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Source: Wildlife Biology, 3(3/4) : 251-259

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.1997.030>

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# Spring social organisation, habitat use, diet, and body mass dynamics of hazel grouse *Bonasa bonasia* in northeastern Asia

Serguei V. Drovetski

Drovetski, S.V. 1997: Spring social organisation, habitat use, diet, and body mass dynamics of hazel grouse *Bonasa bonasia* in northeastern Asia. - Wildl. Biol. 3: 251-259.

Hazel grouse *Bonasa bonasia* encounter more severe climates in northeastern Asia than anywhere else in their range, yet the time between snow melt and laying is shorter here than elsewhere. Birds were able to lay early because they moved to follow the phenology of snow melt, changing their diet as they did so. Before snow melt, habitat distribution and diet were the same as in winter. As soon as the first snow-free patches occurred on terraces, grouse moved there and fed on thawed berries, which were available in great quantities on these terraces only. This habitat shift coincided with the shift in diet; winter foods such as twigs, buds and catkins decreased from 75 to 3%, whereas the proportion of berries increased from 6 to 70%. Females began to lay a few days after all snow had melted, returning to riparian habitats where the variety and abundance of plants were greatest. Foliage increased from 27 to 72% of the diet, and the proportion of berries declined from 70 to 19%. In winter, Asian hazel grouse primarily occur in flocks. In spring males guard their mates rather than their territories; they follow females up to a few kilometres from their riparian breeding habitats, as these move on to terraces to gain weight for egg laying. Such food related movements between habitats have not been reported for this species in Europe.

*Key words:* behaviour, ecology, hazel grouse, Russia, social organisation

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*Associate Editor: Jon E. Swenson*

Diet is especially important to female grouse in spring, when they must build up reserves for reproduction in a short period (Siivonen 1957, Jenkins & Watson 1970, Moss, Watson & Parr 1975, Brittas 1988, Robb, Martin & Hannon 1992). To meet these demands they select foods rich in protein, fat, and phosphorus, and foods that are easy to digest (Schladweiler 1968, McCourt, Boag & Keppie 1973, Herzog 1978, Andreev 1987, Brittas 1988, Naylor & Bendell 1989). The spring diet of hazel grouse *Bonasa bonasia* includes flowers, shoots, new leaves, and seeds of various plants (Shul'pin 1936, Tsvelenov 1938, Donaurov 1947, Kirikov 1952, Belopol'skii 1955, Mishin 1960, Semenov-Tyan-Shanskii 1960,

Kuz'mina 1962, Nechaev 1968, Danilov 1975, Formozov 1976, Swenson 1991a). Access to such foods is restricted by the climatic conditions of each spring (Brittas 1988, Swenson, Saari & Bonczar 1994), with birds breeding earlier in mild springs. There are also sex-specific differences in the allocation of time and energy to reproductive behaviour. Considerable differences in body mass dynamics of the sexes illustrate differences in their reproductive expenditures (Donaurov 1947, Semenov-Tyan-Shanskii 1960, Watson 1987, Swenson 1991a). Females gain weight prior to the onset of egg laying, whereas the body mass of males declines, or remains stable in spring. Females should lay eggs as early as



possible because early young grow faster and survive better (Davies & Bergerud 1988). Thus, hens should gain body mass as fast as possible, and minimise the time between snow melt and the onset of laying.

In northeastern Asia the time between snow melt and the onset of laying is much shorter than it is in other parts of the range of hazel grouse, despite the particularly severe climatic conditions of this region. In this paper I describe the spring social organisation, habitat distribution, diet, and body mass dynamics of hazel grouse *Bonasa bonasia kolyomensis* Buturlin, concentrating on social organisation during the transition from winter to the beginning of incubation. Furthermore, I discuss the influence of phenology, and availability and distribution of different foods on the behaviour and mating system of hazel grouse in northeastern Asia.

## Material and methods

Data were gathered in May and early June 1989 and 1992 in two sites in the Yana and Khasyn valleys in northeastern Russia (59-60°N, 149-150°E).

