Sexual differences in temperature regulation and energetics in the Capercaillie *Tetrao urogallus*

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Rintamäki, H., Karplund, L., Lindén, H. & Hissa, R. 1984: *Sexual differences in temperature regulation and energetics in the Capercaillie* Tetrao urogallus. — Ornis Fennica 61:69—74.

The temperature regulation of male (average mass 4.00—4.11 kg) and female (1.80—1.85 kg) Capercaillie was studied in July-August and February-March in northern Finland. Sex-dependent differences were found in several thermoregulatory parameters, including body temperature, which was on the average 0.5°C lower in male than in female Capercaillie. Seasonal variation in thermoregulation was more obvious in male than in female birds. Male Capercaillie naturally produced more heat than the smaller female birds, but the mass-specific heat production (W/kg) was higher in female birds at all the studied ambient temperatures. The metabolic rate expressed as $W/kg^{0.75}$ did not differ between the sexes in the thermoneutral zone in winter, but was higher in females in the thermoneutral zone in summer and below it in both seasons. The thermal conductance was lower in males than in females.

The present results show clear intersexual differences in the thermoregulation of the Capercaillie. The differences can be partly explained by the great size difference, but those in the metabolic rate below the thermoneutral zone and the differences in body temperature cannot be directly caused by sexual size dimorphism. The results also show that the male Capercaillie is especially well adapted to harsh winter conditions.

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Introduction

The Capercaillie *Tetrao urogallus,* the largest of the tetraonids (Tetraonidae), inhabits an extensive forest zone in Siberia, East Europe and Scandinavia (e.g. Cramp & Simmons 1980). *Tetrao urogallus* can be divided into several subspecies with only slight morphological differences (e.g. Johansen 1957, Koskimies 1958). One of the most interesting features is the conspicuous sexual size dimorphism, which is associated with differences in feeding habits, energy requirements and growth strategies (Seiskari 1962, Lindén 1984a, Lindén et al. 1984).

Gavrilov (according to Kendeigh et al. 1977) has provided experimental data on the temperature regulation of the male Capercaillie, and the energetics of several tetraonids, including the Capercaillie, has been studied in detail by Andreev (1973, 1979). Owing to the unequal size of males and females, sex-related energetic differences are likely to occur and there may be some differences between the subspecies. The subject of the present study was the temperature regulation and energetics of the most northern subspecies of the Capercaillie *Tetrao urogallus urogallus* in winter and summer in Lapland, northern Finland. Interesting material for comparison is provided by a large series of energy consumption experiments carried out with the same birds in semi-natural conditions (Lindén 1984a).

Material and methods

Adult male (7 individuals, age 2—5 years) and female (7—8 individuals, age 2—4 years) Capercaillie were used. The birds were hatched and reared at the Meltaus Game Research Station in Lapland, northern Finland (66°55'N, 25°20'E), from eggs which were collected from a local, racially uniform population of the Capercaillie. For further details of the rearing of the birds, see Lindén (1981). The adult Capercaillies were kept under outdoor conditions: the females in an aviary and the males in an enclosure. Both male and female birds could use a shelter throughout the year. The birds received poultry fodder, oats, green plant material (pine needles in winter), sand and water (snow in winter) *ad libitum.*

The winter measurements were carried out in February-March 1983 and the summer measurements in August-September 1983 in the laboratory of the Meltaus Game Research Station. The daily outdoor temperature during the experiments was —9.1 ± 2.1°C ($\bar{x}$±SE, N = 14 days) in winter and +8.7 ± 1.0°C (N = 15 days) in summer. The photoperiod varied between 7h 3min and 9h 10min in winter, and 14h 33min and 16h 31min in summer.

The measurements were performed daily between 8.30

Table 1. Standard metabolic rate (SMR, $\bar{x}\pm SE$) of the Capercaillie in the thermoneutral zone (TNZ), metabolic rate observed at the lowest ambient temperature at which each bird was measured, and predicted values of basal metabolic rate (BMR, Aschoff & Pohl 1970). Multiplication of metabolism gives the value required to increase the lowest measured metabolic rate (at TNZ) to the observed maximal metabolism (at T_a —27.5 — —31.5°C). * Differs significantly ($P<0.01$) from the summer value.

