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Phenological observations on protected natural areas associated with brown bear (*Ursus arctos* L.) ecology

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Abstract

The Chronicles of Nature (Letopis Prirody) kept in the nature reserves of the Russian Federaton aggregate a wide spectrum of systematic field records. Information of particular interest therein is the timing of ripening of berries and their yields across years, since berries are an important food for many wildlife species, including brown bear (*Ursus arctos*), a core species in boreal European Russia. Such trophic links are most explicit and interesting in the autumn during fattening or hyperphagia period in bears, when the animals depend on berry availability for storing up fat. We aimed to identify the ecological relationships of brown bear applying integrated analysis of field data on the carnivore diet and of records from the Chronicles of Nature of the Kivach Nature Reserves (the middle taiga) and the Pinega Nature Reserve (the northern taiga). We have determined the prevalence (%) of the certain foods in brown bear scats sampled from transects along forest roads and paths. The number and productivity of fruit-bearing rowan trees (*Sorbus aucuparia*) were determined along permanent transects. Bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea*) berries dominate in brown bear diet. Berry ripening dates (19–43 days) and the average yield (scores 1.3 to 5.0) vary greatly over years. Trends in ripening onset dates follow a vector towards earlier dates. In the Pinega NR, the rate of this process is faster in bilberry. The coefficient of rank correlation between the number of fruit-bearing rowans along dirt roads and rowan prevalence in scats was $r = 1$. The same significant correlation was found between the number of fruit-bearing rowan trees and rowan berry yield. The prevalence of different foods in brown bear scats during the hyperphagia period shows the high dietary plasticity of species. A reliable strong correlation was detected in the Pinega NR between the last sighting of brown bear tracks in autumn and the onset of berry ripening in bog bilberry and rowan. The relatively stable food supply for brown bear in the middle and northern taiga of European Russia is one of the factors defining the high numbers and wide distribution of the species.

Keywords: Chronicles of Nature, nature reserves, middle and northern taiga subzones, fattening foods, berry fruiting, trophic links, dietary plasticity, *Ursus arctos*

Introduction

The biology of brown bear *Ursus arctos* (Linnaeus 1758) was addressed in numerous papers (Pazhetnov 2010, Tumanov 2017, Penteriani and Melletti 2020) over the past decades, based both on traditional and on modern research methods. Special attention was always given to studying carnivore trophic links using field observation methods, analysis of stomach content and scats. Outside of Russia, similar studies were employed using stable isotopes (Robbins et al. 2004, Mowat and Heard 2006, Bentzen et al. 2014) and analysis of scats from GPS-tagged animals (Ciucci et al. 2014, Hertel et al. 2016, Klamarova 2019).

The fact that brown bear utilizes different food sources depending on vegetation in the habitat indicates that the high ecological plasticity of this species and its ability to adjust dietary habits to food availability (Dahle et al. 1998, Edwards et al. 2010, Van Daele et al. 2012, Gunter et al. 2014, Hertel et al. 2016, Stenset et al. 2016, Klamarova 2019). In some regions, if fattening foods are deficient and farmed crops attract brown bears, human – bear conflicts may arise (Pazhetnova 1987, Obbard et al. 2014, Sakiyama et al. 2021). This requires a study of the brown bear foraging behaviour during periods of poor yield of forest foods (Pereira et al. 2021). Research in northern Canada

(MacHutchon and Wellwood 2003) has shown that while the frequency of occurrence of animal foods in brown bear scats was high, their volume contribution was a mere 1.6%. On the other hand, animal foods usually have a higher calorific value than plant foods (Gunther et al. 2014). No wonder that brown bears in Norway obtained most of the annual energy supply from consuming ungulates, and in Sweden – from berries and ungulates (Dahle et al. 1998). The most important berry species in Sweden in autumn were bilberry *Vaccinium myrtillus* L., crowberry *Empetrum nigrum* L. and cowberry *Vaccinium vitis-idaea* L. (Stenset et al. 2016), and their consumption was selective (Hertel et al. 2016). In Norway, berries were another important autumn food category in addition to ungulates (Persson et al. 2001).

Most of the Russian academic literature provides data on autumn brown bear foraging based on multipurpose field surveys. Targeted transect surveys for bear scats have been performed much rarer. Materials from the hyperphagia period are even scantier and based on small sample sizes (Pazhetnov 2010, Tirronen et al. 2016). However, this is the time when the animals store up fat to sustain them through the winter and provide for the nourishment of cubs in the first months of their life.

