Ornis Fennica 80:130–136. 2003

The influence of sexual size dimorphism on the dietary shifts of Capercaillie *Tetrao urogallus* during spring

Morten Odden, Per Wegge*, Sigrunn Eliassen & Mats Haneborg Finne

*Odden, M., Wegge, P. & Finne, M. H., Department of Biology and Nature Conservation, Agricultural University of Norway, N-1432 Ås, Norway. (*Corresponding author's e-mail: per.wegge@ibn.nlh.no)*
Eliassen, S., Department of Zoology, University of Bergen, N-5007 Bergen, Norway

Received 6 May 2003, accepted 8 September 2003

In boreal forests during spring, the highly size-dimorphic Capercaillie *Tetrao urogallus* changes its diet from pine needles to more nutritious ground forage. At Varaldskogen in southeast Norway, we compared the dietary shift of males and females from March to end of May based on faecal analysis (n = 199). The proportions of ground plants were significantly higher among the female samples than among the male samples during all three months. Both sexes had significantly higher proportions of ground plants in samples from May than the preceding months. When taking into account actual quantities consumed and the lower digestibility of pine needles, males were estimated to ingest about the same amount of sprouting ground plants as females. Males require much larger quantities of food than females, and thus, a smaller fraction of males' total food requirement is obtained from sparsely distributed ground plants. Consequently, males experience a smaller net benefit from feeding on ground food and supplement their diets with a larger fraction of easily accessible pine needles of lower nutritional quality. Moreover, male lekking activities and mutual avoidance behaviour during daytime may restrict foraging time, and the availability of ground forage is probably lower within the restricted daytime ranges around leks than outside.

1. Introduction

When the snow melts in spring, Capercaillie alters its diet from consisting of almost 100% conifer needles to include an increasing proportion of emerging ground plants. However, females are reported to exhibit a more pronounced change to a higher proportion of ground plants than males (Gjerde & Wegge 1987, Storch *et al.* 1991, Borchtchevski 1995). The following explanations to this trend have been put forward in previous studies: (1) Males divert part of their time into territorial defence and display activity on the lekking grounds, and thus, they have less time available for feeding on sparsely distributed food. Moreover, females' production of eggs increases their demands for more nutritious food (Gjerde & Wegge 1987, supported by Pulliainen & Tunkkari 1991). (2) Differences in metabolic requirements due to sexual dimorphism (Storch *et al.* 1991). (3) Better ability of males to utilize coarse food items due to anatomical differences in the two sexes' intestines (Borchtchevski 1995).

Previous studies have focused on intrasexual differences in the *proportions* of ground food in male and female diets. The relationships between

proportions and *actual quantities* have not been examined thoroughly. In this study we analysed faecal samples to compare the food habits of the two sexes. Even though faecal analysis is considered an appropriate method of describing the diets of galliform birds (Chapuis & Didillon 1987), it only provides rough estimates. However, our aim is not to provide accurate measurements. We only want to illustrate how the general picture of the diets changes when actual quantities and digestibility of ingested foods are considered, compared to the picture so far inferred from proportions of the two food categories.

2. Material and methods

2.1. Study area

This study was carried out in a 40 km^2 forest tract at Varaldskogen (60°10′N, 12°30′E), south-eastern Norway, in the southern part of the middle boreal coniferous zone. The climate is continental with mean temperatures of 16.2 and –7.3 °C in the warmest and coldest month, respectively. The ground is usually covered by snow from late November to the end of April. Norway Spruce *Picea abies* and Scots Pine *Pinus sylvestris* are the dominant tree species, while *Vaccinium* spp. and Heather *Calluna vulgaris* dominate the ground layer. The fauna is typical of the middle boreal zone. Spring density of Capercaillie was 0.5–0.7 males/km^2 and 1.4–1.8 females/km^2, and nearly all mating takes place at the leks during 20–30 April. Average spring weight of males > 2 years of age is 4.3 kg (P. Wegge unpubl.), and that of females > 1 year of age is 2.1 kg (Storaas *et al.* 2000), thus giving a male:female weight ratio of ca. 2.05.

