

- . 1983. Breeding strategies of hole-nesting passerines in northern Lapland. *Ann. Zool. Fennici* 20: 129-149.
- , & H. LINDÉN. 1980. Timing of breeding and the clutch in the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland. *Ornis Fennica* 57: 112-116.
- KLOMP, H. 1980. Fluctuations and stability in Great Tit populations. *Ardea* 68: 205-224.
- KLUIJVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. *Ardea* 39: 1-135.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.
- . 1966. Population studies of birds. London, Methuen.
- MILNE, A. 1957. The natural control of insect populations. *Can. Entomol.* 89: 193-213.
- MURRAY, B. G., JR. 1979. Population dynamics: alternative models. New York, Academic Press.
- NILSSON, S. G. 1983. Clutch size and breeding success of the Pied Flycatcher *Ficedula hypoleuca* in natural tree-holes. *Ibis* 126: 407-410.
- ORELL, M., & M. OJANEN. 1983. Effect of habitat, date of laying and density on clutch size of the Great Tit *Parus major* in northern Finland. *Holarctic Ecol.* 6: 413-423.
- PERRINS, C. 1979. British tits. London, Collins.
- ROBERTSON, R. J., & R. F. NORMAN. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). *Can. J. Zool.* 55: 508-518.
- STRONG, D. R. 1986. Density vagueness: abiding the variance in the demography of real populations. Pp. 257-268 in *Community ecology* (J. Diamond and T. J. Case, Eds.). New York, Harper and Row.
- SZARO, R. C., & R. P. BALDA. 1979. Bird community dynamics in a ponderosa pine forest. *Stud. Avian Biol.* 3: 1-66.
- TOMPA, F. C. 1967. Reproductive success in relation to breeding density in Pied Flycatchers, *Ficedula hypoleuca* (Pallas). *Acta Zool. Fennici* 118: 3-28.
- VIROLAINEN, M. 1984. Breeding biology of the Pied Flycatcher *Ficedula hypoleuca* in relation to population density. *Ann. Zool. Fennici* 21: 187-197.

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### Metabolic Rate and Thermostability in Relation to Availability of Yolk in Hatchlings of Black-legged Kittiwake and Domestic Chicken

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Hatchlings, especially in precocial species, have a relatively large amount of yolk that can be used up to 6 days after hatching if growth, thermoregulatory, and locomotive costs are minimal (Pettit et al. 1985). Marcström (1960, 1966) showed by carcass analyses that yolk is used for both catabolism and synthetic purposes in the Common Capercaillie (*Tetrao urogallus*) and the Mallard (*Anas platyrhynchos*). In Canada Geese (*Branta canadensis*) newly hatched goslings will grow in spite of being starved (Peach and Thomas 1986). If, as suggested by these studies, the yolk reserve is used not only for catabolism but also for synthetic purposes, the result would produce a higher metabolic rate not reflecting a true basal metabolic rate (BMR).

We attempted to estimate the possible difference in metabolic rate in chicks with and without a yolk reserve. The yolk sacs of newly hatched chicks of the Black-legged Kittiwake (*Rissa tridactyla*) and domestic chicken (*Gallus gallus*) were removed surgically. The metabolic rate in these chicks was compared with that measured in sham- and nonoperated chicks.

Hatching eggs of kittiwakes were collected in Kongsfjorden, Spitsbergen, and taken to the laboratory of the Norwegian Polar Research Institute in Ny Ålesund. The eggs were hatched in a commercial in-

cubator, and the chicks were used in experiments 3-6 h after hatching. Newly hatched chickens were obtained from a commercial farm and used in the experiments at the Department of Zoology of the University of Trondheim approximately 2 days after hatching. The hatchlings received only water and were kept under thermoneutral conditions.

Chicks of both species were divided randomly into three groups: operated, sham-operated, and non-operated. Sham- and nonoperated chicks formed the control group. The chicks of the operated and the sham groups were anesthetized with ether; lidocaine was used as a local anaesthesia. In both groups the abdominal cavity was opened. In the operated group the yolk sac was removed and weighed. The chicks recovered within 30 min, and oxygen consumption was measured approximately 3 h later.

