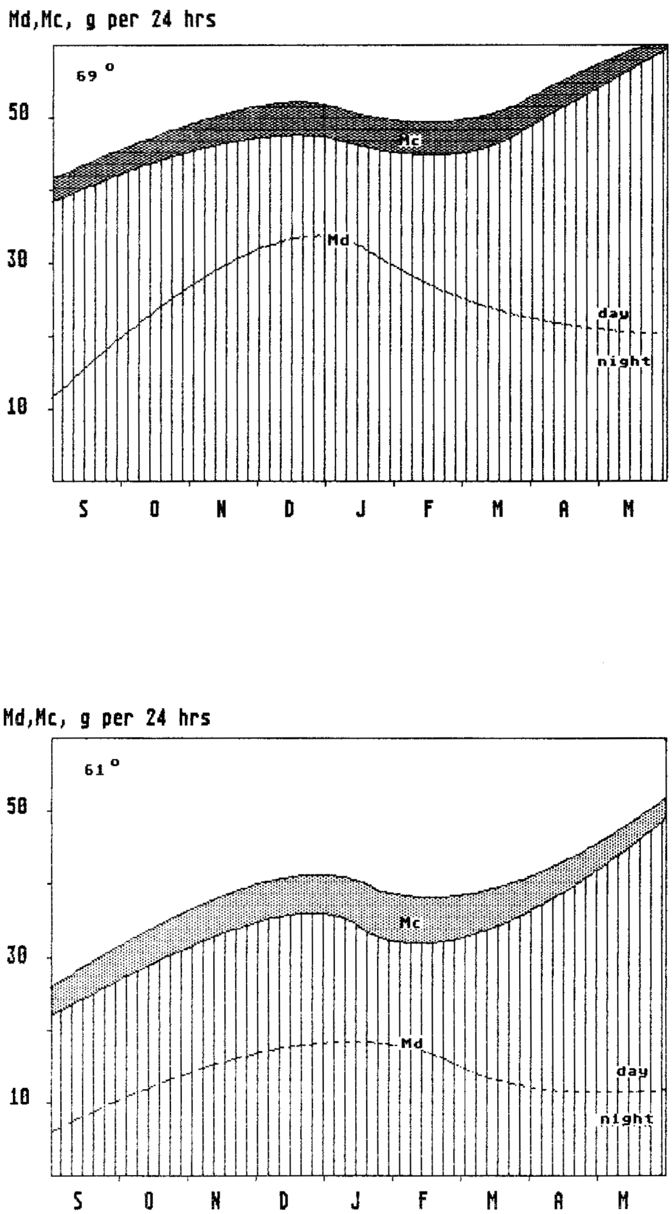

FIG. 8. Statistical trends of daily amount of woody droppings (Md) and caecal excrements (Mc) (both in grams dry weight per day) in Lower Kolyma (upper plot) and the Kolyma Upland (lower plot) throughout the winter (horizontal scale, months). Night samples were collected directly from snow burrows (about 100 samples from each locality). Data for the daytime were calculated from tracking, from the amount of droppings in daily burrows and from the data on activity patterns, assuming that the rate of diurnal excretion is 1.5 times greater than that of the night (Moss, 1973).

At the same time the chemical composition of foods changed as the season progressed. The percentage of fiber tended to increase continually, while protein concentration decreased. As soon as the snow begins to melt or blow away, these changes may be reversed (Fig. 12). Although not statistically proved, this trend coincides with the obvious changes in crop contents. As already mentioned, digestibility of natural diets decreases in parallel with food and grit depletion and weight losses. The process, which is more marked in the north and in males, depends also on the number of birds, ambient temperatures, snow cover and frequency of winds. Together or separately, each of these factors may modify the diet quality and availability, which in turn may bring an individual to certain physiological limits.