Most of northeastern Russia is covered by larch *Larix cajanderi* forest. Hazel grouse inhabit deciduous and mixed forests throughout the year. These habitats are found in river valleys and on some mountain slopes (Swenson, Andreev & Drovetski 1995). Typically they form narrow strips (up to a few kilometres wide) along streams. For short periods in both spring and fall, hazel grouse move out of the mixed forests of the valleys into larch forests.

I analysed the habitat distribution of hazel grouse by measuring the encounter frequency of birds along transects in three valley floor habitats (poplar-chosen-

nia forest, riparian mixed forest, and riparian larch forest) and two habitats on terraces (dry and wet larch forests). Habitats were classified according to the structure and diversity of vegetation (Table 1). In northeastern Asia forest age is not as important in classifying habitats as it is in northern Europe (Swenson & Angelstam 1993), because fires and floods create large tracks of uniform forest. For example, in the Yana Valley, dry larch forest was uniformly ~55 years old along 30 km of the river terrace.

The thickness and diversity of the ground cover was estimated by a visual scale of three grades each (i.e. thick - intermediate - poor, and high - intermediate - low, respectively). Food sources were given five scores indicating their abundance in different habitats (abundant, common, less common, rare, none).

On each of the daily censuses I walked at least 15 km along the transect, which covered approximately the same distance in all five habitats. Grouse were counted by sex when met. Regardless of habitat, birds were easily seen at a distance of up to 30 m; during the entire period of my study there was little or no leaf-out, and the only evergreen species *Pinus pumilla* was sparse in all of the five habitats I surveyed. To minimise possible effects of snow melt and vegetation development on the observability of grouse, I approached, and flushed each grouse encountered to determine sex and group size. Three or more birds, or two individuals of the same sex together separated by  $\leq 20$  m, were considered a flock (Swenson 1993, Swenson & Fujimaki 1994, Swenson et al. 1995). Two birds of opposite sexes were considered a pair if the distance between them was  $\leq 20$  m. Lone birds and individuals  $>20$  m from other birds were treated as solitary birds. In total, I observed 58 social units: flocks, pairs, and lone birds.

Table 1. Characteristics of hazel grouse habitats in northeastern Asia.

Forest	Location	Layers	Grass	Winter foods	Berries	Foliage	<i>Tipulida</i>	Other invertebrates
Poplar-chosenia	Pebble spits along streams	1-2	Poor, low diversity	Abundant	None	Less common	Abundant	Less common
Mixed riparian	Above poplar chosenia; banks of small channels, middle parts of river islands	4-5	Thick, high diversity	Abundant	Less common	Abundant	Less common	Abundant
Riparian larch	Above mixed; high rare flooded parts of river basin	2-3	Thick, intermediate diversity	Less common	Rare	Abundant	None	Common
Dry larch	Edge of the first river terrace	1-2	Poor, low diversity	None	Abundant	Rare	None	Common
Wet larch	Inner parts of river terraces	1-2	Poor, low diversity	None	Abundant	Rare	None	Less common



When I was able to observe a male hazel grouse without disturbing it and to determine whether it was alone or with a female, I noted the reaction of birds to male song imitated with a metal whistle (Swenson 1991b). I distinguished three kinds of reaction: 1) 'no response', when birds completely ignored the imitation of male song, 2) 'vocal response' when males called, but did not move towards the song, and, 3) 'approach' when males flew towards the place of the song imitation.

Measurements of body mass, diet and schedule of laying were taken from 19 collected specimens (8 males and 11 females). Birds were weighed to the nearest gramme. Food composition was determined by weighing different food items after the crop contents had been dried at +50°C for three days (N = 15, the dry mass of food 35.7 g). Food items were separated and weighed to the nearest milligramme.