			SMR at TNZ		SMR at —27.5— —31.5°C			
season	sex	mass of bird (kg)	W/kg	W/kg$^{0.75}$	W/kg	W/kg$^{0.75}$	predicted BMR (W/kg)	multiplication of metabolism
	♂	4.11±0.15	4.4±0.1	6.2±0.1	5.6±0.1	8.0±0.2	3.0	1.37±0.04*
		n=7	27	27	7	7		7
WINTER		P<0.001	P<0.001		P<0.01	P<0.01		P<0.01
	♀	1.85±0.05	5.6±0.1*	6.6±0.2*	9.0±0.6	10.4±0.6	3.7	1.74±0.08
		n=7	20	20	7	7		7
	♂	4.00±0.10	4.3±0.1	6.6±0.2	6.5±0.4	9.1±0.6	3.0	1.55±0.03
		n=7	21	21	7	7		7
SUMMER		P<0.001	P<0.01	P<0.1	P<0.01	P<0.05		P<0.01
	♀	1.80±0.03	5.0±0.2	5.7±0.2	9.1±0.3	10.5±0.4	3.8	1.95±0.09
		n=8	16	16	8	8		8

and 17.00 hrs. A Capercaillie, fasted overnight, was weighed and placed in a dark metabolic chamber, measuring 90 x 40 x 55 cm. When female birds were used, an additional airtight box (52 x 33 x 28 cm) was placed in the chamber to diminish its volume. Compressed air was led through the chamber at a rate of 4—8 l/min, measured with a Rotameter 1100 flow meter. Tubes containing silica gel and soda lime granules were used before and after the chamber, to remove H_2O and CO_2, respectively. The initial temperature of the chamber was ca. 30°C and after an equilibration time of about 1.5 h, the stabilized values for oxygen consumption (vO_2) and cloacal temperature (T_{cl}) were recorded. Thereafter the chamber temperature was reduced by degrees of about 10°C to ca. —30°C, the stabilized values for vO_2 and T_{cl}being recorded after each reduction. The birds usually sat quietly in the metabolic chamber.

Oxygen consumption was measured in an open flow system with a paramagnetic Beckman E2 oxygen analyzer, which was calibrated each morning before the measurements (Hill 1972). For the calculation of heat production, the energy equivalent of 1 ml of O_2 was assumed to be 19.68 J. Cloacal temperature was measured continuously with a diode probe (inserted 50 mm into the cloaca) and a digital thermometer. The ambient temperature (T_a) in the chamber was measured with a similar probe and a mercury thermometer. The relative humidity in the chamber was measured with a hair hygrometer.

For statistical comparisons the one-way analysis of variance and t-test were used when appropriate.

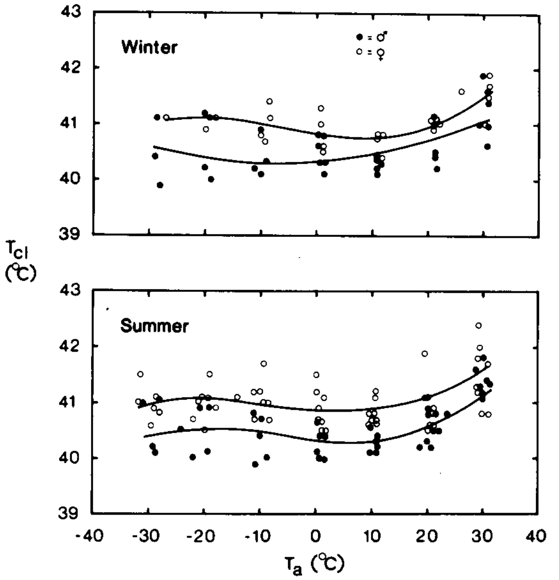

Fig. 1. Cloacal temperature (T_{cl}) of male (closed symbols, lower curve in both seasons) and female (open symbols) Capercaillie in winter and summer. The equations describing the relation of T_{cl} to ambient temperature (T_a) in female birds are:

$T_{cl} = 40.8 - 0.013 \cdot T_a + 0.00046 \cdot T^2_a + 0.000024 \cdot T^3_a$
in winter and
$T_{cl} = 40.9 - 0.008 \cdot T_a + 0.00044 \cdot T^2_a + 0.000021 \cdot T^3_a$
in summer.

