Energy costs during incubation in Svalbard and Willow Ptarmigan hens

GEIR WING GABRIELSEN AND SIGMUND UNANDER

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Studies of wild and captive Willow and Svalbard Ptarmigan hens have allowed us to estimate the daily energy cost during incubation. It was similar for the two species, varying between 70—85 kcal per day depending on number of eggs, nest insulation, ambient temperature, number of foraging periods and total time spent away from the nest. Daily energy cost during incubation was 15—20% above resting metabolic rate in non-incubating hens but only 45—55% of that in free-living non-incubating hens. Incubating hens reduced their energy expenditure through high nest attentiveness. A reduction in food intake during incubation led to loss in body weight.

Geir Wing Gabrielsen, Norwegian Polar Research Institute, Rolfstangveien 12, 1330 Oslo Lufthavn, Norway; Sigmund Unander, Division of Environment, Regional Commissioner of Aust Agder, Holbergsgate 54, 4600 Kristiansand.

Several Galliform species live and breed in arctic and subarctic regions where temperatures below 0° C and snow are not uncommon during nesting. Successful reproduction involves regulation of egg-temperature within optimal limits for embryonic development, a process dependent upon heat flow from the bird, nest attentiveness and nest insulation. Ptarmigan hens *(Lagopus* sp.) leave the nest to forage 2—5 times a day (Barth 1949; Pulliainen 1978; Erikstad 1985). The rate of egg cooling depends mainly on ambient temperature and the time spent away from the nest. As in many single-sex incubators, ptarmigan hens have to rewarm the eggs after each foraging period, as well as keeping the clutch of eggs at incubation temperature.

Indirect methods of estimating the cost of avian incubation include measurements of heat loss from the eggs (Kendeigh 1963), the clutch mass method (West 1960; Ricklefs 1974) and heat budget modelling (Walsberg & King 1978). Direct measurements of incubation cost have included measurement of food intake (Riddle & Brancher 1934; El-Wailly 1966; Brisbin 1964) and oxygen consumption or carbon dioxide production (Norton 1973; Mertens 1977, 1980; Biebach 1979; Gessaman & Findell 1979; Vleck 1981; Grant & Whittow 1983; Haftorn & Reinertsen 1985). Gabrielsen & Steen (1979) measured heart rate and egg temperature in incubating Willow Ptarmigan hens and suggested a relationship between egg temperature and energy cost of incubation.

In the present study measurements of body weight, food intake, egg, nest and ambient temperature, heart and respiration rate, oxygen consumption and carbon dioxide production of wild and captive Willow Ptarmigan *(Lagopus lagopus lagopus)* and Svalbard Ptarmigan *(Lagopus mutus hyperboreus)* hens are used to determine the energy cost of incubation and the nesting strategy of these birds.

Methods

Field investigations on wild birds were conducted during the summers of 1981 and 1982. Five Willow Ptarmigan hens were studied on Karlsøy Island, Troms County, Norway (70° N), and four Svalbard Ptarmigan hens at Ny-Ålesund on the western coast of Spitsbergen (79° N).

Ptarmigan hens were netted on the nest and fitted with ECG transmitters (SINTEF, TRE—1) fastened to a wire frame that was mounted on the bird in rucksack fashion. Insertion of the electrodes was performed under local anesthesia with one electrode placed close to the heart and the other under the abdominal skin (Gabrielsen & Steen 1979). Total weight of the rucksack and the 100 mHz transmitter (with batteries for 400—600 hrs operation) was 23 g. Heart rate signals were received through a directional Yagi antenna to a commercial FM-radio and recorded on cassette tapes for later analysis. Heart and respiration rates were later derived by means of an on-line microcomputer. Heart and respiration rates were averaged for 5 sec periods during resting, walking and when hens started incubating cold eggs. The values were calculated as the average of these 5 sec periods. Behavioural observations were made by a hidden observer through a telescope from at least 50 m distance. Egg, nest and ambient temperatures were recorded on a data logger (Aanderaa DL—1). One unfertilized ptarmigan egg, with copper-constantan thermocouple glued sub-surface on the upper side of the egg, was fastened in a fixed position in the middle of the nest. Other thermocouples were placed at the bottom of the nest to record nest temperature, and 10 cm above the ground level to record ambient temperature. Daily precipitation was measured at the meteorological stations in Tromsø and Ny-Ålesund. Ptarmigan hens of both species were caught and weighed 2—3 times during the incubation period.