In nature reserves (NRs) of the taiga zone of European Russia, studies of brown bear have a long history, but the interest in this species was particularly high in the second half of the XX century (Ecology… 1987, Pazhetnov 1990). Materials from the Darwin NR stands out as one of the most detailed studies of brown bear foraging (Razumovsky 1966, Kaletskaya 1973, 2002, Kaletskaya and Filonov 1986). Publications are also available on such nature reserves as the Pechora-Ilych (Nejfeld and Sokolsky 2002), Nizhne-Svirsky (Grachev 1987, Oliger 2002), Pinega (Rykov 1987), Kivach (Shcherbakov 1990), and Tsentralno-Lesnoi ones (Pazhetnova 1987). They report summary data on seasonal patterns in brown bear diet. Meanwhile, year-by-year data on the timing of ripening and yields of berries are missing.

The Chronicles of Nature is a key scientific record kept by nature reserves – aggregate a wide spectrum of annual phenological field observations of plants and animals (Filonov and Nakhimovskaya 1985). This activity in the Kivach Nature Reserve started in 1951 (Romanovskaya 1969). Since 1966, the effort has been expanded to cover 280 phenological parameters (Skorokhodova 2006). In the Pinega Nature Reserve, the Chronicles of Nature have been kept since 1978 and cover 184 phenological phenomena (Zakharchenko 2000, Fedchenko 2008). The observation series in the Kostomuksha Nature Reserve are shorter, since 1993.

The Chronicles of Nature annually record the last sightings of brown bear tracks in late autumn and the first tracks in spring, and the dates when a steady snow cover forms. This enables an integrated assessment of the conditions and timeframe of the species' active life period, and the duration of stay in the den. The Chronicles of Nature contain the dates for the emergence of first berries (cloudberry *Rubus chamaemorus* L., bilberry, crowberry, bog bilberry *Vaccinium uliginosum* L., cowberry, cranberry *Vaccinium oxycoccos* L., and rowan *Sorbus aucuparia* L.) and their mass ripening, when seasonal shifts happen in the brown bear food supply. Records of berry yield scores provide a rationale for seasonal and annual dietary patterns in brown bear. McLellan and Hovey (1995) argue that the availability and ripening dates of foods can be of higher significance for the food being selected by brown bear than its quality, i.e. calorie and protein content. The onset and duration of seasonal shifts in the diet of brown bear in Italy were considered using randomized tests (Ciucci et al. 2014).

Information from the Chronicles of Nature is usually utilised by specialists in application to specific taxonomic groups of plants or animals (Makarova et al. 2001, Skorokhodova and Scherbakov 2013a, b) and much more rarely in its integrated form (Ovaskainen et al. 2013). As has been demonstrated, a special role in the analysis of the spatial variation of phenological reactions belongs to large-scale and long-term multitaxon databases (Ovaskainen et al. 2020). The same applies to the studies of brown bear ecology, i.e. the species' sensitivity to climate variability and its effect on the denning phenology (Delgado et al. 2018).

Long-term phenological data from nature reserves permits tracing the seasonal and annual patterns in the trophic links of brown bear in the protected areas and their neighbourhoods and assessing the conditions for individual subpopulations. Our aim was to reveal the ecological links of brown bear through an integrated analysis of the materials contained in the Chronicles of Nature kept in the nature reserves of the middle (Kivach) and northern (Pinega) taiga subzones and data collected through field surveys of the carnivore foraging. The tasks included are the following: investigation of the chronological patterns of berry ripening in the Kivach, Kostomuksha and Pinega Nature Reserves; study of phenological parameters as the basis for identifying the timeframes in the fattening/hyperphagia period in brown bear; analysis of brown bear diet qualities and quantities during the hyperphagia period; assessment of the species' dietary plasticity; testing of the method for transect surveys of fruit-bearing rowan trees and their productivity.

Material and methods

The study area has a humid temperate continental climate. The northern taiga subzone of Karelia is dominated by pine (bilberry- and cowberry-type) forests (81%), whereas the middle taiga has nearly equal shares of pine (42%) and bilberry-type spruce (39%) forests (Volkov 2008). In the Arkhangelsk region, spruce forests prevail in both subzones (65 and 53%, respectively), while the shares of pine forests are much lower (26 and 28%, respectively). In the Kivach NR (10,900 ha in area), pine forests occupy 44%, spruce forests 32%, and birch forests 19% of the forested land. In the Pinega NR (51,900 ha in area), spruce

forests prevail considerably (73% of the forested land) over pine (16%) and birch (12%) forests.