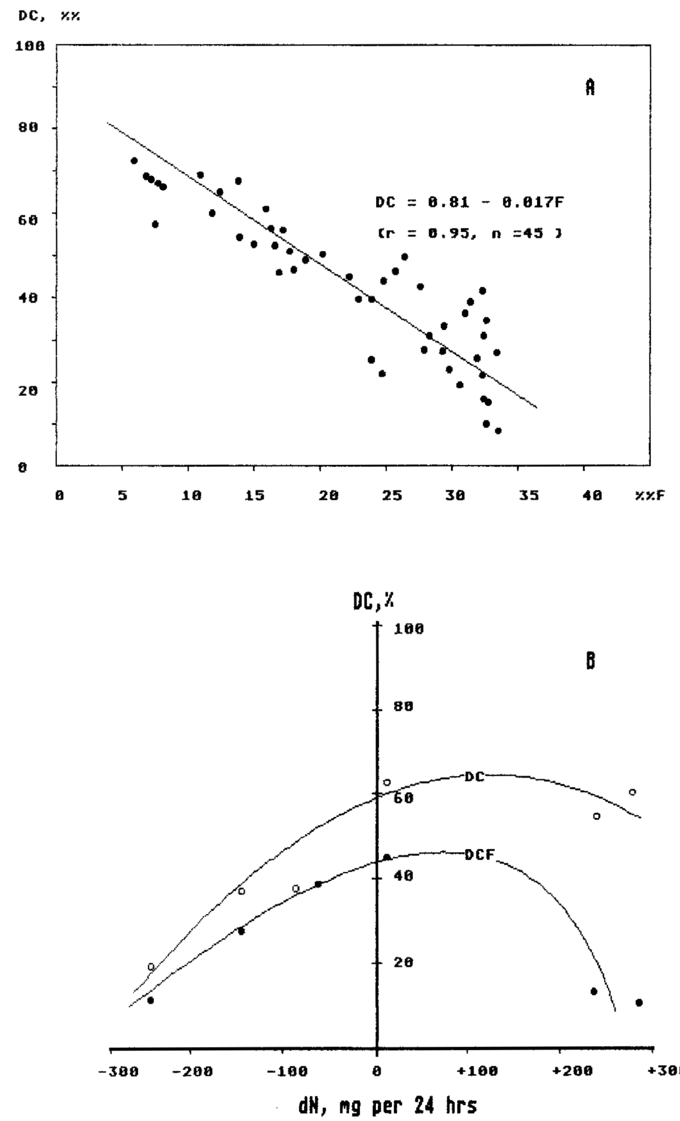

FIG. 9. Digestibility coefficients (DC, percent) in the willow ptarmigan as related to the fiber content of a diet (F, percent) (A) and to the nitrogen balance (dN) of a bird (B). DCF on plot B indicates the partial digestibility of fiber.

To compensate for all these changes, ptarmigan must eat more food as the season progresses, so that the process of digestion must be more rapid. More time is spent feeding. Data on rates of food consumption and excretion clearly illustrate this seasonal process.

CONCLUSION

To summarize, only rarely in nature may a willow ptarmigan individual keep its homeostatic parameters within optimal limits throughout the winter. More commonly, a ptarmigan must pay for the energy gained from the food with its own body reserves of nitrogen. The rougher the diet (i.e., the more fiber content), the faster the bird exhausts its reserves. Body protein reserves recover only from proteins in the diet. Early in winter, the nitrogen gains and losses are in balance, because the birds can feed selectively on the most nutritious twigs and buds. Later, the choice diminishes or