Experiments on two captive hens of each species were carried out at the Department of Arctic Biology, University of Tromsø, Norway. Each hen with her mate was placed in an outdoor room (0.5 x 2 m) containing a metabolic chamber in which the eggs were laid. All four hens laid a normal clutch of 8—12 eggs. The males were removed just prior to incubation. Modified pelleted chicken food (Moss & Hanssen 1980) and water were given *ad libitum*. Food intake was measured every other day before, during and after the incubation period. After two weeks of incubation one hen of each species was equipped with an ECG transmitter, and one egg with a thermocouple was placed in the middle of the nest. Ambient temperature was recorded both inside and outside the metabolic chamber by thermocouples connected to a Fluke (2190 A) digital thermometer. Metabolism was measured in an open system, the metabolic chamber (40 x 30 x 25 cm) was connected to a carbon dioxide (Leybold-Heraeus, BINOS—2) and an oxygen (Applied Electro-Chemistry Inc. S—3 A, R—1 and N—22 M) analyzer through a plastic tube from the outdoor room. Air was dried ($CaCl_2$) and pumped through the system with a flow of 2.5—3.0 l/min. Airflow was measured in each experiment with a Tri-Flat flowmeter (Fischer & Porter, Type 10 A 3200). All results are given at STP. An energy equivalent of 4.8 kcal per l oxygen/hour was used (Schmidt-Nielsen 1975). 1 kcal corresponds to 4.185 KJ (Kleiber 1975). Cooled eggs (+4°C) were exchanged with the hens' own clutch during each experiment. Simultaneous measurements were made of the hens' heart and respiration rates, carbon dioxide production and oxygen consumption, egg and ambient temperature, following the initiation of incubation of each cooled clutch.

Two-tailed t-test was used to determine the significance of differences between means. Results are reported as mean ± standard deviation. The regression line in Fig. 7. was calculated by using least-squares method of linear regression.

Results

Field investigation

Willow Ptarmigan. — In wild Willow Ptarmigan hens the heart rate increased at each inspiration and decreased at each expiration (Fig. 1). The mean for incubating and undisturbed hens was 138 beats/min (b.p.m.) and respiratory rate was 25.2 breaths/min (br.p.m.) (Table 1; Fig. 1a). Within 5 to 10 sec after settling on the eggs, after a foraging period, heart rates rose to a mean maximum of 534 b.p.m. and respiratory rate to 35.2 br.p.m. (Table 1; Fig. 1b). The duration of the tachycardia period was associated with the length of time spent away from the nest and the ambient temperature (Gabrielsen & Steen 1979). Normally 40 to 80 minutes passed before heart and respiration rates had returned to resting levels. A temporary increase in heart and respiration rates occurred each time the eggs were turned and during periods of low ambient temperature. Hens left the nest 3—5 times a day (Table 2; Fig. 2).

Willow Ptarmigan hens were away from the nest for mean periods of 16.2 minutes during which the egg temperature dropped from 32°C

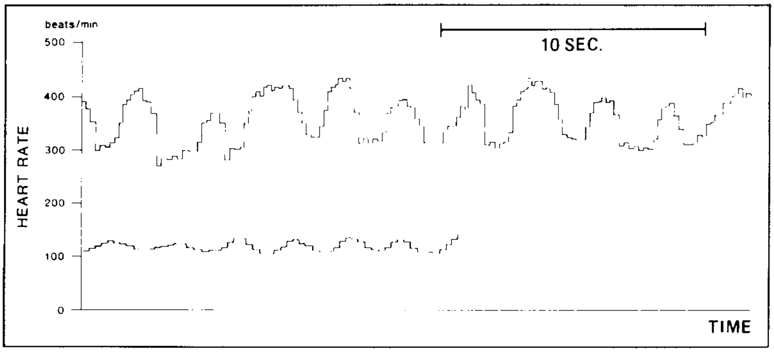

Fig. 1. Example of heart and respiration rates of a wild incubating Willow Ptarmigan hen: a) Incubating, b) 5 min after settling on cold eggs. Heart rate increased at each inspiration and decreased at each expiration.

