

COLD-HARDINESS OF THE NEWLY HATCHED YOUNG IN
RELATION TO ECOLOGY AND DISTRIBUTION IN TEN
SPECIES OF EUROPEAN DUCKS

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FIELD observations and experimental investigations (Böni, 1942; Pynnönen, 1954; Ryser and Morrison, 1954; Höglund, 1955; Salminen, 1957; Koskimies, 1962) have shown that the young chicks of gallinaceous birds are very sensitive to low environmental temperatures. They soon lose their capacity for thermoregulation and coordinated activity if exposed to even moderately low summer temperatures. Their sensitivity to cold is, to a large extent at least, the result of insufficient metabolic heat production (Koskimies, *op. cit.*).

Casual field experience suggested that young ducklings may be less sensitive to cold than gallinaceous chicks. They are capable of a more continuous independent search for food and are not brooded so much as gallinaceous chicks.

It also seemed probable that there might be measurable differences in cold-sensitivity between the ducklings of various species, as had been found to be the case among gallinaceous chicks (Koskimies, 1962, and MS), and at the same time this aroused interest in the bioenergetic basis of such differences.

In consequence, a series of experiments was undertaken, the results of which are described in the present paper.

ACKNOWLEDGMENTS

This paper is part of a larger project dealing with the bioenergetics of precocial and semi-precocial bird chicks (see also Koskimies, 1962). The project has been aided by grants from the National Research Council of Canada and the Finnish Government Board for Natural Sciences (Valtion luonnontieteellinen toimikunta). We also wish to thank Professor Paavo Suomalainen for the facilities and equipment made available to us at the Department of Physiological Zoology of the University of Helsinki. Our thanks are also given to Professor Donald S. Farner and Dr. Vidar Marcström for their valuable criticism of the manuscript.

THE BIOENERGETIC BASIS OF COLD-HARDINESS IN HOMEOTHERMS

The bioenergetics of thermoregulation and cold-hardiness of homeotherms have been thoroughly reviewed by Scholander *et al.* (1950a, b, and c), Hart (1957), and King and Farner (1961). By applying the simple physical principle of Newton's law of cooling, Scholander *et al.* (1950b) presented a simplified model of the heat economy of a homeothermic organism and discussed the quantitative relationships involved and the significance of insulation and thermogenesis, in particular, in thermoregulation.

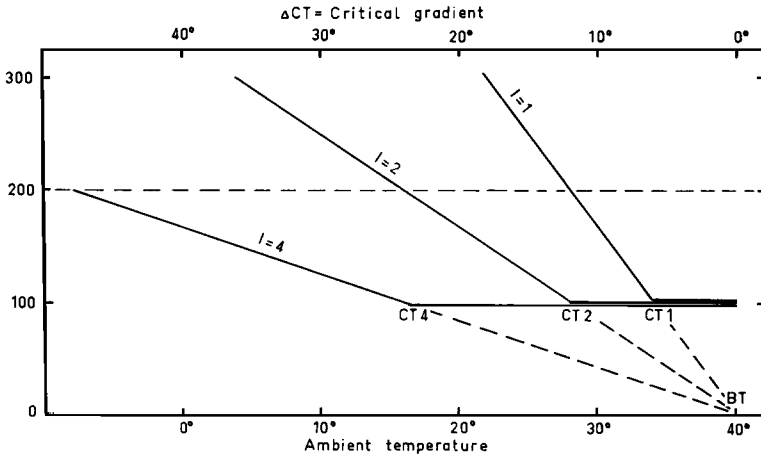


Figure 1. A simplified model of the thermal system of a homeotherm (modified from Scholander *et al.*, 1950b). The solid lines represent the relative energy output (metabolic rate) necessary to maintain a body temperature of 40°C for different ambient temperatures, with the minimum energy level (basal metabolic rate) set equal to 100 and insulations of 1, 2, and 4 units. Vertical axis equals relative metabolic effort. Further explanations in text.

Figure 1 is a modification of the model of Scholander *et al.* (1950b: 241). The lowest metabolic rate by means of which the animal is able to maintain a body temperature of 40°C under thermoneutral conditions (the basal metabolic rate) is given the value 100. Within certain temperature limits (the zone of thermal neutrality) the animal is able to maintain its heat balance by purely physical means (i.e., by changing the effectiveness of its insulation).