Food items were categorised into five groups, according to differences in digestibility, nutrition value, and time needed to find them: 'winter foods', 'berries', 'foliage', 'seeds', and 'invertebrates'. 'Winter foods' included buds and catkins of shrub alder *Alnaster fruticosa* and birches *Betula platiphylla* and *B. middendorffii*, twigs of chosenia *Chosenia arbutifolia* and twigs and flower buds of willows *Salix schwerini* and *S. rorida*. All foods from this group are typical of hazel grouse diet in northeastern Russia (Andreev 1979, 1980, Drovetski 1992a,b). 'Berries' included berries of *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *Empetrum androgynum*, *Rosa* spp., *Padus asiatica*, *Sorbus sambucipholia*. 'Foliage' included leaves of *Stellaria media* and *Vaccinium vitis-idaea*, buds of *Vaccinium vitis-idaea* and *Vaccinium uliginosum*, young leaves of chosenia, *Salix schwerinii*, *Sorbaria sorbifolia*, *Betula exilis* and horsetail sporangia. 'Invertebrates' included larvae *Tipulida* spp., ants *Componotus* spp., beetles *Coleoptera* and terrestrial molluscs *Gastropoda*.

The calculation of dates for the onset of egg laying was based on the number of collapsed follicles, the size and stage of development of the largest ovum, and an average inter-egg interval of 1.33 days (Pynnonen 1954, Semenov-Tyan-Shanskii 1960).

## Results

### Spring phenology

The first small patches of thawed ground appeared in poplar-chosenia and dry larch forests in April. Snow

melted first around trunks of trees, stumps, and fallen logs, which were heated by the sun during daytime. Poplar-chosenia and dry larch forests are exposed to more sun than other habitats because they are situated on the edges of streams (poplar-chosenia forest) and on the edges of terraces (dry larch forest). Snow melt is earliest in poplar-chosenia forests, because habitat is warmed by underground water that comes close to the surface, and because a significant amount of snow in this habitat is blown away by winter winds.

Intensive snow melt began a few days after the average daily temperature exceeded 0°C (10 May 1989 and 8 May 1992). In both years the snow disappeared first from the poplar-chosenia forest, and then from terraces. The snow melt started on the edges of terraces in dry larch forests and then moved into wet larch forests, situated above the dry larch forests. Snow melt did not begin in riparian mixed forests until the average daily temperature was high enough for the melt to become independent of direct solar radiation. Snow melted last in the riparian larch forest because of its great depth due to ground cover of low bushes trapping the snow and because the valley floor mixed forest on one side and the protection from wind and sun provided by mixed forest on one side and up-slope terraces on the other side of the valley.

In the larch forests, the ground cover on the terraces consisted of mosses, lichens and several species of low-bush berries. These berries, frozen throughout winter, became available for hazel grouse in thawed areas (first in dry and then in wet larch forests). Just a few days after snow melt, these low-bush berry plants began forming flower buds, also extensively consumed by hazel grouse.

Invertebrates were available during two periods. As soon as snow melted in poplar-chosenia forest, *Tipulida* larvae were abundant in the layer of dead leaves. Other invertebrates appeared in all habitats in early June, and were most abundant in the riparian mixed forests.

Vegetation development followed the snow melt. New growth started at different times in different habitats. Among the valley floor habitats vegetation started first in poplar-chosenia forests, then in riparian mixed forests, and last in the riparian larch forests. In just a few days after snow melt, the first horsetail shoots with sporangia began to grow; next the first shoots of grasses appeared, the earliest being *Stellaria media*. This sequence was similar in all valley-floor habitats.

On my study area females laid earlier relative to



Table 2. Frequency of encounters of lone birds, pairs and flocks in February - March (1989), May, and early June (1989, 1992).