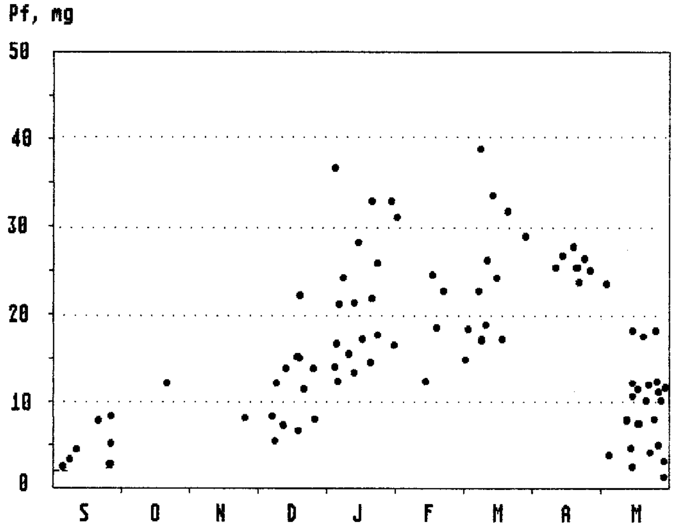

FIG. 10. Seasonal changes in the weight (Pf, mg dry weight) of pieces of willow from the ptarmigan's crops. Each point represents an average from 100-150 pieces. Data from Lower Kolyma only.

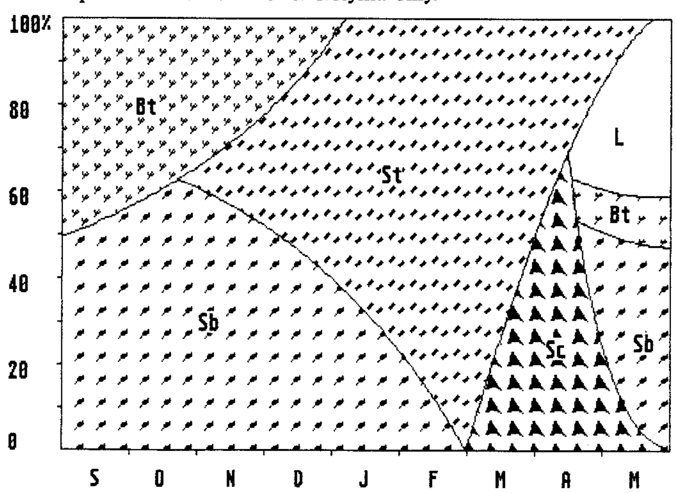

FIG. 11. Changes in the composition of winter diets of willow ptarmigan (vertical scale, percent dry crop contents) throughout winter (horizontal scale, months). Data from Lower Kolyma, winter 1979/80 (a peak of the population cycle). Bt — twigs of *Betula exilis*; Sb — twigs and buds of *Salix* sp.; St — twigs of *Salix* sp.; Sc — willow bark; L — green leaves and berries.

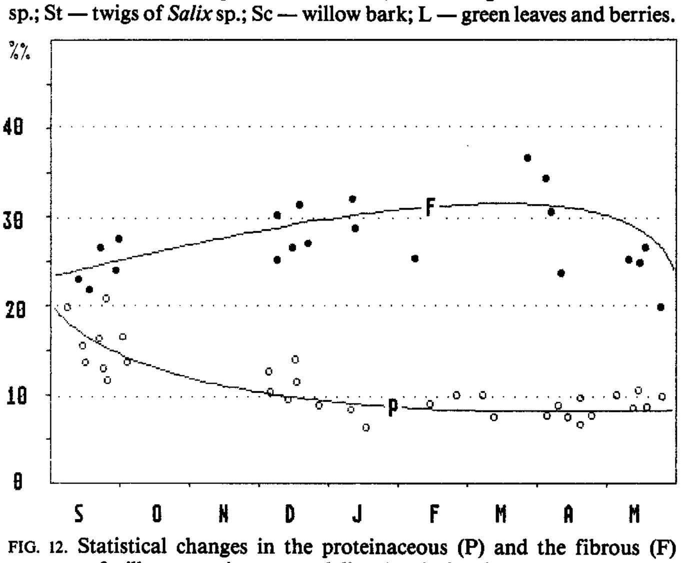

FIG. 12. Statistical changes in the proteinaceous (P) and the fibrous (F) contents of willow ptarmigan natural diets (vertical scale, percent dry matter) throughout winter (horizontal scale, months). F is at its peak in March and April, indicating the diet is least nutritious.

disappears, owing to depletion of willow twigs and the increased snow depth. As progressive weight loss compensates the nitrogen imbalance in individuals, significant changes may occur later in the structure of the breeding population and its reproductive output (Andreev, 1988b).

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