At the lower limit of the zone of thermal neutrality, at the critical temperature (CT), an elevation of heat production (chemical thermoregulation) becomes necessary to compensate for the increased heat loss. It is assumed that, below the critical temperature, insulation is maintained at its maximal efficiency. The heat loss, as well as the heat production necessary to compensate for it, now increases in proportion to the fall in the ambient temperature. The difference between the body temperature and the ambient critical temperature is called the critical temperature gradient (ΔCT). It is seen from Figure 1 that the critical temperature gradient is dependent on both the over-all insulation (I) and the basal metabolic rate (BMR). The relationship is determined by the formula $\Delta CT = K \times I \times BMR$, in which K is a constant denoting units of measurement.

We have not been able to find a generally accepted definition or quantitative measure of cold-hardiness. For the purposes of the present paper,

cold-hardiness is taken to mean the ability to withstand low environmental temperatures with as low a metabolic effort (increase over the basal metabolic rate) as possible.

From Figure 1 it is obvious that the most cold-hardy type is basically the one with the greatest critical gradient (ΔCT). However, in our primarily ecological comparisons we prefer to use, in conformity with our definition, as an inverse index of cold-hardiness, the metabolic effort (expressed as a percentage of the basal metabolic rate) required at an arbitrarily selected, ecologically pertinent, low ambient temperature. Such a measure also indicates the relationship of this effort to the general "maximum metabolic effort" (see Depocas *et al.*, 1957) attainable by homeotherms (usually between 300 and 400 per cent).

In animals with equal basal heat production ($BMR = 100$) differences in cold-hardiness are determined solely by differences in over-all insulation. A doubling of the insulation (from $I = 1$ to $I = 2$) produces two effects characteristic of increased cold-hardiness: the critical temperature gradient (i.e., the temperature zone within which physical thermoregulation alone is sufficient to combat heat loss) is doubled and the metabolic effort required at each ambient temperature below the critical temperature is halved.

A doubling of the basal metabolic level (from $BMR = 100$ to $BMR = 200$) leads to the same changes in cold-hardiness as a doubling of the insulation.

On the basis of these relationships it is possible to make quantitative comparisons of cold-hardiness and of the relative significance of insulation and heat production in the thermoregulation of homeotherms.

The technique of such investigations is relatively simple and involves only the determination and comparisons of the curves relating metabolic rate with ambient temperature (corresponding to the curve in Figure 1). The metabolism-temperature response has previously been successfully employed to relate functional characteristics of a bird or mammal to its ecology or distribution by, for instance, Scholander *et al.* (1950b, c), Salt (1952), Hart and Heroux (1953), Cook and Hannon (1954), Wallgren (1954), Murie (1961), and Pearson (1962).

Scholander *et al.* (1950c) state that the phylogenetic adaptation of birds and mammals to cold or heat may theoretically take place along three lines: (1) by changing the body-to-environment temperature gradient, (2) by changing the insulation, and (3) by changing the basal metabolic rate. From their discussion these authors conclude that both body temperature and basal metabolic rate are independent of environmental conditions and do not show differences correlated with climate. Hence, phylogenetic adaptations of homeothermic organisms to cold or heat are

thought to take place only or primarily through changes in insulation.

As far as adult true homeotherms are concerned the conclusions of Scholander *et al.* (1950c) can be accepted, at least insofar as they refer to the inadaptability of body temperatures (see also Morrison and Ryser, 1952; Irving and Krog, 1954; Scholander, 1954). As regards the basal metabolic rate, the present evidence is inconclusive. However, regardless of any doubts as to the rigid inadaptability of basal metabolic rates, the great importance of insulation in climatic adaptations is obvious.

In young homeotherms, in which full thermoregulation has not yet been established, the situation is more complicated. None of the premises listed above appears to hold. First, the body temperature in young homeotherms is very labile, and in many cases it had been shown, or it can be considered probable, that short-term adjustments of body temperature in response to climatic stresses take place in young homeotherms. Furthermore, the thermogenesis of young precocial homeotherms does not bear as close a relationship to body weight as that of the adults. Instead, their thermogenesis starts at a level corresponding to only 30–70 per cent of the heat production of an adult homeotherm of the same weight (Koskimies, 1962). The presence of adaptive differences in basal metabolic rates is thus by no means so absolutely precluded as has been alleged for adult homeotherms on the basis of the general quantitative relation of their basal metabolic rate to body weight. Furthermore, in the case of young animals, efficient adaptation in surface insulation, which is the main method of climatic adaptation in adult homeotherms, is probably “technically” a difficult state to achieve, because of their generally small size and rapid, continuous changes of size. Also the rapid movements and lively activity which are necessary to young precocial chicks make heavy insulation impractical, not only because of the mechanical difficulties involved but also because of the difficulty of dissipating the excess heat produced in muscular work.