2.2. Faecal analysis

From 11 March to 30 May of 1997 we collected fresh faecal droppings from males (n = 140) and from females (n = 59) at locations marked by pointing bird dogs, or where birds were flushed. Determining sex was simple, as their droppings differ in size (Gjerde 1990). The proportions of different categories of plants in 3.5 ml sub-samples were visually estimated. All plant fragments large enough to distinguish with a binocular microscope were classified into two main categories: Pine needles and ground plants. The latter category was further divided into Bilberry buds and twigs (*Vaccinium myrtillus*), stems and leaves of Bog Rosemary (*Andromeda polyfolia*), buds of Bog Cottongrass (*Eriophorum vaginatum*), graminoids or forbs, seeds of Cowberry (*Vaccinium vitis-idéa*), seeds of Cranberry (*Oxycóccus quadripétalus*), and seeds of Crowberry (*Émpetrum hermaphrodítum*).

Fragments too fine grained to classify constituted approximately 20%–30% of the material, with the same proportions in each sampling period. Berry seeds constituted insignificant proportions in the samples, and hence they were only counted to obtain an index of the changes in the amount of berries consumed over time. The seeds are hereafter expressed as number of seeds per ml sample.

Sixty-eight of the samples from males stemmed from 7 different radio-marked individuals, whereas 20 of the female samples were collected from one marked bird. The remaining samples were collected from unmarked birds. The number of marked birds varied throughout the season due to death or new captures. Thus, in order to examine the influence of individual variation in diet composition we used only data from March and April, at which time the number of birds was constant. No difference between individuals in the proportion of ground plants in the faecal samples was detected among males (Kruskal-Wallis One Way Analysis of Variance on Ranks, $H_4 = 2.37$, $P = 0.668$). Moreover, there was no difference between the radio-marked female and the unmarked females in the proportion of ground plants in their samples (Mann-Whitney U-Test, $U = 133$, $P = 0.276$). Thus, we concluded that pseudo-replication did not affect the data, and in the further analysis we grouped the data according to sex and month.

2.3. Converting proportions of food categories in the faecal samples into quantities consumed

The pronounced sexual size dimorphism among Capercaillie entails large differences in energy

requirements between the sexes (Lindén 1984). Among the tetraonids, both Black Grouse *Tetrao tetrix* and Capercaillie exhibit marked sexual size dimorphism, and sexual differences in daily amounts of food consumed in these species are virtually similar as the sexual differences in body size (Andreev 1988, cited from Potapov & Andreev 1973: Black Grouse; Semenov-Tjan-Sanskij 1960: Capercaillie). Thus, a comparison between the sexes of quantities consumed was obtained by multiplying the average proportions of different food categories in the faecal samples from males by the proportional difference in body weight (2.05).

3. Results

Pine needles and bilberry stems and leaves were the only two food items that were consumed by both sexes during the whole study period (Table 1). Both sexes consumed Bog Cottongrass and Bog Rosemary only during April and May, whereas the proportion of graminoids and forbs increased abruptly in the female samples from May. This category was practically nonexistent in the samples from males. The only berries available in spring are those that are conserved under the snow during winter. Of these, only Cowberries and Cranberries showed up rather frequently in the faecal samples of both sexes, while Crowberries occurred sporadically (Table 2). Only one tiny fragment of an invertebrate leg was found in one of the female samples.

The proportion of ground plants in the faecal samples from females was significantly higher than among males both in March ($U = 454$, $P = 0.012$), April ($U = 1101$, $P = 0.010$) and May ($U = 993$, $P < 0.001$) (Fig. 1). The proportion of ground plants differed significantly between the three months in both sexes (males: $H_2 = 22.2$, $P < 0.001$, females: $H_2 = 20.0$, $P < 0.001$). In males, the pro-

Table 1. The average proportions (%) of plant categories (berry seeds excepted) in the faecal samples of male and female Capercaillies in Varaldskogen during the spring of 1997.

Period	March		April		May	
Sex	Males	Females	Males	Females	Males	Females
N	46	14	56	22	38	23
Pine needles						
Average	96.9	81.5	88.3	71.1	68.2	23.5
SD	5.4	32.3	19.8	33.1	35.4	35.2
Freq*	100	92.9	100	90.9	100	47.8
Bilberry stems and leaves						
Average	3.1	18.5	6.8	20.5	20.4	30.8
SD	4.1	32.3	13.2	25.5	27.5	35.3
Freq*	34.8	71.4	44.6	77.3	62.5	78.3
Bog cottongrass						
Average	0	0	3.8	6.3	9.7	12.8
SD	0	0	11.4	19.0	23.3	22.7
Freq*	0	0	16.1	27.3	26.3	47.8
Bog rosemary						
Average	0	0	1.1	2.1	0.1	1.4
SD	0	0	5.9	4.7	0.6	5.4
Freq*	0	0	7.1	22.7	2.6	8.7
Graminoids and forbs						
Average	0	0	0	0	1.6	31.5
SD	0	0	0	0	8.3	25.0
Freq*	0	0	0	0	5.3	39.1