In male birds the equations are:
$T_{cl} = 40.3 + 0.008 \cdot T_a + 0.00061 \cdot T^2_a$ in winter and
$T_{cl} = 40.4 - 0.008 \cdot T_a + 0.00048 \cdot T^2_a + 0.000023 \cdot T^2_a$
in summer.

Results

In both summer and winter the body mass of the female birds was 55 % lower than that of the males (Table 1). In both sexes the mass was only 3 % (nonsignificant) lower in the summer than in the winter experiments (there is, however, significant seasonal variation in body mass during the year, see Lindén 1984a). The relative humidity in the chamber fluctuated widely, showing an average of 51.3 ± 1.0 % ($\bar{x}\pm SE$, N = 174).

Body temperature. In both summer and winter the mean cloacal temperature (T_{cl}) in the male birds was 0.4—0.5°C lower ($P<0.001$) than in the females (Table 1, Fig. 1). The same pattern is seen in all the T_{cl} curves: after maximal T_{cl}'s at high T_a's, T_{cl} declines by 0.7—0.9°C and then increases again as T_a decreases further. In the female birds, T_{cl} is lowest at almost at the same T_a (6.5—8.5°C) in the two seasons, but in the male birds the minimum shifts from ca. 6°C in summer to ca. —6°C during the winter (Fig. 1).

Metabolic rate. After oxygen consumption has been converted to Watts, three different dimensions are used for the metabolic rate: W/bird, W/kg (mass-specific metabolic rate) and W/kg$^{0.75}$(for the use of metabolic body size, see Bligh 1973, Kleiber 1975).

In the male Capercaillie, the standard metabolic rate (SMR) in the thermoneutral zone (TNZ) showed no marked seasonal changes, being 17.0±0.7 W/bird (N = 22) in summer and 18.0±0.5 W/bird (N = 27) in winter (see also Table 1 and Fig. 1). In the female birds, metabolism at TNZ was 8.9±0.4 W/bird (N = 16) in summer and 10.3±0.2 W/bird in winter, thus showing seasonal variation ($P<0.01$). The mass-specific metabolic rate at TNZ was 12 % lower in summer than in winter in the females (Table 1). The metabolism/bird was 74 % (in winter) and 91 % (in summer) higher in the males than in the females, but due to the size difference the metabolic rate/kg was 27 % (in winter, $P<0.001$) and 16 % (in summer, $P<0.01$) higher in the females.

When the metabolic rate is expressed as W/kg$^{0.75}$ instead of W/kg, sex-dependent differences in SMR at TNZ disappear in winter. In summer, however, the metabolic rate/kg$^{0.75}$ is 16 % higher in male birds than in females (Table 1). Only female birds showed significant seasonal variation.

In the females, the highest metabolic rates observed at the lowest T_a's (—27.5 — —31.5°C in different birds) were 16.3±0.8 W/bird (N = 8) in summer and 17.3±1.1 W/bird (N = 7) in winter. In the males the corresponding values were significantly higher ($P<0.001$), being 25.8±1.9 W/bird (N = 7) in summer and 23.1±0.9 W/bird (N = 7) in winter. The maximal mass-specific metabolic rates of the female birds were, however, 41 % higher in summer ($P<0.01$) and 59 % higher in winter ($P<0.01$) than those of the males, and the same trend is seen when metabolism is expressed as W/kg$^{0.75}$ (Table 1).

Irrespective of the dimension of the metabolic rate, the lowest metabolic rate of the females has to be multiplied by a significantly ($P<0.01$) larger coefficient than in the male birds to obtain the metabolic rate seen at the coldest end of the T_a range (Table 1). In males the coefficient was, moreover, significantly ($P<0.01$) higher in summer than in winter.

The lower critical temperature shifted to a lower T_a in winter than in summer in both sexes (Table 2, Fig. 2). In both seasons the critical temperature was lower in male birds than in females.

Thermal conductance. Thermal conductance was calculated according to the equation (Calder & King 1974):

$$C = M/(T_{cl}—T_a)$$

where C = conductance (W/kg/°C)
M = metabolic rate (W/kg)
T_{cl} = cloacal temperature (°C)
T_a = ambient temperature (°C)

As shown in Table 2, the mean thermal conductance of the male Capercaillie is 20—44 % lower than that of the female ($P<0.001$ in both seasons). The thermal conductance of male birds was also 25 % lower ($P<0.001$) in winter than in summer.