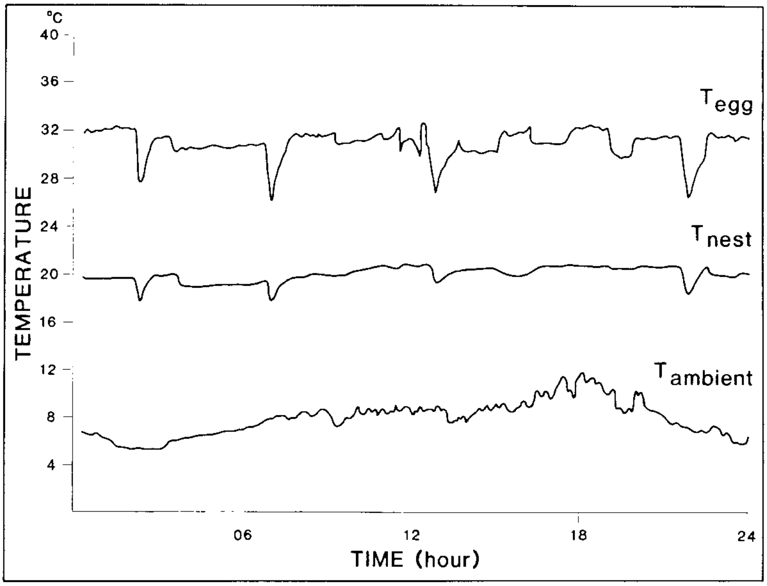

Fig. 2. Egg, nest and ambient temperature during one day of incubation in a wild Willow Ptarmigan hen. Drops in egg and nest temperature indicate periods away from the nest.

to a mean of 26.7°C (Table 2). Drop in egg temperature was related to ambient temperature and time spent away from the nest. Ambient temperatures and mean daily precipitation during the month of June, which was the main incubation period, are given in Table 3. The number of foraging trips was reduced from 4.1 to 3.3 per day ($p < 0.02$, t-test) during periods of precipitation. Body weight dropped on the average 19.5% (or 100 g) from the end of egg laying until hatching (Table 4). Hen weights at the end of the incubation period showed a wide range, from 450 to 550 grams (mean 498.6 g). Two of seven hens that were captured late at incubation deserted the nest. Both had low body weights (440 and 475 g).

Svalbard Ptarmigan. — The mean heart rate of incubating and undisturbed Svalbard Ptarmigan hens was 155 b.p.m. and the respiratory rate 25.3 br.p.m. When moving to or from the nest, mean heart rate was 205 b.p.m. and respiratory rate 28.5 br.p.m. (Table 1). Heart rate rose to a mean maximum of 442 b.p.m. within 5—10 sec after settling on the eggs after a foraging period, and the respiratory rate to 35.5 br.p.m. (Table 1; Fig. 3). Heart and respiration rates then declined gradually to resting level within 30—60 min, but increased each time the hen turned her eggs. Periods of increased heart and respiration rate occurred during normal incubation at intervals of about 10 minutes (Fig. 3).

Table 1. Mean heart (b.p.m.) and respiration (br.p.m.) rates of wild and captive ptarmigan hens.

Species		Number of birds	Resting		Walking		Start of incubating cooled eggs	
			b.p.m. X ± SD	br.p.m. X ± SD	b.p.m. X ± SD	br.p.m. X ± SD	b.p.m. X ± SD	br.p.m. X ± SD
Willow Ptarmigan hens	wild	5	138 ± 15.0	25.2 ± 1.3	224 ± 17.0	28.0 ± 1.4	534 ± 24.0	35.2 ± 1.1
	captive	2	190 ± 14.0	26.0 ± 1.4	290 ± 14.0	31.0 ± 1.4	460 ± 14.0	36.0 ± 1.0
Svalbard Ptarmigan hens	wild	4	155 ± 19	25.3 ± 1.0	205 ± 19.0	28.5 ± 1.9	442 ± 71.4	35.5 ± 1.9
	captive	2	200 ± 28	26.0 ± 1.0	270 ± 14.0	33.0 ± 1.4	400 ± 28.0	37.0 ± 1.4

Table 2. Mean values for nest attentiveness, duration of absence and drop in egg and nest temperature in wild incubating ptarmigan hens.

Species	Number of birds/days	Number of times away from nest per day (X ± SD)	Duration of absence (min) (X ± SD)	Egg temperature (°C) upon returning to the nest (X ± SD)
Willow Ptarmigan hens	3/17	4.1 ± 0.7	16.2 ± 6.0	26.7 ± 0.9
Svalbard Ptarmigan hens	2/7	2.9 ± 0.4	14.3 ± 3.6	25.6 ± 1.2

Table 3. Mean daily ambient temperature and precipitation in Tromsø and Ny-Ålesund (meteorological data) during the incubation period (June 1 to July 1 1981-82 for Willow Ptarmigan hens, and June 15 to July 15 1981-82 for Svalbard Ptarmigan hens).