*Frequency of occurrence

portion of ground plants was significantly higher in May than in any of the previous months (Dunn's method, May vs. April: Q = 3.07, P < 0.05, May vs. March: Q = 4.66, P < 0.05), whereas the proportion of ground plants did not differ significantly between samples from March and April (Q = 2.09). The comparison between months of female samples revealed a similar pattern as among males (May vs. April: Q = 3.45, P < 0.05, May vs. March: Q = 4.06, P < 0.05, April vs. March: Q = 1.02, ns).

The average number of food categories per male sample was 1.32 in March (SD = 0.48), 2.38 in April (SD = 1.81) and 2.74 in May (SD = 1.66). The corresponding numbers in female samples were 2.27 (SD = 1.49), 3.18 (SD = 1.76) and 3.52 (SD = 1.75). The number of food categories per sample was significantly higher among females than among males during March (U = 479, P = 0.024). During the two following months female samples tended to contain more food categories than male samples, but the differences were not significant (April: U = 1045, P = 0.051, May: U = 833, P = 0.075). A significant difference between months in the number of food categories per sample was detected among males (H_2 = 20.6, P < 0.001), but not among females (H_2 = 5.50, P = 0.064). Male samples contained significantly less food categories during March than the two following months (March vs. April: Q = 2.94, P < 0.05, March vs. May: Q = 4.51, P < 0.05), while no significant difference was detected between April and May (Q = 2.03, ns).

The estimated quantities of ground plants consumed did not differ significantly between the sexes in any of the three months (March: U = 422, P = 0.074, April: U = 1003, P = 0.138, May: U = 788, P = 0.268). As illustrated in Fig 2, the consistent consumption of much larger quantities of pine needles among males was the most pronounced diet difference when comparing quantities.

4. Discussion

Sexual differences in the proportions of ground plants in their spring diets, and a more pronounced increase of this food category among females, have been reported earlier (Gjerde & Wegge 1987, Storch *et al.* 1991, Borchtchevski 1995). Such proportional differences were also confirmed in this study. On a quantitative basis, as shown in this study, the most apparent diet difference was the much larger quantities of pine needles among males, whereas the difference in the amount of ground foods was negligible. Our estimates of quantities consumed are approximate since less digestible foods are over-represented in the fae-

Table 2. The average number of berry seeds per ml. of faecal samples of male and female Capercaillies in Varaldskogen during the spring of 1997.

Period	March		April		May	
Sex	Males	Females	Males	Females	Males	Females
N	46	14	56	22	38	23
Cowberry seeds						
Average	0	1.0	1.0	4.5	1.1	2.7
SD	0	2.7	3.0	12.3	3.6	6.0
Freq*	0	14.3	19.6	27.3	23.7	34.8
Cranberry seeds						
Average	0	0.1	1.6	1.1	1.0	1.8
SD	0	0.3	3.5	2.2	2.4	3.2
Freq*	0	14.3	28.6	27.3	23.7	43.5
Crowberry seeds						
Average	0	0	0	0	0	0
SD	0	0	0	0.1	0.1	0.1
Freq*	0	0	0	4.6	2.6	8.7