It is thus obvious that what is known of the climatic adaptations in adult homeotherms is not applicable to their young. In the present study an attempt is made to explore the characteristics of thermoregulation and cold-hardiness in young ducklings and to find out whether the characteristics involved show species-specific differences which should be explained as climatic adaptations.

MATERIALS AND METHODS

The experiments upon which this paper is based were performed in the summers of 1961 and 1962 at the Evo Research Station of the Finnish Game Research Institute.

The main experimental procedure was the determination of the responses of the metabolic rate of resting young birds to temperatures normal, or at least possible, in their natural habitats.

The birds were placed in individual airtight containers, which were remodeled from

new half-liter paint tins with soldered copper inlets and outlets for air and equipped with an inserted thermocouple probe to indicate the temperature inside the chamber. Atmospheric air, from which carbon dioxide had been removed in tubes of soda lime with Ascarite as indicator, and excess moisture had been removed by calcium chloride with silica gel as indicator, was pumped through the chambers with low-pressure aquarium air pumps, one for each channel used.

In the system used for most of the experiments (in 1962), CO₂ and water were absorbed from the exhaled air as above and the percentage of oxygen in the air was determined by means of a Beckman paramagnetic oxygen analyzer (Model E-2), the accuracy being within 0.025 per cent O₂. From the rate of air flow (150 to 250 cc/min), measured with an Elster and Co. 1,000 cc wet test flow meter, and the difference in the percentage of oxygen between the atmospheric air and the expired air, the absolute oxygen consumption per unit time was derived. By taking samples in sequence for two to five minutes it was possible, after some practice, to work with up to three birds simultaneously.

In 1961, a modified Haldane method was used, in which the respiratory water was absorbed in concentrated sulphuric acid with silica gel as indicator, and the carbon dioxide into two tubes of Ascarite, which were weighed on a Mettler H-15 balance to 0.1 mg before and after each experimental period of 10 minutes. The experiment was run with up to six individual channels simultaneously. The flow rate in this system varied between 300 and 500 cc/min.

The entire apparatus, from the initial CO₂ absorbent (in the Haldane system, also the pumps) to the animal chamber, was kept inside a constant temperature cabinet with continuously adjustable temperature between -3 and +50°C. The temperature within the cabinet ranged within ±1°C of the desired value.

The birds were taken directly from their normal brooders and, after their body temperature and weight had been recorded, were placed in the apparatus. They were first kept, as a rule, at a temperature within, or a few degrees above, the expected thermoneutral range (i.e., at 36-38°C) and were left inside the apparatus for at least 1½ hours before readings were started. The temperature was then gradually lowered at the rate of 12 ± 2°C per hour until the thermoneutral zone had been passed and the rate of subsequent increase in thermogenesis in response to further decrease in temperature had been established. The lowest value of oxygen consumption (or CO₂ output, in the case of the Haldane method) was used to compute the basal metabolic rate in terms of heat production. In the computations a caloric equivalent of 4.7 cal/cc O₂ (using unreduced gas volumes) and a respiratory quotient of 0.70 were assumed.

The duration of an experiment, including the period of adjustment, averaged three to four hours. The experiments were carried out at various times of day. Fifty-four per cent of the basal values were obtained between 2100 and 0300 hours; the remainder were fairly evenly distributed between 0900 and 2100 hours. No disturbing activity was experienced at any time of the day, as the newly hatched young remained quiet for most of the time.

Each bird was used in only one experiment. A record was kept of the time of hatching of each chick, and all were classified 0 day old or one day old, depending on whether the basal rate of metabolism was determined at the age of 10 (rarely less) to 24 hours or 24 to 36 (rarely to 48) hours. No food or water was given to the chicks prior to the experiment. They were kept at room temperature and given free access to electric brooders.

Although the clutches were transferred to the station and placed in incubators as late

in incubation as possible, some of the eggs were in the machine for the greater part of their incubation period. The hatching percentage was good, and no definite ill effects of transportation or artificial incubation could be detected. All chicks originated from southern Finland, between 60°10' and 61°10' N lat. and 24°55' and 26°25' E long.

The methods used in the cooling experiments and in the treatment of the data are explained in their appropriate connections.

RESULTS

EFFECT OF EXPOSURE ON BODY TEMPERATURE

The reaction of body temperature is a simple but practical measure of the capacity of a homeotherm to resist environmental cold or heat stresses. The body temperature of an adult homeotherm is generally stable to within 1 to 2°C in all environmental temperatures it normally encounters in its natural habitat (e.g., Baldwin and Kendeigh, 1932; Udvardy, 1953; King and Farner, 1961). Young precocial chicks, on the other hand, have a much more labile body temperature, as is clearly shown in a number of species of gallinaceous birds (see p. 281).