Before measurement of oxygen consumption the chicks were weighed, and, in the case of the kittiwakes, a copper-constantan thermocouple was inserted into the rectum. Oxygen consumption in kittiwakes was measured using a manometric respirometer (Bech et al. 1984). In the chickens oxygen consumption was measured using an open-flow system in which the air was sucked through a 0.9- or 2.4-l metabolic chamber with a flow rate of 1 l/min. After drying over silica

TABLE 1. Oxygen consumption at 35°C in kittiwake and chicken hatchlings. Values are means ± SD with sample sizes in parentheses. *t*-tests were conducted using pooled variances (variances were not significantly different; *F*-test,  $P_2 < 0.05$ ).

	Kittiwake oxygen consumption		Chicken oxygen consumption	
	ml O <sub>2</sub> · h <sup>-1</sup> · g <sup>-1</sup>	ml O <sub>2</sub> · h <sup>-1</sup> · g <sub>yolk-free</sub> <sup>-1</sup> · a	ml O <sub>2</sub> · h <sup>-1</sup> · g <sup>-1</sup>	ml O <sub>2</sub> · h <sup>-1</sup> · g <sub>yolk-free</sub> <sup>-1</sup>
Operated	1.41 ± 0.09 (6)	1.41 ± 0.09 (6)	1.41 ± 0.31 (12)	1.41 ± 0.31 (12)
Sham	1.40 ± 0.13 (3)	1.49 ± 0.13 (3)	1.48 ± 0.38 (12)	1.60 ± 0.42 (12)
Nonoperated	1.41 ± 0.05 (5)	1.50 ± 0.05 (5)	1.38 ± 0.39 (10)	1.51 ± 0.41 (10)
Control	1.41 ± 0.08 (8)	1.50 ± 0.08 (8)	1.43 ± 0.38 (22)	1.56 ± 0.41 (22)
<i>t</i> -tests for comparison of groups				
Operated, sham	<i>t</i> (7) = 0.09, $P_1 = 0.46$	<i>t</i> (7) = 1.09, $P_1 = 0.16$	<i>t</i> (22) = 0.53, $P_1 = 0.30$	<i>t</i> (22) = 1.29, $P_1 = 0.11$
Operated, nonoperated	<i>t</i> (9) = 0.12, $P_1 = 0.45$	<i>t</i> (9) = 2.05, $P_1 = 0.04$	<i>t</i> (20) = 0.19, $P_1 = 0.43$	<i>t</i> (20) = 0.69, $P_1 = 0.25$
Operated, control	<i>t</i> (12) = 0.02, $P_1 = 0.49$	<i>t</i> (12) = 1.93, $P_1 = 0.04$	<i>t</i> (32) = 0.22, $P_1 = 0.42$	<i>t</i> (32) = 1.14, $P_1 = 0.13$
Sham, nonoperated	<i>t</i> (6) = 0.20, $P_2 = 0.86$	<i>t</i> (6) = 0.20, $P_2 = 0.86$	<i>t</i> (20) = 0.63, $P_2 = 0.54$	<i>t</i> (20) = 0.50, $P_2 = 0.62$

<sup>a</sup> Yolk-free body masses of sham- and nonoperated chicks were assessed using mean yolk mass of operated chicks.

TABLE 2. Decrease in body temperature during 1 h of exposure to an ambient temperature of 26°C for kittiwake chicks. Values are means ± SD, with sample sizes in parentheses. *t*-tests were conducted using pooled variances (variances were not significantly different; *F*-test,  $P_2 < 0.05$ ).

	Cooling rate (°C/h)
Operated	1.6 ± 0.5 (6)
Sham	0.3 ± 0.7 (2)
Nonoperated	0.8 ± 0.3 (5)
Control	0.6 ± 0.4 (7)
<i>t</i> -tests for comparison of groups	
Operated, sham	<i>t</i> (6) = 3.90, $P_1 < 0.01$
Operated, nonoperated	<i>t</i> (9) = 5.43, $P_1 < 0.01$
Operated, control	<i>t</i> (11) = 5.16, $P_1 < 0.01$
Sham, nonoperated	<i>t</i> (5) = 0.75, $P_2 = 0.48$

gel, the oxygen concentration of the effluent air was determined using a Servomex 1100A or an S-3A Applied Electrochemistry oxygen analyzer. All experiments were conducted under thermoneutral conditions (35°C; Freeman 1963, Bech et al. 1984) and lasted for about 2 h. Calculation of oxygen consumption was based on stabilized readings only. After the oxygen-consumption measurements, the hatchlings of the chicken control group were sacrificed and the yolk sac removed and weighed.