*Frequency of occurrence

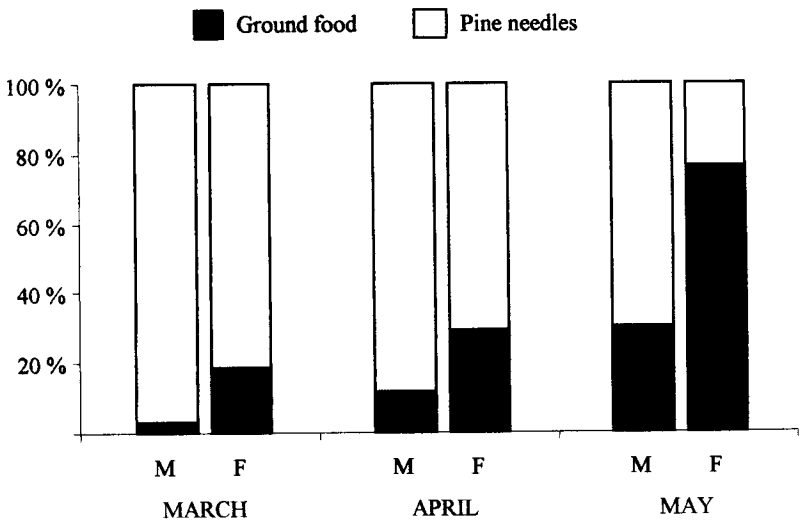

Fig 1. Average proportions (%) of ground plants and pine needles in the faecal samples from male (M) and female (F) Capercaillies at Varaldskogen during March, April and May 1997.

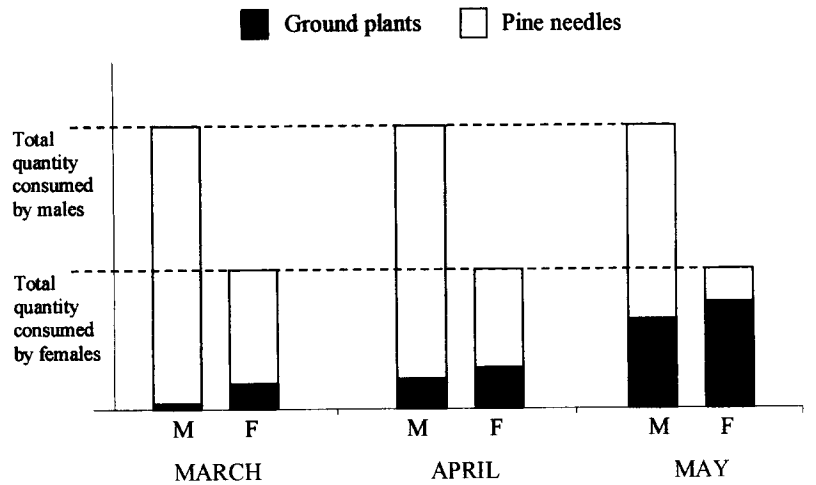

Fig 2. Relationship between quantities of ground plants and pine needles consumed by male (M) and female (F) Capercaillies at Varaldskogen during March, April and May 1997, assuming that the sexual difference in total quantity ingested is similar to the extent of the sexual size dimorphism (1:2.05).

cal samples. In our case, pine needles are the least digestible food due to their low protein content (Andreev 1988, Pulliainen & Tunkkari 1991). Thus, the quantity of ground food consumed was probably more under-estimated among males than among females. Consequently, more precise estimates of quantities of ground plants consumed would probably have further reduced, or eliminated the slight sexual disparity.

Both sexes' utilisation of ground food was probably somewhat constrained by limited availability, since they supplemented their diets with a large fraction of the easily available and less digestible pine needles during most of the spring season. However, males' exploitation of ground foods may be more severely affected by limited availability because they require much more food each day than females do. Males must consume approximately twice the amount of ground food per day in order to obtain a similar proportion of this food in their diet as females. Intake of twice the amount of food can be obtained by ingesting larger quanta per unit of time, or by prolonging foraging time. The larger beak size of males may facilitate higher rate of food intake, but probably only when feeding on specific types of food. For instance, over-wintering berries and the phenology of buds of bog cottongrass exclude the possibility of taking large bites. Furthermore, larger bites may decrease the benefit from feeding on

certain food items because a larger proportion of the ingesta will consist of crude fiber. Thus, it is probable that males must prolong foraging time substantially in order to consume a similar proportion of ground plants as females.

Prolonging foraging time may not be a sustainable strategy for several reasons. Firstly, the time available for feeding per day may be limited by physiological constraints on resource acquisition (i.e. foraging, digestion and absorption) and energy expenditure (Weiner 1992, Ydenberg *et al.* 1994, Houston 1995). Secondly, foraging animals are likely to experience greater predation risk per unit of time (Lima 1986, McNamara & Houston 1987), due to decreased vigilance (Milinski 1984). Thirdly, the net benefit from feeding on ground plants will be smaller among males if they must prolong foraging time substantially in order to consume similar proportions of these plants as females. This may promote distinct feeding strategies between the sexes where males limit their activity in order to conserve energy instead of spending time on selective ground feeding. Contrary to females, which have to invest in egg-laying, males may postpone intensive exploitation of ground foods until the moulting period in early summer.