Brown bear numbers in Karelia have remained quite stable, some 3,100 animals, over the past decades (Danilov et al. 2014). The species' density in the Kivach NR is about the same as the middle-taiga average, i.e. 0.5 ind./1,000 ha of habitats. Brown bear numbers in the Arkhangelsk Region are more dynamic, estimated at around 10,000 animals (Borisov et al. 2009), while the species' density in the Pinega NR is 0.4 ind./1,000 ha of habitats.

We analyzed material from the Chronicles of Nature of the Kivach, Kostomuksha and Pinega nature reserves (Figure 1). We have augmented and processed primary archival and published tabled information from the Chronicles of Nature regarding the fruiting phenology and yields of berries. Sources for the Kivach NR cover the period 1951–2005 (Romanovskaya 1969, Skorokhodova 2006, Skorokhodova and Scherbakov 2013a, b), with the addition of archival material for 2006–2014. Sources for the Kostomuksha NR include some published tabular data (Adrianova 2003) and primary archival material for years 1993–2010. Phenological records for the Pinega NR (1977–2019) were obtained and systematized by the authors using materials of Fedchenko (2008).

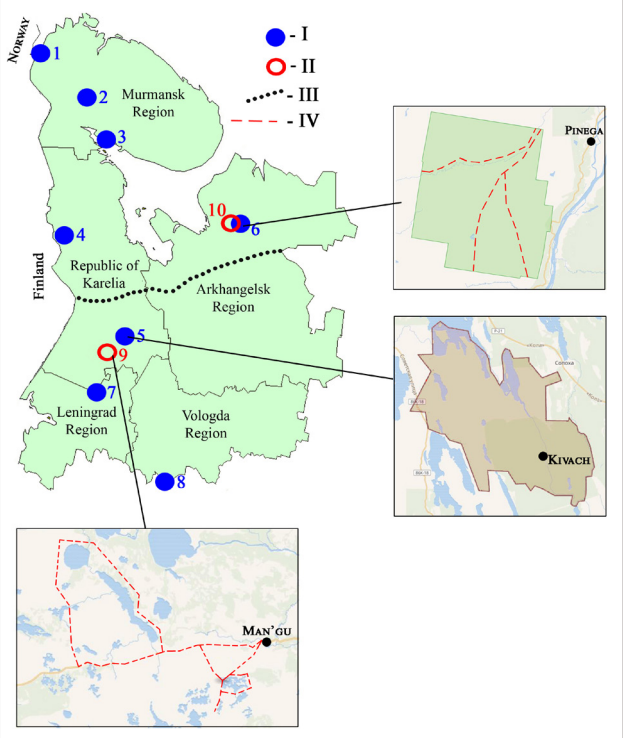

Figure 1. Map of protected areas (I) and sampling locations (II) in the boreal zone of European Russia

Legend: 1 – Pasvik Nature Reserve, 2 – Lapland Nature Reserve, 3 – Kandalaksha Nature Reserve, 4 – Kostomuksha Nature Reserve, 5 – Kivach Nature Reserve, 6 – Pinega Nature Reserve, 7 – Nizhne-Svirsky Nature Reserve, 8 – Darwin Nature Reserve, 9 – Pryazhinsky district, Republic of Karelia, 10 – Pinega Nature Reserve territory, Arkhangelsk Region; III – borders of the northern and middle taiga, IV – survey routes.

Data on brown bear foraging during the hyperphagia period (August–October) were collected from the Pryazhinsky District of Karelia and from the Pinega Nature Reserve. Transect surveys of brown bear and its traces in Karelia during the hyperphagia period were performed in 1981–1984 and in 2012–2014. They yielded a sample of 60 bear scats. In the Pinega NR, 176 scats were collected along transects in August–October in 1978–2019. The transect surveys for brown bear scats followed forest roads and paths. This sort of sampling is rather laborious and has low efficiency, especially in wilderness areas with a limited road network.

The sampled scats were disassembled into components. Plant components are usually well discernible and separable: berries of bilberry, cowberry, bog bilberry, cranberry, crowberry, rowan, vegetative parts of plants (shrub leaves and herbaceous vegetation), and oat *Avena sativa* L. For our purposes, it was enough to determine the prevalence of individual foods in scats (% of the total number of scats). No laboratory determinations of individual food fractions in scats were carried out.

Permanent transects totalling 138 km were covered in the Pryazhinsky district of Karelia in 2012–2014, in which 653 fruit-bearing rowan trees were counted. The survey width was 5 m on each side of a forest dirt road or asphalt paved road, and on the border of the forest with agricultural fields. One or two surveyors were involved. Simultaneously, the number of trees with different berry productivity were determined using a 5-point scale suggested by Kapper (Filonov and Nakhimovskaya 1985) and supplemented by Stolyarskaya (2012). All brown bear scats from the autumn season (287 pcs.) were recorded inside the rowan survey strip and during all research activities in the forest within these years. They were used to estimate the prevalence of rowan in brown bear scats.