Location	Year	Mean daily amb. temp. °C during the incubation period (X ± SD)	Absolute max. temp. °C during the incubation period	Absolute min. temp. °C during the incubation period	Number of days with precipitation	Mean daily precipitation (> 1 mm)
Tromsø	1981	6.1 ± 3.4	13.5	-0.8	9	4.4
	1982	5.3 ± 4.1	17.5	-1.2	14	4.2
Ny-Ålesund	1981	2.6 ± 1.8	9.4	-2.0	5	2.9
	1982	2.9 ± 2.6	6.9	-0.8	3	2.4

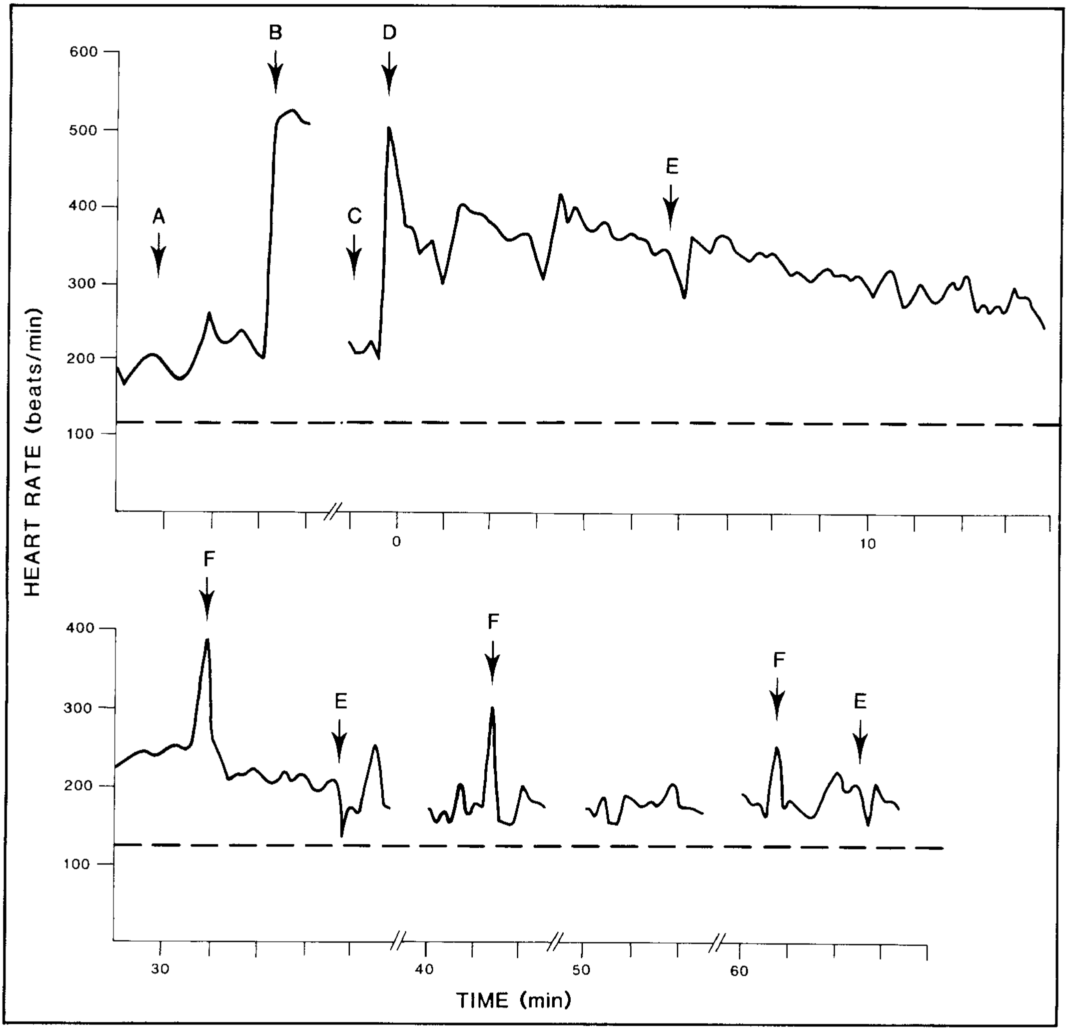

Fig. 3. Heart rate recordings from a wild nesting Svalbard Ptarmigan hen.
A — walking after leaving the nest.
B — flying away from the nest.
C — at the nest just prior to incubation.
D — initiation of incubation (and start of time scale).
E — a Fulmar *(Fulmarus glacialis)* flies over the nest.
F — a period of tachycardia without any change in behavior, probably due to shivering and heating of the clutch.