Different feeding strategies between the sexes, in which males spend less time with selective ground feeding than females, may also be promoted by other factors. In their report on male spacing pattern around leks, Wegge and Larsen (1987) proposed that the more or less exclusive daytime territories, or mutual avoidance behaviour (Wegge *et al.* in press), limited confrontations with conspecifics. Thus, males' movement during daytime and their choice of feeding sites may be restricted. Moreover, males spend more time than females on the leks, and their activity tends to be distributed in a more bimodal fashion at the current time of year (Gjerde & Wegge 1987). This pattern implies that male lekking activities consume time that could be used for ground feeding, and as a consequence, males' dependence upon readily available pine needles increases further. Hypothetically, the larger size and less cryptic plumage may expose males for a higher predation pressure while foraging on the ground than females. If so, they may be more constrained in their search for patchily distributed new ground foods than females; they may spend proportionally less time on the ground or avoid feeding in "risky" but richer sites.

In this study, the number of food categories per sample was consistently higher among females, and graminoids and forbs were almost solely detected among the female samples. The larger number of food categories among females was probably caused by a smaller probability of detecting rare food items in the males' faecal samples due to their consumption of a much larger amount of pine needles. Conversely, the difference in the utilisation of graminoids and forbs, which showed up in the females' samples during the last month, may be due to different access to these food sources between the two sexes. Males are linked to small home ranges surrounding one geographical point, the lekking ground, during most of April and the whole of May (Wegge & Larsen 1987, Storch 1997). Females are also tied to one point, the nest, but not before the beginning of May. Leks tend to be located in late winter habitats (Gjerde *et al.* 2000) on relatively low site quality (Rolstad & Wegge 1987). In contrast to males, females are wider roaming and free to settle in habitats richer in spring forage (Wegge 1985, Storch 1997). Evidence supporting this difference in access to richer ground food is the abrupt movement away from the lekking grounds to richer forest types by males immediately after the lekking period has come to an end (Wegge & Larsen 1987, Rolstad *et al.* 1988, Hjeljord *et al.* 2000). Presumably, they move away to get access to richer food resources that were in short supply within their spring ranges.

Acknowledgements: We thank Ellen Arneberg, Nina E. Eide, Vegard Gundersen and Trond Wegge for assistance in the field. Torstein Storaas gave constructive input to the manuscript. The study was funded by the Directorate for Nature Management and the Forestry Division of the Ministry of Agriculture.

Selostus: **Sukupuolten kokoeron vaikutus metson ruokavalion muutokseen keväällä**

Artikkelin kirjoittajat tutkivat ulostenäytteisiin perustuen koirasmetsojen ja koppeloiden keväis-

tä ruokavalion muutosta Varaldskogenissa, Kaakkois-Norjassa. Kenttäkerroksen kasvilajien osuus oli koppeloiden ulostenäytteissä (n = 59) kaikkina tutkimuskuukausina (maaliskuu–toukokuu) suurempi kuin koirasmetsojen ulostenäytteissä (n = 140). Kenttäkerroksen kasvien osuus oli sekä naaraiden että koiraiden näytteissä suurempi toukokuussa kuin maalis- tai huhtikuussa. Kun huomioitiin käytetyn ravinnon määrä ja männynneulasten huono sulavuus, havaittiin koirasmetsojen käyttävän ravinnokseen lähes saman verran kenttäkerroksen kasveja kuin koppeloiden. Koirasmetso on kooltaan kaksi kertaa koppeloa suurempi. Koirasmetsot tarvitsevatkin huomattavasti enemmän ravintoa kuin koppelot. Koiraat näyttävät hyötyvän vähemmän maassa tapahtuvasta ruokailusta ja hyödyntävän vähän ravintoaineita sisältäviä, mutta helposti saatavilla olevia männynneulasia. Lisäksi koiraiden soidinkäyttäytyminen ja päiväreviirillä oleskelu voivat lyhentää ruokailuun käytettävissä olevaa aikaa. Kenttäkerroksen kasveja on ilmeisesti vähemmän saatavilla soidinpaikan ympäristössä sijaitsevilla koiraiden päiväreviireillä kuin niiden ulkopuolella.

References

Andreev, A. V. 1988: Ecological energetics of Palearctic Tetraonidae in relation to chemical composition and digestibility of their winter diets. — Can. J. Zool. 66: 1382–1388.