The quantitative material was processed by common statistical methods with MS Excel spreadsheet of the Microsoft 365 suite of software (Microsoft 2017) and StatGraphics Plus 5.0 (StatGraphics 1992) software package. Depending on size and conformance to the normal distribution, dataset comparisons were done using parametric (Student's t-test) or non-parametric (Mann-Whitney U-test) tests. Differences were regarded significant with $p < 0.01$. Relationships between the studied parameters were investigated by correlation and regression analyses. The power of the effect of different factors on the studied parameters was estimated by multivariate analysis of variance. Dates in the analysis were accommodated to a 365-day year so that January 1st was the first day of the given year.

Results

The fattening/hyperphagia period for brown bear in the middle taiga subzone (Kivach NR) begins with mass fruiting of bilberry (11.07–9.08; 25.07. on average) and ends in mid-October after mass fruiting of cowberry

(6.08– 11.09; 25.08. on average) and cranberry (4.09–2.10; 17.09. on average). This period in the northern taiga (Pinega NR) is more concise and begins 7–10 days later due to a later mass berry ripening in bilberry (18.07–26.08; 4.08. on average) and cowberry (20.08–15.09; 1.09. on average), and due to a fortnight earlier formation of a lasting snow cover. This is in line with the general pattern of phenological change across latitudes.

Berry ripening dates in the Kivach and Pinega Nature Reserves vary widely among years (19–43 days) (Figure 2), and partially overlap, especially in the Pinega NR. Average berry yields vary among years from 1.3 to 5.0 points, and the fruiting period lasts up to two months, creating a complex mosaic of available principal and subsidiary foods and a generally adequate supply of food combinations for brown bear in both European taiga subzones.

The number of fruit-bearing rowan (trees/km transect) and their productivity (scores) are closely interrelated parameters, indicating the real abundance of this component of the brown bear diet in habitats. Taken together, they define the prevalence of rowan berries in brown bear scats (Table 1). The coefficient of rank correlation between the number of fruit-bearing rowan trees along dirt roads and rowan prevalence in scats was $r = 1$. The same significant correlation was detected both between the number of fruit-bearing rowan trees in field margins, along asphalt-paved roads, and on average across all survey sites and with rowan berry yields.

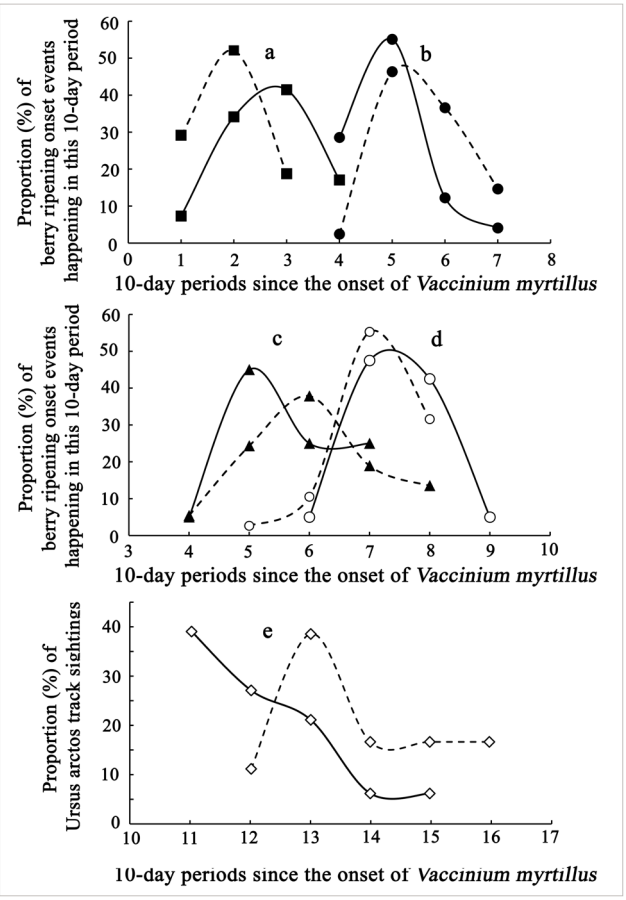

Figure 2. Chronology of berry ripening in bilberry (a), cowberry (b), rowan (c), cranberry (d) and sightings of the last brown bear (e) tracks in autumn in the Kivach (dotted line) and Pinega (solid line) Nature Reserves

Variations in the prevalence of different foods in brown bear scats during the hyperphagia period (Table 2) are associated with the availability, time of ripening, and changes in the dietary value of the foods, and exhibit the species' high dietary plasticity. The principal natural fattening foods for brown bear are bilberry and cowberry.