The hens left the nest 2—3 times a day (Table 2) and were away from the nest an average of 14.3 minutes at each absence. During the absence, egg temperature dropped from 32°C to a mean of 25.6°C (Table 2), depending on ambient temperature and duration of absence. Ambient temperature during the main incubation period and mean daily precipitation, between June 15 and July 15, is given in Table 3. Body weights dropped on the average 20.8% (or 105 g) from the end of egg laying until hatching (Table 4).

Table 4. Body mass (mean in grams ± SD) of wild and captive Svalbard and Willow Ptarmigan hens at the end of egg laying and at hatching.

		Body mass at the end of egg laying (g) (X ± SD)	Body mass at hatching time (g) (X ± SD)
Svalbard Ptarmigan hens	wild	613.4 ± 37.9 (n = 19)	507.9 ± 23.0 (n = 12)
	captive	617.5 ± 10.6 (n = 2)	507.5 ± 38.9 (n = 2)
Willow Ptarmigan hens	wild	595.6 ± 30.2 (n = 9)	498.6 ± 32.5 (n = 7)
	captive	602.5 ± 17.7 (n = 2)	497.0 ± 14.1 (n = 2)

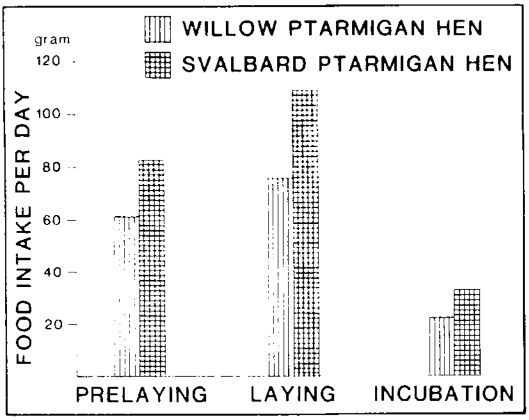

Fig. 4. Food intake (dry weight) before, during and after incubation in one captive Willow Ptarmigan and Svalbard Ptarmigan hens.

Food intake during incubation was 32% of that prior to egg laying (Table 5; Fig. 4). Body weight decreased 22% (Table 4; Fig.5) during incubation.

Laboratory experiments

Willow Ptarmigan. — The two captive incubating Willow Ptarmigan hens had a mean resting heart rate of 190 b.p.m. and a respiratory rate of 26.0 br.p.m. Heart rates increased to 460 b.p.m. and respiration rates to 36.0 br.p.m. when returning to an artificially cooled clutch and declined to resting level within one hour (Table 1). During this period the egg temperature reached a stable level of 36—38°C. The increase in heart and respiration rate was accompanied by a more than two-fold increase in metabolic rate (Table 5). The metabolic rate declined as the egg temperature rose.

Svalbard Ptarmigan. — Captive incubating Svalbard Ptarmigan hens had a resting heart rate of 200 b.p.m. and a respiratory rate of 26.0 br.p.m. Heart rate increased to a mean maximum of 400 b.p.m. and the respiratory rate to 37.0 br.p.m. after returning to artificially cooled eggs (Table 1). At the same time the metabolic rate increased and reached a maximum of about 2 times resting level (Table 5; Fig. 6). Heart and respiratory rates and metabolism gradually declined to resting levels 40—60 min after returning to the eggs. There was a significant correlation between heart and metabolic rate (Fig. 7, least-squares regression analysis; $F_{1,11}$ = 152.49, $p < 0.01$).

Food intake during incubation was 37% of that prior to egg laying (Table 5; Fig. 4). Body weight decreased 18% during incubation (Table 4; Fig. 5).

Table 5. Metabolic rate (mean in kcal/day ± SD) and food intake (mean in gram ± SD, dry weight) in captive Willow and Svalbard Ptarmigan hens.

	Metabolic rate (kcal/day)		Food intake (gram)		
	Resting (X ± SD)	Start of incubating cooled eggs (X ± SD)	Prelaying (X ± SD)	Egglaying	Incubation
Willow Ptarmigan hens	67.5 ± 2.5	169.0 ± 4.2	61.3 ± 11.9	74.3 ± 4.8	19.9 ± 3.9
Number of birds/ measurements	1/5	1/5	2/10	2/10	2/10
Svalbard Ptarmigan hens	62.0 ± 4.5	163.2 ± 2.9	78.3 ± 2.9	100.5 ± 5.1	29.2 ± 2.4
Number of birds/ measurements	2/6	2/6	2/8	2/8	2/8