Period	Lone males	Lone females	Total lone birds	Pairs	Flocks
November - January <sup>1</sup>	2	-	2	-	26
February - March <sup>1</sup>	2	1	3	5	4
Early May <sup>2</sup>	2	1	3	8	2
February - early May <sup>3</sup>	4	2	6	13	6
Middle May <sup>2</sup>	10	6	16	15	-
Late May - early June <sup>2</sup>	9	2	11	3	-

<sup>1</sup> Drovetski 1992a

<sup>2</sup> This study

<sup>3</sup> Combined data from Drovetski 1992a and this study

snow melt than they do in northern Europe. Snow melt was completed on 23 May 1989 and on 24 May 1992. Average first egg dates were 28 May 1989 (N = 2) and 29 May 1992 (N = 3). At the same latitude in central Sweden, the long-term average last day with snow cover was April 10 (Dahlström 1995). Average first egg dates were 7 May 1988 (N = 3), 4 May 1989 (N = 2) and 26 April 1990 (N = 4; Swenson 1991a). Thus, in northeastern Asia females begin laying 2-3 weeks earlier, relative to snow melt, than they do in northern Europe.

### Social organisation

Hazel grouse are encountered almost exclusively in flocks from November through January in this region (Drovetski 1992a). As weather conditions improved in late February and March, hazel grouse began to spend much less of the day in snow burrows, ceased to lose weight (as they did in December-January), and males began to display and whistle. During the same period of improving weather conditions, pairs began to form, but if the weather turned cold birds regrouped into flocks.

Social organisation of hazel grouse in early May did not differ significantly from the social organisation in February and March 1989 ( $G = 1.34$ ,  $df = 2$ ,  $P = 0.51$ ; Table 2). In early May, pairs were encountered much more frequently than lone birds and flocks. No birds were encountered in flocks during and after mid-May (see Table 2), and all birds in the two flocks encountered in early May were females.

With the rapid melting of snow in mid-May, I began to encounter relatively more lone birds. The frequency with which pairs were encountered declined considerably between February - early May and mid-May, and encounters with lone birds increased between these periods ( $\chi^2 = 10.16$ ,  $df = 2$ ,  $P = 0.006$ ). On 17 May 1989, I observed one copulation in dry larch forest on the edge of the river terrace.

### Reaction of males to song imitation

Lone males responded to song imitation significantly more strongly than males in pairs (Fishers exact  $P = 0.005$ ; one paired male that failed to respond was excluded from the test). Fourteen (88%) of 16 males that were with females when tested responded to the song imitation vocally, only one (6%) approached, and one (6%) failed to respond at all. None of the 14 lone males tested failed to respond to the song imitation, six (43%) responded vocally, and eight (57%) approached.

Lone males responded to the song imitation vocally and by approach in both valley floor and terrace habitats. I found no significant difference in the frequencies of vocal responses and approaches by lone males between the valley floors, where birds breed, and the terraces, where they forage during snow melt (Fishers exact  $P = 0.627$ ; valley floor, four vocal responses and two approaches; terraces, four vocal responses and four approaches).

On two occasions, in dry larch forest on the terrace, I was able to position myself between the male and female of presumably mated pairs separated by 80 m. On each of these occasions, the male response to vocal imitations was extreme; both were much more aggressive than any other male I have observed, and neither ceased aggressive demonstrations until I left. In contrast, males that were close to females only responded vocally, and one male failed to respond even when I mimicked male song just 20 m from a pair.

### Diet

The diet of both sexes changes dramatically during spring (Table 3; two-way ANOVA; food  $\times$  period interaction,  $F = 18.1$ ,  $P < 0.0001$ ). 'Winter foods' predominated hazel grouse diet prior to snow melt. As soon as thawed patches appeared on the terraces, birds began to visit both dry and wet larch forests and



Table 3. Hazel grouse spring diet (% of dry mass of crop content).