Trends in the timing of berry ripening follow a vector towards earlier dates, and if this tendency persists, the dates of the hyperphagia period in brown bear can be expected to change in the future. In the Kivach NR, the tendency was detected for the onset of berry ripening in bilberry (*V. myrtillus* = 524.412 – 0.167901 × year), cowberry (*V. vitis-idaea* = 498.604 – 0.139592 × year), cranberry (*V. oxycoccos* = 612.649 – 0.183758 × year), and mass ripening of the latter (*V. oxycoccos* = 758.291 – 0.251801 × year). This process in bilberry is faster in the Pinega NR (*V. myrtillus* = 645.341 – 0.223868 × year) than in the Kivach NR (Figure 3).

The variation in the dates of the last sightings of brown bear tracks differs among the Kivach and the Pinega Nature Reserves (Figure 2). A reliable correlation between berry

Table 1. Dynamics of the number of fruit-bearing rowan trees along the permanent transects in the Pryazhinsky district of Karelia, trees/km of transect

Parameter	Years			Average
	2012	2013	2014	
Dirt roads, trees/km	1.3	6.4	88.0	26.4
Field margins, trees/km	3.0	0.2	28.6	6.5
Asphalt-paved roads, trees/km	1.5	0.3	20.9	5.0
Average	1.5	1.3	40.8	10.7
Yield score	4	3	5	4
Prevalence in scats, %	14.9	15.1	43.0	26.1

Table 2. Prevalence of specific foods in brown bear scats during the hyperphagia season in the Pinega Nature Reserve in 1978–2019, % of scats containing the respective food

Food	August (*n* = 73)	September (*n* = 82)	October (*n* = 21)	Total (*n* = 176)
Plant foods	94.5	98.8	100.0	97.2
incl.:				
Cloudberry	1.4	-	-	0.6
Bilberry	61.6	32.9	19.1	43.2
Crowberry	6.9	13.4	14.3	10.8
Bog bilberry	34.3	25.6	4.8	26.7
Cowberry	31.5	50.0	42.9	41.5
Rowan	5.5	24.4	14.3	15.3
Cranberry	-	3.7	4.8	2.3
Vegetative parts of plants	38.4	29.3	47.6	35.2
Animal foods	34.3	7.3	4.8	18.2

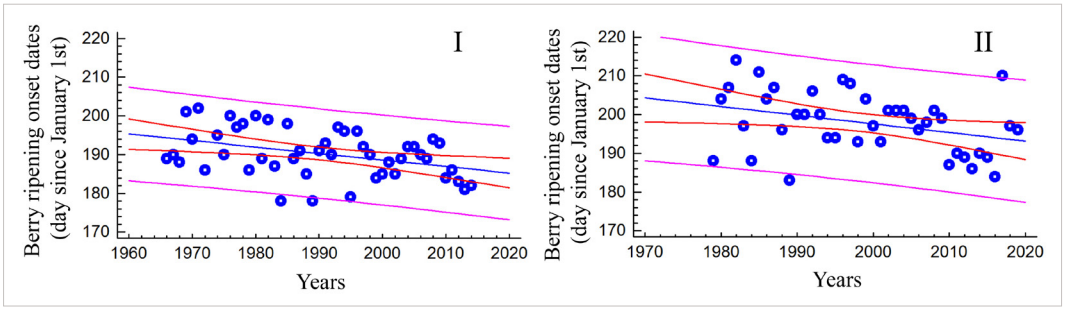

Figure 3. Trends in bilberry ripening onset in the Kivach (I) and Pinega Nature Reserves (II)

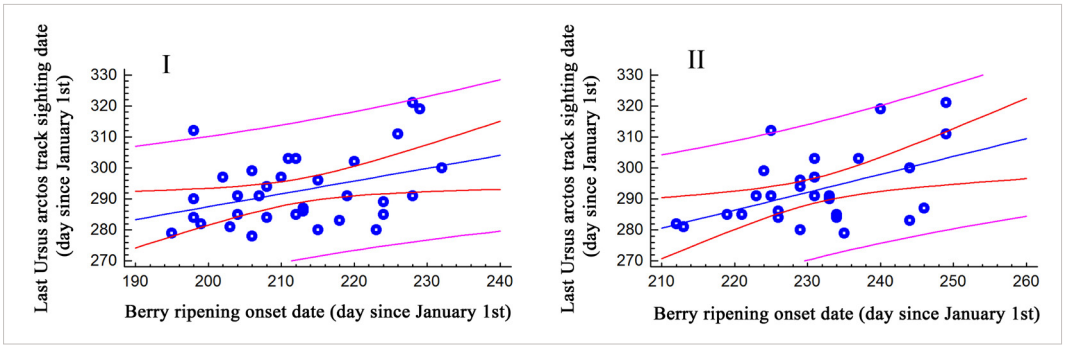

Figure 4. Relationship between the onset of bog bilberry (I) and rowan (II) ripening and the last sightings of brown bear tracks in the Pinega Nature Reserve