Energy budget calculations

Based on measurements of oxygen consumption, carbon dioxide production and nest attentiveness we calculated the energy expenditure for wild, incubating hens of the two species in the following way:

Expenses: Incubating Willow and Svalbard Ptarmigan hens had a mean resting metabolic rate (RMR) of 67.5 and 62 kcal/day, respectively. The energy cost for foraging activity (2 times RMR, 15 min away each time the hens left the nest) and re-heating of eggs after foraging (2 times RMR, 60 min after foraging) was calculated to be 3.5 and 3.2 kcal (Willow and Svalbard Ptarmigan hens, respectively) each time they left the nest. Each species left the nest on average 4.1 (Willow) and 2.9 (Svalbard) times a day ($p < 0.01$, t-test). This added another 14 kcal/day in Willow Ptarmigan and 10 kcal/day in the Svalbard Ptarmigan to the daily energy budget (Table 6).

Income: While away from the nest both species eat 15—25 grams (wet weight) of food (Gabrielsen, Parker & Elvebakk unpublished; Unander et al. 1985). A food intake of 20 grams corresponds to an energy intake, based on experiments of food digestibility (Moss & Hanssen 1980) and caloric equivalent of protein (Schmidt-Nielsen 1975), of 18 kcal per meal (70% water, 70% metabolic efficiency). The energy intake was therefore 72 kcal/day (4 foraging trips) in Willow and 54 kcal/day (3 foraging trips) in Svalbard Ptarmigan hens (Table 5).

Wild Willow Ptarmigan lost 100 g while wild Svalbard Ptarmigan lost 105 g during incubation. While Svalbard hens show a decrease in body fat from June to July (Mortensen et al. 1983), there is only 2% body fat available in Willow Ptarmigan hens (Grammeltvedt 1978). 98 g protein and 2 g fat correspond to 10 kcal/day, 21 days of incubation, 60% body water, caloric equivalent of protein 4.8 kcal/g (d.w.) (Kleiber 1975) and 7.7 kcal/g for fat (Mortensen & Blix 1985b). Svalbard Ptarmigan hens lose ~ 30 g of fat and ~ 75 g of proteins during incubation (Mortensen et al. 1983). This gives an energy gain of 18 kcal/day, 7.7 kcal/g for fat (Mortensen & Blix 1985b) (Table 6).

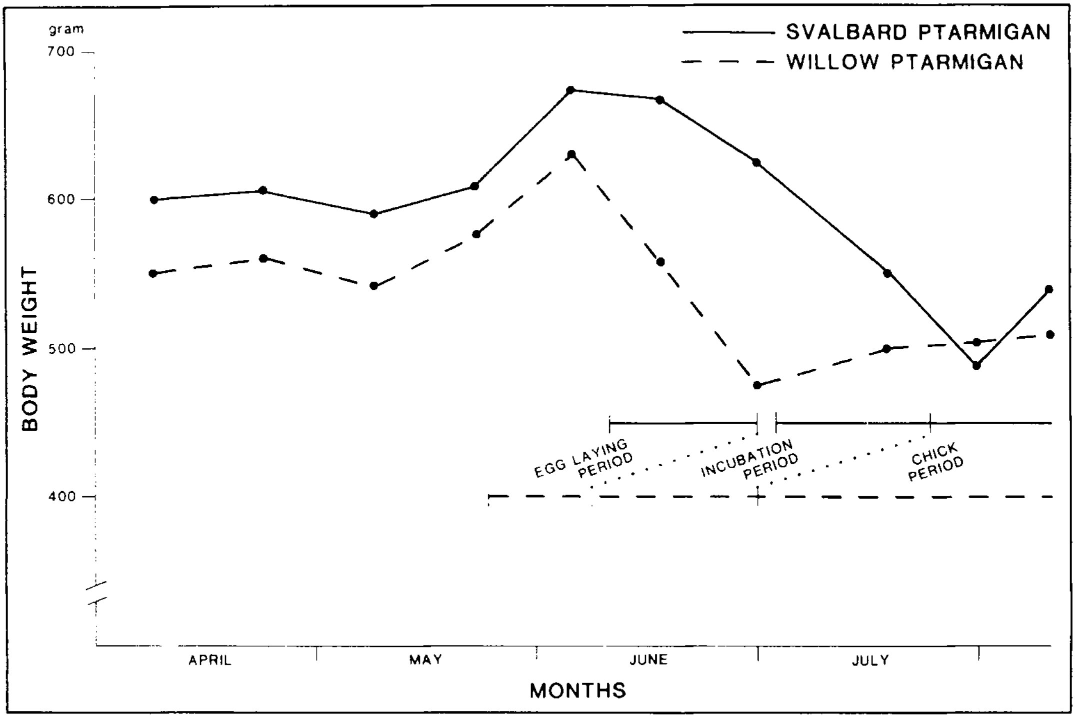

Fig. 5. Body weights measured from April to the middle of August in one captive Willow Ptarmigan and one Svalbard Ptarmigan hen.