Discussion

The present results suggest that several sex-dependent differences exist in the thermoregulation of the Capercaillie. They show unequivocally that

Table 2. Mean ($\bar{x}$±SE) cloacal temperature (T_{cl}) of the Capercaillie in the ambient temperature range of —31.5 — 31.5°C, observed thermal conductance (C), theoretical C predicted by the equation of Herreid & Kessel (1967), and lower critical temperature (LCT). * Differs significantly ($P<0.01$) from the summer value.

season	sex	T_{cl} (°C)	C below TNZ (W/kg/°C)	predicted C (W/kg/°C)	LCT (°C)
WINTER	♂	40.6±0.1 n=31	0.089±0.003* 10	0.070	—3
		P<0.001	P<0.001		
	♀	41.0±0.1 n=26	0.159±0.004 12	0.106	9
SUMMER	♂	40.6±0.1 n=40	0.120±0.005 20	0.071	6
		P<0.001	P<0.001		
	♀	41.1±0.1 n=58	0.148±0.004 38	0.108	12

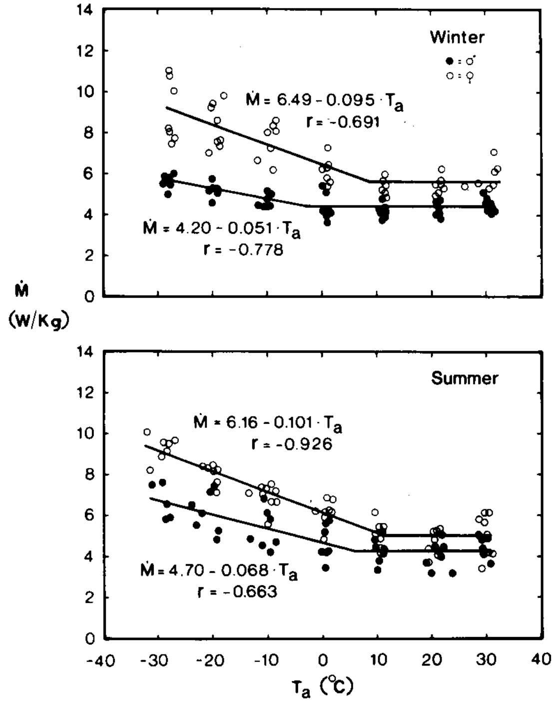

Fig. 2. Relation of metabolic rate ($\dot{M}$) to ambient temperature (T_a) in male (closed symbols, lower curve in both seasons) and female (open symbols) Capercaillie in winter and in summer.

even the body temperature is dependent on sex. The large size difference between the sexes can hardly explain the higher T_{cl} of the females. Body weight does not significantly affect the temperature of nonpasserine birds during the daily activity time, although the range of the circadian oscillation of body temperature decreases with increasing body size (Aschoff 1982). The circadian patterns of body temperature in the Capercaillie are still to be resolved, though some measurements have been made throughout a winter night in outdoor conditions (Marjakangas et al. 1984). The different environmental conditions in that study are probably the reason why Marjakangas et al. (1984) could not demonstrate any sex-dependent T_{cl} differences. The explanation of the higher T_{cl} in the female Capercaillie than in the male in the present study may be the higher mass-specific metabolic rate. The present values for the two sexes fit well within the body temperature range of other Galliformes, 40.0—42.4°C (Dawson & Hudson 1970).

The biological optimum temperature (BOT) is the T_a at which an animal is under minimal thermal stress. BOT can be determined from the relationship between T_a and T_{cl} being taken at the T_a at which T_{cl} is minimal (excluding T_{cl} during extreme cold exposure) (Nichelmann 1983). The curvilinear variation of T_{cl} in relation to T_a does not indicate any seasonal change in the BOT of female Capercaillie. In males, however, the lower BOT in winter than in summer suggests that some kind of acclimatization occurs.