ripening onset and the last sighting of brown bear tracks was noted in the Pinega NR (Figure 4) only for bog bilberry (last brown bear tracks = 204.722 + 0.413838 × *V. uliginosum* ripening) and rowan (last brown bear tracks = 159.231 + 0.577868 × *S. aucuparia* ripening), which exhibited the greatest scatter of the dates of berry ripening onset (43 days).

Discussion

Phenological observations reveal significant and explicable latitude-wise differences in the dates of berry ripening, last records of brown bear tracks in the autumn, and formation of a steady snow cover in protected areas of European Russia situated in different taiga subzones

Table 3. Last brown bear track sightings in the autumn (1) and formation of the snow cover (2) in protected areas of the boreal zone of European Russia, long-term annual averages

Protected area	1	2	Source
	Northern taiga		
Lapland NR	28.10.	28.10.	Semenov-Tyan-Shansky and Ablaeva 1983
Pinega NR	23.10.	29.10.	Fedchenko 2008, authors' own data
Kostomuksha NR	24.10.	5.11.	Adrianova 2003, archival data
	Middle taiga		
Kivach NR	12.11.	11.11.	Skorokhodova 2006
Nizhne-Svirsky NR	5.11.	16.11.	Oliger 2002, Stolyarskaya 2012
	Southern taiga		
Darwin NR	28.11 (solo animals); 5.11 (females with cubs)	-	Kaletskaya and Filonov 1986

(Table 3, Figure 2). These data offer a reference point for determining the potential dates of the onset and end of the hyperphagia period in brown bear. Considering the berry ripening dates (Table 4, Figure 2), intensive foraging period in the carnivore in the middle taiga appears to begin with bilberry in the second half of July and to end with rowan and cranberry in mid-October. Because of the timing of bilberry and crowberry ripening, the hyperphagia period in brown bear in the northern taiga begins somewhat later than in the middle taiga and ends earlier. On average, mass ripening of bilberries in the Kivach NR happens 10 days earlier, and that of cowberries 7 days earlier than in the Pinega NR. Judging by the studies carried out in the Kola Peninsula (Makarova et al. 2001), ripening in bilberry, cowberry, and rowan in the Kandalaksha and Pasvik nature reserves happens even later. Mass ripening in bog bilberries in the Kivach NR takes place almost a month earlier than the formation of first berries in the Pinega NR. On the other hand, cranberry in the southern taiga subzone (Darwin NR) ripen 6 days earlier on average than in the Kivach NR (Table 4).

The chronology of berry ripening in the Kivach NR shows that the dates of the first berries appearing in cowberry, rowan, and cranberry partially overlap and vary widely among years (33, 31, and 30 days, respectively). Mass ripening of bilberries, bog bilberries, cowberries, and cranberries also occurs in a wide time range (26, 19, 36, and 28 days, respectively). Knowing how long these berries remain on the plants, it is obvious that brown bear can forage even on bilberries for a prolonged time, up to two months.

Similar or even more extreme berry ripening dates among years are observed in the Pinega NR: bilberry – 32, crowberry – 35, bog bilberry – 43, cowberry – 31, row-

Table 4. Emergence of first berries and their mass ripening in protected areas in the boreal zone of European Russia, long-term annual averages