Date	Sex	Dry mass (mg)	'Winter foods'	Berries	Foliage	Seeds	Invertebrates
Before intensive snow melt (early May)							
8 May 1989	♂	10693	99.6	-	0.4	-	-
8 May 1989	♀	1535	96.0	-	1.0	-	3.0
8 May 1989	♀	2885	54.0	-	2.5	-	43.5
9 May 1992	♀	2193	31.5	22.5	-	46.1	-
10 May 1992	♀	5891	92.8	7.2	-	-	-
During intensive snow melt (mid-May)							
11 May 1989	♀	1069	4.3	40.7	55.0	-	-
11 May 1989	♀	1384	-	87.4	12.6	-	-
21 May 1992	♀	2371	9.5	87.6	2.9	-	-
23 May 1992	♀	1169	-	96.1	3.9	-	-
23 May 1989	♀	1315	4.9	55.5	39.6	-	-
23 May 1992	♀	358	-	52.8	47.2	-	-
After complete snow melt (early June)							
2 June 1992	♂	647	-	33.1	65.4	1.5	-
2 June 1992	♀	1954	-	13.0	84.5	-	2.5
2 June 1992	♀	26	-	30.8	38.5	-	30.8
8 June 1989	♀	2256	-	-	100.0	-	-

switched from 'winter foods' to berries exposed by the snow melt. 'Berries' predominated the diet until hens started to lay eggs. 'Foliage' became the main food for both sexes during laying, which began five days after the snow had melted completely in late May. After snow melt, all of the birds I encountered (3 pairs and 10 lone birds), except for one male, were in riparian habitats, where the diversity and abundance of grassy plants are greatest. 'Berries' continued to comprise up to 33% of hazel grouse diet after snow melt. Unlike the period of snow melt, when hazel grouse fed on low-bush berries (*Vaccinium vitis-idaea*, *V. uliginosum*, *Empetrum androgynum*), they took high bush or tree berries (*Rosa* spp., *Sorbus* spp., *Prunus asiatica*) when feeding in riparian habitats.

During the three periods, I found no differences between the sexes in consumption of the three most important groups of food: 'winter foods', 'berries', and 'foliage' (see Table 3; all three ANOVA P-values = 0.47). However, I found a negative correlation between the body mass of females that ate invertebrates and the proportion of invertebrates in their crop con-

tent ( $r = -0.97$ ,  $df = 3$ ,  $P = 0.03$ ), suggesting that females may consume invertebrates when they are in poor condition to help attain laying condition. *Tipulida* larvae may be especially important to females in early spring before snow begins to melt on terraces. These larvae are found on the edges of streams in poplar-chosenia forests. In early May 1989, I found much evidence of the leaves having been turned over by grouse, presumably as they searched for tipulids. I measured the biomass of these insects in four 25 × 25 cm squares. Their biomass was 2.5 g dry mass/m<sup>2</sup>.

#### Habitat use

Birds increased their use of terraces in spring when melting of snow exposed last-year's berries. Terraces were seldom used in winter, and when they were used it was apparently because birds were seeking protection from the wind in dense larch thickets when the snow was either too thin or too crusty to allow grouse to roost in it (Drovetski 1992a).

In early spring, terraces were used no more frequently than in winter. However, birds made frequent

Table 4. Hazel grouse encounters in five habitats (numbers represent groups, not individuals)

Period	Valley floor forests				Terrace forests		
	Poplar-chosenia	Riparian mixed	Riparian larch	Combined	Dry larch	Wet larch	Combined
Winter - early May <sup>1</sup>	16	28	9	53	17	-	17
Mid-May <sup>2</sup>	4	14	-	18	7	6	13
Late May-early June <sup>2</sup>	1	8	4	13	1	-	1

<sup>1</sup> Combined data from Drovetski 1992a and this study

<sup>2</sup> Data from this study



use of terrace habitats as they became snow free in middle May (Table 4;  $G = 7.1$ ,  $df = 2$ ,  $P = 0.03$ ). The birds apparently shifted into terrace habitats because of the abundance of thawed berries newly exposed by the snow melt. By the completion of snow melt in late May birds ceased to use the terraces and switched to foraging on new leaves and shoots as soon as they become available in the riparian habitats of the valley floors.

### Body mass dynamics

Sex and age classes of hazel grouse do not differ in body mass during winter in northeastern Asia (Drovetski 1992a). However, body mass changes considerably over the course of winter. It increases from October to December, but then declines until February.