Borchtchevski, V. G. 1995: Comparison of the spring diets of male and female Capercaillies Tetrao urogallus in the Russian taiga. — Gibier Faune Sauvage, Game Wildl. 12: 303–320.

Chapuis, J. L. & Didillon, M. C. 1987: Methods for research on the food habits of Galliformes. — Gibier Faune Sauvage. 4: 295–320.

Gjerde, I. 1990: Determination of sex in Capercaillie by means of winter dropping size. — Fauna Norv. Ser. C. Cinclus 13: 91–92.

Gjerde, I. & Wegge, P. 1987: Activity patterns of Capercaillie, Tetrao urogallus, during winter. — Holarct. Ecol. 10: 286–293.

Gjerde, I., Wegge, P. & Rolstad, J. 2000: Lost hotspots and passive female preference: the dynamic process of lek formation in Capercaillie Tetrao urogallus. — Wildl. Biol. 6: 291–298.

Hjeljord, O., Wegge. P., Rolstad, J., Ivanova, M. & Beshkarev, A. B. 2000: Spring-summer movements of male Capercaillie *Tetrao urogallus*: A test of the 'landscape mosaic' hypothesis. — Wildl. Biol. 6: 251–256.

Houston, A. I. 1995: Energetic constraints and foraging efficiency. — Behav. Ecol. 6: 393–396.

Lima, S. L. 1986: Predation risk and unpredictable feeding conditions: determinants of body mass in wintering birds. — Ecology 67: 377–385.

Lindén, H. 1984: Annual patterns in the ecological energetics of the Capercaillie Tetrao urogallus in captivity. — Finn. Game. Res. 42: 19–27.

McNamara, J. M. & Houston, A. I. 1987: Starvation and predation as factors limiting population size. — Ecology 68: 1515–1519.

Milinski, M. 1984: A predator's cost of overcoming the confusion effect of swarming prey. — Anim. Behav. 32: 233–242.

Potopov, R. L. & Andreev, A. V. 1973: On the black grouse bio-energetics in winter. — Rep. Acad. Sci. USSR, Biol. Ser. 210: 499–500. (In Russian).

Pulliainen, E. & Tunkkari, P. S. 1991: Responses of the Capercaillie Tetrao urogallus, and the willow grouse Lagopus lagopus, to the green matter available in early spring. — Holarct. Ecol. 14: 156–160.

Rolstad, J. & Wegge, P. 1987: Habitat characteristics of Capercaillie display grounds in southeastern Norway. — Holarct. Ecol. 10: 219–229.

Rolstad, J., Wegge, P. & Larsen, B. B. 1988: Spacing and habitat use of Capercaillie during Summer. — Can. J. Zool. 66: 670–679.

Semenov-Tjan-Sanskij, O. I. 1960: Ecology of grouse in the Lapland reserve. — Proc. Lapland Reserve 5: 1–318. (In German).

Storaas, T., Wegge, P. & Kastdalen, L. 2000: Weight-related renesting in Capercaillie Tetrao urogallus. — Wildl. Biol. 6: 299–303.

Storch, I., Schwarzmüller, C. & von den Stemmen, D. 1991: The diet of Capercaillie in the alps: A comparison of hens and cocks. — In : Trans. XX. IUGB-Congress. Gödöllö, Hungary: 630–635.

Storch, I. 1997: Male territoriality, female range use, and spatial organisation of Capercaillie Tetrao urogallus leks. — Wildl. Biol. 3: 149–161.

Wegge, P. 1985: Spacing patterns and habitat use of Capercaillie hens in spring. — In: Hudson, P. J. & Lovel, T. W. I. (eds), Proc. Int. Grouse Symp. 3: 261–274.

Wegge, P. & Larsen, B. B. 1987: Spacing of adult and subadult common Capercaillie during the breeding season. — The Auk 104: 481–490.

Wegge, P., Kvalsgård, T., Hjeljord, O. & Sivkov, A. 2003: Spring spacing behaviour of Capercaillie males does not limit numbers at leks. — Wildl. Biol. (In press).

Weiner, J. 1992: Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. — Trends Ecol. Evol. 7: 385–388.

Ydenberg, R. C., Welham, C. V. J., Schmid-Hempel, R., Schmid-Hempel, P. & Beauchamp, G. 1994: Time and energy constraints and the relationship between currencies in foraging theory. — Behav. Ecol. 5: 28–34.