Protected area	Bilberry	Crowberry	Bog bilberry	Cowberry	Rowan	Cranberry	Source
				Northern taiga			
Lapland NR							Semenov-Tyan-Shansky and Ablaeva 1983
first berries	28.07.	26.07.	-	25.08.	-	-	
mass ripening	-	-	-	-	-	-	
Pinega NR							Fedchenko 2008, authors' own data
first berries	21.07.	22.07.	4.08.	19.08.	25.08.	4.09.	
mass ripening	4.08.	-	-	1.09.	-	-	
Kostomuksha NR							Adrianova 2003, archival data
first berries	19.07.	16.07.	-	23.08.	26.08.	15.09.	
mass ripening	-	-	-	-	-	-	
				Middle taiga			
Kivach NR							Romanovskaya 1969, Skorokhodova 2006, Skorokhodova and Scherbakov 2013a,b, archival data
first berries	12.07.	-	-	12.08.	20.08.	7.09.	
mass ripening	25.07.	-	6.08.	25.08.	-	17.09.	
Nizhne-Svirsky NR							Stolyarskaya 2012
first berries	9.07.	-	18.07.	12.08.	19.08.	5.09.	
mass ripening	-	-	-	-	-	-	
				Southern taiga			
Darwin NR							Nemtzeva 1983
first berries	-	-	-	-	-	28.08.	
mass ripening	-	-	-	-	-	11.09.	

an – 43, and cranberry – 31 days. The sequence of ripening onset in berry sites is quite meaningful. Bilberry annually began bearing fruit 15–47 days (31.3 days on average) earlier than cowberry. Crowberry began to come into berry 14–42 days (28.5 days) earlier than cowberry. Bog bilberry began to fructify 1–31 days (14.8 days on average) earlier than cowberry. In most years, cowberry started to berry 2–22 days (4.2 days on average) earlier than rowan, and in all years, 1–36 days (15.6 days on average) earlier than cranberry. Similarly with the middle taiga, this mosaic sequence of berry ripening onset secures the necessary interchangeability of principal and subsidiary foods of brown bear in any given year (Figure 5).

Transect surveys of fruit-bearing rowan trees in the middle taiga of Karelia, including permanent transects in the Pryazhinsky district of Karelia, showed the number of such trees to vary manifold from year to year (Table 1). In 2013, 55.2% of rowan trees produced poor yield (score 2); 44.1% gave medium yield (score 3), and 0.7% afforded high yield (score 4). In 2014, these proportions changed notably: 27.8% (score 2) – 49.7% (score 3) – 25.5% (score 5). The abrupt change in the number of fruit-bearing rowans in 2014 concurred with an increase in the share of high yield trees, leading to a proportionally abrupt rise in the prevalence of rowans in brown bear scats. The manifold increase in the number of high-yield rowan trees provides a comprehensive idea of the fruiting intensity and abundance of this food for brown bear.

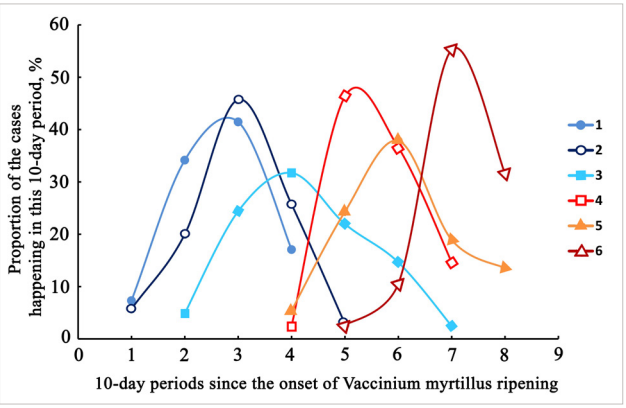

Figure 5. Chronology of berry ripening for bilberry (1), crowberry (2), bog bilberry (3), cowberry (4), rowan (5), and cranberry (6) in the Pinega Nature Reserve within 1978–2019

The average productivity of rowan in Karelia is 150 kg/ha in roadsides, and 400 kg/ha in forest and field margins (Sakovec and Litinsky 1982). In high-yield years, which in the Kivach NR happened 17 times over the 29 years of surveys (Skorokhodova and Scherbakov 2013a), these values can be much higher. High abundance of fruit-bearing rowans tells more on brown bear diet in years with low yields of forest fruit, especially cowberries. In the Tsentralno-Lesnoy NR (southern taiga), rowan, alongside bilberry, is a principal fattening food for brown bear (Pazhetnova 1987).

Average berry yield scores of bilberries, cowberries, rowans, and cranberries in the Kivach NR varied among years from 1.3 to 5.0, being 3.5 points on average over the period covering 1981–2014. Similar scores (3.3 on average) were reported for the Kostomuksha NR in 1993–2010. The scores in the Nizhne-Svirsky NR in 1985–1995 were

Table 5. Brown bear diet during the hyperphagia period in the boreal zone of European Russia, data from scat surveys (prevalence, % of scats containing the food)