In this study the body mass of males in early May ( $370 \pm 17$  g,  $N = 3$ ) was similar to the values I found for February and March ( $\bar{x} = 372 \pm 18$  g,  $N = 15$ ; Drovetski 1992a). However, during the May-June mating season, male body mass declined significantly ( $BM = 375.9 - 2.2 \times d$ ; where  $d$  is number of days counted from 8 May;  $r = -0.71$ ,  $df = 7$ ,  $P = 0.05$ ; Fig. 1). This rate of weight loss was twice as great (test for difference of slopes:  $F = 7.9$ ,  $P = 0.011$ ) as the  $1.1$  g/day that birds lost during January - February ( $400.7 - 1.1 \times d$ , with days counted from 23 January;  $r = -0.77$ ,  $df = 15$ ,  $P < 0.001$ ; data from Drovetski 1992a).

By the time I began this study in early May, females had already gained considerable weight. The mean weight of the four females that I collected in early May ( $\bar{x} = 407 \pm 26$  g) was much higher than that

of 15 birds from February and March 1989 ( $\bar{x} = 371 \pm 18$  g; Drovetski 1992a; Mann-Whitney  $U = 9.0$ , two-tailed  $P = 0.037$ ). One of these four early-May females was light (371 g) and had the same body mass as birds from February and March. Female body mass did not change significantly during the study period ( $BM = 415.7 - 0.7 \times d$ ; with days counted from 8 May;  $r = -0.32$ ,  $df = 10$ ,  $P = 0.34$ ; see Fig. 1).

## Discussion

### Spring movements and timing of reproduction

The phenology of snow melt, development of vegetation, and changes in availability of different foods appeared to be the major factors influencing spring behaviour of hazel grouse in northeastern Asia. On my study area, snow melt began along streams, and shortly after that on the edge of terraces. Gradually the melt moved into interior habitats of the riparian zone, terraces and mountain slopes. This sequence determined the beginning of vegetation development and availability of various foods in different habitats.

Hazel grouse responded quickly to these changes in environmental conditions. As soon as the first large snow-free patches appeared in the poplar-chosenia forests along the water courses, the grouse moved there, apparently to exploit the abundance of *Tipulida* larvae. Shortly thereafter snow melt progressed to the exposed terraces, uncovering huge quantities of frozen berries that had been there since the past fall. Until new shoots began to grow these berries predominated the diet of grouse during mid-May. As fresh shoots of horsetail and new grasses began to appear, the birds returned to their primary habitat in riparian mixed forest up to 2 km away.

A particularly surprising result of my study was the discovery that in northeastern Asia the time between snow melt and laying is shorter than it is in Europe. Despite the severe climatic conditions of northeastern Asia, so much food is exposed by the snow melt, that females can form eggs very rapidly, when they move to exploit the appearance of the food sources.

### Territoriality patterns in northeastern Asia

During the breeding season male hazel grouse experience a trade-off in time allocation among two major activities: social competition (guarding a mate to ensure paternity, and guarding territory to protect food from conspecifics), and maintaining body condition (foraging). The severity of such a trade-off is revealed

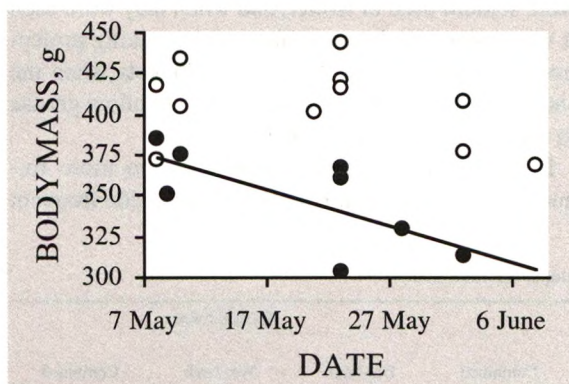


Figure 1. Spring body mass dynamics of hazel grouse in northeastern Asia. Unfilled circles = females; filled circles = males; solid line = regression line for the body mass dynamics of males ( $BM = 375.9 - 2.2 \times d$ ; where  $d$  is number of days counted from 8 May;  $r = -0.71$ ,  $df = 7$ ,  $P = 0.05$ ).



by the fact that male hazel grouse lose weight twice as fast (0.6% of body mass per day) during the breeding season as they do during the coldest months of winter.