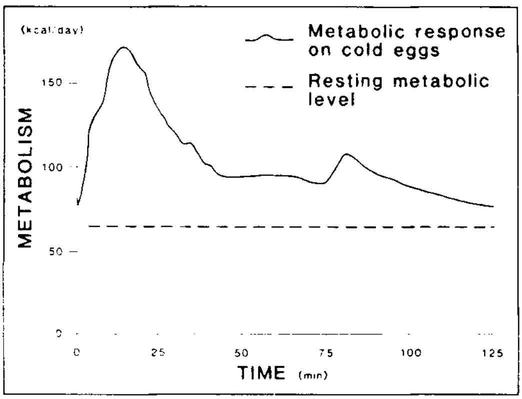

Fig. 6. Metabolism upon returning to cold eggs in one captive Svalbard Ptarmigan hen (Ta = 10°C).

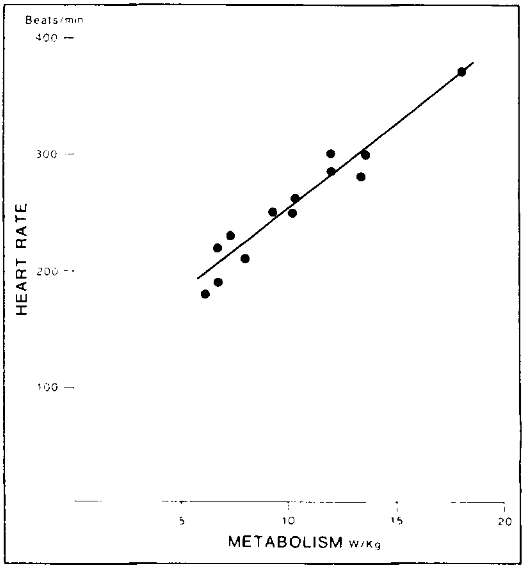

Fig. 7. The relationship between heart (BPM) and metabolic rate (W/kg) in an incubating Svalbard Ptarmigan hen.

Table 6. Daily energy budget (kcal/day) calculations of wild Svalbard and Willow Ptarmigan hens.

	Energy output			Energy intake		
	Resting metabolic rate	Extra cost during incubation: to keep eggs warm, foraging activity and re-heating of eggs, heating of eggs after foraging.	Total energy output	Food intake	Weight loss	Daily energy cost during incubation
Willow Ptarmigan hens	67.5	14	81.5	72	10	82
Svalbard Ptarmigan	62.0	10	72,0	54	18	72

Discussion

The daily energy cost during incubation in wild Ptarmigan hens varied between 70—85 kcal/day. This was 15—25% above resting metabolic rate in non-incubating hens, which corresponds to 20—30% found in smaller birds (Biebach 1981; Vleck 1981; Haftorn & Reinertsen 1985), but 45—55% of the metabolism of free living Willow Ptarmigan (Moss 1973).

Heating of cold eggs is probably achieved by shivering thermogenesis (Tøien et al. 1986). Aulie (1976) found a coupling between activation of the pectoral muscles and the heart rate during shivering in the Ptarmigan. Increased circulation during shivering will provide sufficient oxygen to the muscles, and the heat produced is immediately distributed to the brood patch. Midtgård et al. (1985) found vasodilation and increased blood flow at the brood patch site of cooling. This supports suggestions by Gabrielsen & Steen (1979) that warming of the eggs is facilitated by increased blood flow to the brood patch.

Wild Willow Ptarmigan hens quadrupled while captive hens were found to double their heart rate when returning to cold eggs (Gabrielsen & Steen 1979). This difference in heart rate between wild and captive hens is probably related to physical fitness; wild birds showing a lower resting rate and a higher maximum heart rate compared to captives. In captive ptarmigan hens of both species the two-fold increase was accompanied by a two-fold increase in metabolic rate. Despite the good relationship between heart and metabolic rate in laboratory studies, one should be aware of this when transforming heart and metabolic relationships to the wild birds.