Survey location	Bilberry	Crowberry	Bog bilberry	Cowberry	Rowan	Cranberry	Plant vegetative parts	Oat	Animal foods	Source
Tersky district, Murmansk Region (*n* = 131)	44.3	60.3	-	59.5	5.3	-	34.4	-	23.7	Tirronen et al. 2016
Pinega NR (*n* = 176)	43.2	10.8	26.7	41.5	15.3	2.3	35.2	-	18.2	authors' data
Kivach NR (*n* = 110)	70.9	-	-	28.2	3.6	0.9	10.9	2.7	11.8	Shcherbakov 1990
Pryazhinsky district, Republic of Karelia (*n* = 60)	35.0	-	-	30.0	33.3	3.3	30.0	13.3	3.3	authors' data
Nizhne-Svirsky NR (*n* = 57)	19.6	-	-	25.5	3.9	23.5	7.8	11.8	7.9	Oliger 2002
Darwin NR (*n* = 89)	48.3	-	-	38.3	4.5	21.4	2.4	18.0	9.0	Kaletskaya 1973

also similar (Oliger 2002). On the other hand, very low berry yields happened only once in each of these nature reserves, and considering that brown bears are quite mobile, this could only make them move to nearby areas in search of more productive sites. Such conditions have been reported from the southern Kola Peninsula (Tirronen et al. 2016) and from Scandinavia (Hertel et al. 2016). In the Darwin NR, too, only one year with a simultaneously poor yield of bilberry and cranberry happened over 34 years of surveys (Kaletskaya and Filonov 1986).

Comparison of our results from long-term transect surveys for brown bear scats during the hyperphagia period in the Pryazhinsky district of Karelia with similar surveys in the Kivach and Nizhne-Svirsky Nature Reserves demonstrates that the prevalence of bilberries and cowberries are the highest in all samples from the middle taiga. A similar pattern is observed in the Pinega and Darwin Nature Reserves, and in the Tersky district of the Murmansk region (Table 5). However, at high latitudes of European Russia, crowberry gains in importance. In central Sweden and north-eastern Norway (area adjoining the Pasvik NR in the Murmansk region), crowberry is a principal fattening food for brown bear (Dahle et al. 1998, Persson et al. 2001, Stenset et al. 2016, Klamárová 2019). It shows high prevalence in the carnivore scats in the south of the Kola Peninsula as well (Tirronen et al. 2016). For the Kandalaksha NR, Bojko (2016) places crowberry first among the principal fattening foods of brown bear. Compared to berries, plant vegetative parts are a less nutritive food (Gunter et al. 2014). That said, they play a noticeable role in brown bear diets in the middle and northern taiga (prevalence 7.8–35.2%). In the surroundings of the Central-Forest NR (southern taiga), oat, alongside plant vegetative parts, is a principal fattening food for brown bear (Pazhetnov 2010). Further northwards into the forest zone, the role of the oat declines, remaining relevant only locally, in areas with specially planted self-feeding patches or oat crops (Belkin 2016).

Data from the Pinega NR illustrate the significance of different foods both in specific months and over the hyperphagia period at large (Table 2). In August, there prevail scats with bilberries, bog bilberries, cowberries, and vegetative parts of plants. In September, the list of dominant species is complemented with rowan. Brown bear scats in October feature a high prevalence of cowberries and plant vegetative parts. The preferences of other foods are several times lower. The lowest preferences throughout the hyperphagia period are demonstrated by cranberry.

Speaking of the hyperphagia period in general, the range of principal and subsidiary natural foods (bilberry, cowberry, bog bilberry, rowan, and vegetative parts of plants) is wider in the Pinega NR in comparison with Karelia due to bog bilberry (Table 5). Up to 64° N, crowberry and cranberry serve as subsidiary foods, which come into play in years with poor yield of other berries (crowberry) or late in the hyperphagia period (cranberry). Further to the north of the region, the role of crowberry grows, while that of cranberry declines because of a pronounced geographic variability of its stock and yield (Antipin and Tokarev 2010).

Conclusions

Phenological records accumulated in the Chronicles of Nature of Russian nature reserves constitute a unique source of information for integrated ecological research, especially monitoring. The key factors for variations in the fattening diet of brown bear in the middle and northern taiga of European Russia are the dates of ripening and yield of the principal and subsidiary foods, abundance of berry sites and their distribution across the ranges of the species. The same parameters are responsible also for the dietary plasticity of brown bear. Bilberry and cowberry demonstrate the highest prevalence in brown bear scats. Vegetative parts of plants, being the most steadily available component of brown bear diet, remain in demand throughout the hyperphagia period. Brown bear exhibits its dietary plasticity in years with different berry yields and in areas differing in the stock of berry plant sites. It helps avoid problems with over-wintering in the middle and northern taiga subzones and secure high population numbers and wide distribution of the species.

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