The standard metabolic rate at TNZ (basal metabolic rate, BMR, *sensu* Kendeigh et al. 1977) in the present study is clearly higher than the BMR's predicted by theoretical equations; e.g. it exceeds the values predicted by the equation of Aschoff & Pohl (1970) by 32—51 % (Table 1). A higher BMR than that predicted by allometric equations is a common observation in northern avian species (see e.g. Schwan & Williams 1978, Weathers 1979, Rintamäki et al. 1983). Weathers (1979) has proposed that the geographical location of the bird species influences the SMR predicted from the bird's mass in such a way that SMR increases by 1 % with each degree of latitude. This could partially but not entirely explain the difference between the observed and predicted values.

The present results also clearly exceed the BMR observed in the male Capercaillie at night (ca. 3 W/kg; Gavrilov according to Kendeigh et al. 1977). The higher metabolism observed in the present study is partly explained by the fact that in day-active avian species BMR is lower at night than in daytime (see Aschoff & Pohl 1970).

The results showed seasonal variation in the SMR at TNZ in the female Capercaillie. In birds weighing more than 0.1 kg, the variation of BMR is usually only slight (Weathers & Caccamise 1978, Weathers 1979) and in some gallinaceous birds the basal metabolism is even lower on winter nights than in summer (Gavrilov according to Kendeigh et al. 1977), which suggests good adaptation to harsh winter conditions. Our results show no seasonal variation at TNZ in the metabolic rate of the male Capercaillie and are thus in agreement with those of Gavrilov (op. cit.).

Further seasonal changes in the thermoregulation of the Capercaillie are seen in the extent to which the birds have to increase their TNZ metabolism at T_a around —30°C. Both sexes increase their metabolism relatively more in summer than in winter. In the male Capercaillie the reason may be the greater conductance in summer than in winter. In female birds, however, the reason is the lower SMR at TNZ in summer than in winter: a larger coefficient is needed in summer than in winter to reach maximal metabolism.

When the metabolic rate is expressed per unit body weight raised to the exponent 0.75, the metabolic rates of animals of unequal body size should be comparable (Kleiber 1975). Therefore the difference between the maximal metabolic rates (per $kg^{0.75}$) of male and female Capercaillie suggests that the body size is not the only explanation of the different metabolic rates of male and female birds.

The lower critical temperatures (LCT) of the male Capercaillie were 4°C (in summer) and 7°C (in winter) below the corresponding values of Gavrilov (given in Kendeigh et al. 1977).

As shown in Table 1, the observed values of thermal conductance at T_a below TNZ exceed the values predicted by the equation of Herreid and Kessel (1967) by 29—71 %. It seems possible, however, that above a critical body weight the value of thermal conductance ceases to depend on body weight in the manner supposed in theoretical equations (see Bech 1980). The winter plumage of tetraonids is well-developed compared with the summer plumage (Kuzmina 1961), which suggests that the insulation of the plumage is better in winter than in summer. The present results for male birds show clearly lower conductance in winter than in summer. The conductance of the female Capercaillie seems to be constant throughout the year, except possibly during moulting. The conductance of female birds is essentially the same as that of juvenile Capercaillie of similar size (Hissa et al. 1983). Of course the conductance does not depend only on the properties of the plumage but also on subcutaneous fat deposits and on the flow of blood in the skin and subcutaneous tissues.

When the present results are compared with those of existence metabolism experiments *(sensu* Kendeigh et al. 1977) carried out throughout the year in outdoor conditions with caged Capercaillie (see Lindén 1984a), some interesting differences may be observed. Firstly, contrary to the present results, the existence metabolism, when expressed as multiples of BMR, is significantly higher in males than in females in both summer and winter, which suggests that in the wild males live under stronger energetic selective pressure than females. Secondly, the energy existence requirements of females and males seem to be only 50—60 % and 80—85 %, respectively, of the SMR values recorded in this study. This disagreement is very probably due to some methodological differences (e.g. duration of measurements: this study 6—8 hrs in daytime, Lindén 1984a 48 hrs in succession), but the existence energy requirements of Capercaillie, especially in winter, are evidently small.

The costs of free-living in winter are surprisingly small considering the following energy-demanding features in the life of the Capercaillie:

- The Capercaillie is almost monophagous in winter, feeding on pine needles, which are rich in resins and phenols and have low digestibility (see Lindén 1984b).
- The winter weight gain of the male Capercaillie male is remarkable: over 0.5 kg from October to March. This is connected with the need to be strong and successful in the lek in spring (Lindén 1984a).
- Low temperatures and wind usually increase energy requirements, but in the existence metabolism measurements no significant increments could be observed (Lindén 1984a).