In northern Europe, where food apparently is concentrated in relatively small, almost randomly distributed patches, both sexes hold and defend territories (Swenson & Boag 1993). Females apparently hold territories to defend food. By defending territories that overlap those of females, males simultaneously defend food for themselves and their mates from other males. As the result, males spend less than half (37%) of their time with females prior to the onset of laying (Swenson & Boag 1993). European males continue to defend their territories after the peak of mating, probably to protect food for themselves later in the season and to mate with reneating females.

In northeastern Asia, the situation differs considerably. Important spring food sources (berries, foliage, and invertebrates) are abundant, but situated in different habitats that can be far from each other. In contrast to European females that are resident on their territories with diameters of 600-700 m during the whole breeding season (Swenson & Boag 1993), birds in northeastern Asia move up to 2 km between habitats, to follow the phenology of snow melt and to improve their diet.

Also, in early May, before the period of copulations, the ratio of encounters of lone birds to pairs was 32% to 68% (N = 19; see Table 2). In mid-May, when I observed a copulation (some birds might have mated already, and others might not) the ratio was 52% to 48% (N = 31). In late May - early June, when females began laying, the ratio was 79% to 21% (N = 14). This suggests that females are attended by males much more often prior to and during mating in northeastern Asia than in Europe. After that, when females were laying lone birds predominated.

Finally, in northeastern Asia the response of males to song imitation varied primarily with whether or not they were attending females and not whether they were encountered in habitats used for breeding or habitats used only for foraging. I observed extreme aggressive responses only from two males with females, and then only after I imitated the song while positioned between these males and their mates. On both occasions the birds were encountered in dry larch forest on the river terrace, far from the mixed riparian forest, where hazel grouse breed. When males were attending females, they answered song imitations, but seldom approached. In contrast lone

males approached much more often, perhaps to see if their partner was close to the 'other male' that was whistling, or if the 'other male' had a mate that they might compete for. These data are consistent with the view that hazel grouse whistles may serve as contact calls and that calls coordinate activities among individuals (Swenson 1991a, Swenson et al. 1995, Drovetski 1992a), as well as announce ownership of territories.

In northeastern Asia spring food apparently is unlimited and grouse do not seem to defend it. However, Asian birds move considerable distances between habitats tracking food exposed by snow melt. These movements between habitats make all-purpose territories uneconomical for males to defend because breeding and foraging habitats may be separated by 1-2 km. Consequently, males spend more time guarding mates than territories.

### Body mass dynamics

In northern Europe, the body mass of male hazel grouse declines, or sometimes remains stable in spring. The body mass of females increases prior to laying and then drops rapidly (Semenov-Tyan-Shanskii 1960, Swenson 1991a). I found similar patterns of weight change at my study site in northeastern Asia.

Interestingly, males in northeastern Asia lose weight more rapidly during the spring than they do in January, the most severe winter month; body mass declines only when the temperature drops below -25°C (Drovetski 1992a). During January - February of 1989, when the average daily temperature was -29°C, the body mass of both sexes declined by 1.1 g/day. Remarkably, results from this study show that males lost weight in spring twice as fast as in January. In the mild climate of Utah, Pekins, Gessaman & Lindzey (1994) found winter conditions not to be challenging for blue grouse *Dendragapus obscurus*. Surprisingly, this also seems true for hazel grouse that confront the extreme winter conditions of northeastern Asia.

*Acknowledgements* - this study was supported by Mr. Garret Eddy and the Burke Museum's Eddy Endowment for Excellence in Ornithology. I thank Sievert Rohwer for his help with this manuscript. I am grateful to Jon Swenson and two anonymous reviewers for helpful reviews of the manuscript.



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