Both species incubate within the thermal neutral zone but close to the lower critical temperature which for Willow Ptarmigan hens in summer plumage is 0° C (Mortensen & Blix 1985a). It was suggested by Haftorn & Reinertsen (1985) that the energy cost of incubation increases when air temperature falls below the lower critical temperature. This is true, but as shown in the present study, the energy cost in ptarmigan hens is also increased above this lower critical temperature during certain periods. While incubating at low ambient temperatures, above 0° C, both species showed short periods (20—30 seconds) of increased heart and metabolic rate. These periods of increased heart rate and oxygen consumption, which were 15—30% above resting level, must be regarded as being due to the extra cost of keeping the eggs at incubation temperature. The eggs must be regarded as a poorly insulated extension of the bird's body that usually does not contribute to the heat production. An incubating bird and her eggs must be treated as one organism. After foraging the eggs are cooled, and the incubating hen must produce additional heat to compensate for a lowered egg temperature, or she must increase heat production due to a lowered body temperature.

During periods of precipitation and low ambient temperature wild Willow Ptarmigan hens reduced foraging periods from 4 to 3 times a day. Eggs cool faster under these conditions and the cost of rewarming would then be greater. A reduction of one foraging period per day is calculated to have a negative effect of 14 kcal/day in Willow Ptarmigan hens. Less energy necessary for feeding, locomotion and warming will have a positive effect on the total energy budget for the bird, provided that it has extra energy resources (i.e. body fat, as Svalbard Ptarmigan hens) to compensate for one less meal per day. The result will be, as observed in our study, that Willow Ptarmigan hens must fast when the external temperature reaches minimal levels and precipitation is high. During cold weather, and especially when it is raining, the tendency for gulls to remain sitting on the nest is very high (Baerends 1959). An earlier study of ptarmigan hens (Pulliainen 1978) showed that both eggshifting and resettling decreased in frequency during cold periods.

Differences in energy household during incubation are illustrated by comparison of Common Eiders, Svalbard and Willow Ptarmigan hens. Eiders carry 20% fat prior to incubation (Milne 1976; Parker unpublished), Svalbard Ptarmigan hens less than 10% fat (Mortensen et al. 1983) and Willow Ptarmigan hens less than 2% fat (Grammeltvedt 1978). The Eiders do not feed throughout the incubation period but rely on two sources of energy, the skeletal muscles and body fat. These energy resources are used during the incubation period, causing a 30—45% loss of body weight (Milne 1976; Korschgen 1977; Parker unpublished). Both wild and captive ptarmigan hens eat somewhat throughout the incubation period. However, both species lose about 20% of their body weight during incubation. Svalbard Ptarmigan hens receive one less meal per day compared to Willow Ptarmigan hens. Less energy input per day in Svalbard Ptarmigan hens was partly compensated for by less energy used for locomotion, foraging and re-heating the eggs. Svalbard Ptarmigan hens, in contrast to Willow Ptarmigan hens, store body fat as an energy reserve to be used during incubation. Because Willow Ptarmigan hens have little or no body fat prior to incubation they are more vulnerable to periods of fasting. In Willow Ptarmigan hens the energy content of one less meal per day would have a total negative effect of 14 kcal/day, energy which would have to come mainly from body protein.

Both Willow and Svalbard Ptarmigan hens incubate eggs of the same average weight. They show the same reduction in food intake and the same loss of body weight. The only major difference is that Svalbard Ptarmigan hens use body fat as an energy reserve during incubation. Such fat reserves enable the hen to increase nest attentiveness while at the same time reducing energy expenditure due to lowered activity and less reheating of the eggs. More precipitation falls in Troms County, but the ambient temperature is lower in Svalbard. The low ambient temperature is suggested to be the most important factor stimulating the high nest attentiveness in Svalbard Ptarmigan hens. Slagsvold's (1975) analysis of previous Willow Ptarmigan data showed a positive correlation between ambient temperature at the end of the incubation period and the production of chicks. Steen & Unander (1985) concluded that the physical condition of Svalbard Ptarmigan hens prior to breeding seemed to be the most important factor in determining chick production. In a study of Willow Ptarmigan hens at Dovre (62 °N), Erikstad (1985) showed that hens in good condition took fewer recesses than hens in poor condition. However, differences in incubation behaviour did not influence hatching success. For ptarmigan hens, a high rate of nest attendance is dependent upon sufficient internal reserves and food intake. Low ambient temperatures and much precipitation during the incubation period may hasten the drain of reserves and limit food intake, thereby weakening hens and indirectly influencing chick production.

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