From the present results we may conclude that intersexual differences exist in several thermoregulatory features of the Capercaillie. Most of them are obviously caused by the great size difference between the sexes, which leads to a less advantageous weight/surface area ratio in the female than in the male. Male Capercaillie also show clear seasonal changes in the lower critical temperature and thermal conductance, with the result that cold-exposed males have to increase their metabolism to a lesser extent in winter than in summer. In female Capercaillie clear seasonal variation is seen only in SMR at TNZ; a light variation in the lower critical temperature. We may also note that Capercaillie roosting in the snow (see Semenov-Tjan-Šanskij 1960) are living at or near TNZ, and that the short foraging time and the use of a superabundant food source (pine needles) are thus important adaptations (see also Marjakangas et al. 1984).

Acknowledgements. We are grateful to Mr. Albin Ylisuvanto and Mr. Ilkka Pesonen for technical assistance. This study was supported by a grant (to H.R.) from the Academy of Finland.

Selostus: **Sukupuolten välisiä eroja metson lämmönsäätelyssä ja energetiikassa**

Metson lämmönsäätelyä tutkittiin Rovaniemen maalaiskunnassa Meltauksen riistantutkimusasemalla helmi-maaliskuussa ja elo-syyskuussa 1983. Päivisin tehdyissä kokeissa mitattiin pimeässä aineenvaihduntakammiossa lämmönsäätelyvasteet linnuilta, joita oli paastotettu yli yön.

Tulokset osoittavat, että koirasmetso ja koppelo poikkeavat toisistaan miltei jokaisessa lämmönsäätelyyn liittyvässä tekijässä, jopa lintujen lämpötilakin on erilainen eri sukupuolilla (koirasmetsolla keskimäärin 0.5°C alhaisempi kuin koppelolla, kuva 2, taulukko 2).

Lämmöntuotosta epäsuorasti laskettu konduktanssi (lämmönhukan mitta) on koirasmetsolla merkitsevästi pienempi kuin koppelolla. Koirasmetsojen termoneutraalivyöhykkeen alaraja (alempi kriittinen lämpötila) oli myös molempina vuodenaikoina alemmassa lämpötilassa kuin koppelolla.

Kookkaan koirasmetson lämmöntuotto on luonnollisesti suurempi kuin koppelon, mutta kun se suhteututaan linnun painoon, on koppeloiden lämmöntuotto voimakkaampaa kuin koiraan sekä termoneutraalissa että kylmässä ympäristössä (kuva 1, taulukko 1). Kun linnun paino korotetaan potenssiin 0.75 ja lämmöntuotto suhteutetaan tällä tavalla korjattuun painoon, pitäisi tulosten olla painoerosta huolimatta vertailukelpoisia. Tällainen muunto pienentääkin eri sukupuolten lämmöntuottoarvojen välistä eroa termoneutraalissa ympäristössä mutta kylmässä on edelleen selvästi nähtävissä koppeloiden kiihkeämpi lämmöntuotto. Riippumatta tavasta, millä lämmöntuotto ilmaistaan osoittautuu, että koppelot kohottavat kylmäaltistuksen aikana lämmöntuottoaan suhteellisesti enemmän kuin koirasmetsot. Pelkällä kokoerolla ei siis voi selittää sukupuolten välisiä lämmönsäätelyeroja, vaan ilmeisesti eri sukupuolet poikkeavat tavassaan reagoida lämpötilaärsykkeisiin. Metson lämpötilassa ilmenevää sukupuolten välistä poikkeamaa ei kokoero voi selittää lainkaan, sillä linnun lämpötila ei ole riippuvainen koosta.

Saadut tulokset osoittavat, paitsi selviä sukupuolten välisiä eroja lämmönsäätelyssä, myös että koirasmetson lämmönsäätelyssä tapahtuu selkeämpää vuodenaikaisvaihtelua kuin koppelolla, mikä ilmeisesti merkitsee hyvää sopeutumista energeettisesti vaativiin talviolosuhteisiin.

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Received November 1983