Following the 2 h of exposure to 35°C, the kittiwake chicks were placed in an ambient temperature of 26°C. At this temperature, which is below thermoneutrality, kittiwake hatchlings maintained metabolic rate at a peak level, which does not prevent a moderate body temperature decrease (Bech et al. 1984). Body temperature changes were monitored for 1 h.

The mass of the chicks, including the yolk sac, was 32.6 g (SD = 2.2,  $n = 14$ ) for kittiwakes and 33.5 g (SD = 3.3,  $n = 34$ ) for chickens. Yolk-sac masses were 1.9 g (SD = 0.4,  $n = 6$ ) and 2.5 g (SD = 1.7,  $n = 34$ ) and represented 5.8% and 7.5% of total body mass of kittiwakes and chickens, respectively.

Body temperatures in kittiwake hatchlings under thermoneutral conditions were 38.9° (SD = 0.3,  $n = 6$ ), 38.6° (SD = 0.3,  $n = 3$ ), and 38.8°C (SD = 0.4,  $n = 5$ ) for the operated, sham-, and nonoperated groups, respectively. These values did not differ significantly (in all cases  $P_2 > 0.12$ ).

There were no differences in mass-specific oxygen consumption among the three experimental groups for either kittiwake or chicken hatchlings (Table 1). Because yolk has only a negligible metabolic capacity (Steen and Gabrielsen 1986), however, the mass-specific oxygen consumption was recalculated using the yolk-free body mass. This resulted in a significantly higher oxygen consumption in the control group compared with the operated kittiwakes (Table 1). The same tendency was apparent in the chickens, but because of large variances the results were not signifi-

cant (Table 1). The high variance could be caused by the larger variation in body and yolk masses compared with those in kittiwake chicks. We conclude that the yolk was responsible for an elevation of the metabolic rate on the order of 6–13%. The increased metabolism was presumably due to the use of yolk reserve for synthetic purposes. For this reason, BMR cannot be measured in newly hatched chicks because they continuously use yolk as substrate for tissue synthesis. Therefore, "basal metabolic rate" is an inappropriate term when applied to hatchlings, and we encourage the use of the prefix "hatchling."

The removal of the yolk sac from kittiwake hatchlings significantly increased the cooling rate (Table 2). The results demonstrate the importance of the yolk sac as a nutrient reserve for catabolism.

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#### LITERATURE CITED

- BECH, C., S. MARTINI, R. BRENT, & J. RASMUSSEN. 1984. Thermoregulation in newly hatched Black-legged Kittiwakes. *Condor* 86: 339–341.
- FREEMAN, B. M. 1963. Gaseous metabolism of the domestic chicken IV. The effect of temperature on the resting metabolism of the fowl during the first month of life. *Brit. Poultry Sci.* 4: 275–278.
- MARCSTRÖM, V. 1960. Studies on the physiological and ecological background to the reproduction of the Capercaillie (*Tetrao urogallus*). *Viltrevy* 2: 1–71.
- . 1966. Mallard ducklings (*Anas platyrhynchos*) during the first days after hatching. A physiological study with ecological considerations and a comparison with Capercaillie chicks (*Tetrao urogallus*). *Viltrevy* 4: 343–369.
- PEACH, H. C., & V. G. THOMAS. 1986. Nutrient composition of yolk in relation to early growth of Canada Geese. *Physiol. Zool.* 59: 344–356.
- PETTIT, T. N., G. C. WHITTOW, & G. S. GRANT. 1985. Caloric content and energetic budget of tropical seabird eggs. Pp. 113–138 in *Seabird energetics* (G. C. Whittow and H. Rahn, Eds.). New York and London, Plenum Press.
- STEEN, J. B., & G. W. GABRIELSEN. 1986. Thermogenesis in newly hatched Eider (*Somateria mollissima*) and Long-tailed (*Clangula hyemalis*) ducklings and Barnacle (*Branta leucopsis*) goslings. *Polar Research* 4: 181–186.

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