There is hardly any previous information about the body temperatures or thermoregulation of young ducklings. The only relevant observation on the cold-resistance of young ducks widely quoted is that of Rolnik (1948), who found a fairly well established thermoregulation in the young of the [Common] Eider, *Somateria mollissima*, in the Barents Sea soon after hatching.

To obtain an idea of the cold-hardiness of our ducklings in 1961 we first exposed them to moderate cooling, similar to that used in earlier studies on gallinaceous chicks (Koskimies, 1962). The birds were put into small, individual, wire netting compartments in a darkened constant temperature cabinet, where they remained for 20 minutes. Body temperatures recorded immediately before and after the experiment indicated the total change in body temperature during this exposure. Body temperatures were taken in the rectum at a depth of at least 15 to 20 mm, with a flexible plastic-coated thermocouple probe (Ellab RM-4), and read to the nearest 0.1°C by means of an Ellab TE-3 thermometer.

At 20°C, an exposure of 20 minutes produced no definite effects exceeding the normal physiological variation in any of the ducklings studied (Mallard, *Anas platyrhynchos*; [Common] Teal, *A. crecca*; [Common] Goldeneye, *Bucephala clangula*; see Figure 2). Under similar and comparable conditions, gallinaceous chicks of the same age already experience a distinct drop in body temperature (Figure 2; see also Ryser and Morrison, 1954; Höglund, 1955; Koskimies, 1962).

At 10°C, indications of differences in cold-hardiness between the three species of ducks were clearly apparent (Figure 3). In addition, the difference between gallinaceous birds and ducks became more distinct. The

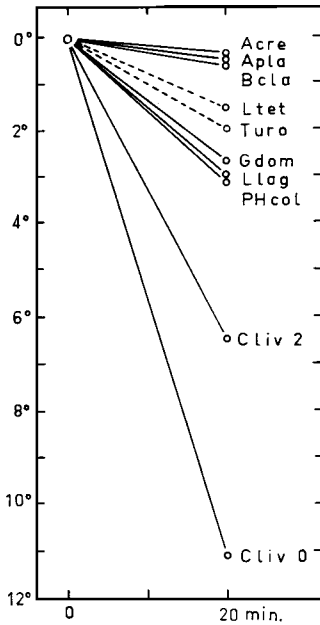


Figure 2 (above, left). Changes in body temperatures of some one-day-old precocial chicks, and, for comparison, of some domestic pigeons, when exposed for 20 minutes to temperatures of 20°C. Ltet = *Lyrurus tetrix*, Blackcock (after Salminen, 1957); Turo = *Tetrao urogallus*, Capercaillie (after Höglund, 1955); Acre = *Anas crecca*; Apla = *A. platyrhynchos*; Bcla = *Bucephala clangula*; Gdom = *Gallus domesticus*; Llag = *Lagopus lagopus*, Willow Ptarmigan; PHcol = *Phasianus colchicus*; Cliv 0 = 0-day-old domestic pigeons, *Columba livia*; Cliv 2 = two-day-old domestic pigeons.

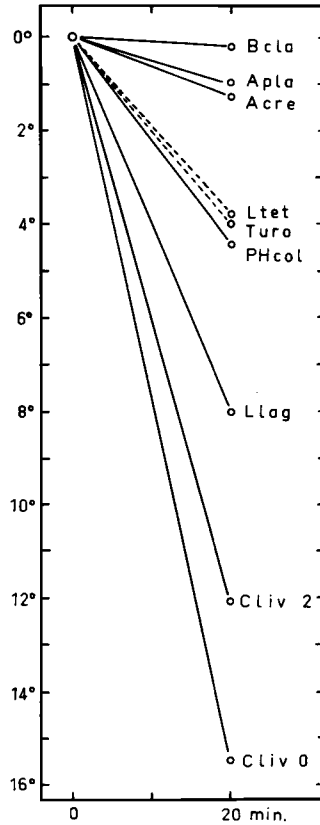


Figure 3 (above, right). Changes in body temperatures of chicks when exposed for 20 minutes to temperatures of 10°C. Otherwise as in Figure 2.

drop in body temperature of the two species of *Anas* at 10°C (computed as a means of all experiments) was 1.1°C, probably already indicating a thermogenic debt. An exposure of longer than 20 minutes to this temperature would possibly have caused a continuous drop in body temperature of (at first) roughly the same rate. This was clearly the case in the gallinaceous chicks studied, in which the drop in body temperature both at 10°C and 20°C increased in proportion to the length of exposure. In *Bucephala* the body temperature at 20°C, and probably also at 10°C, was still under complete control.

In 1962, additional experiments were undertaken, which permitted

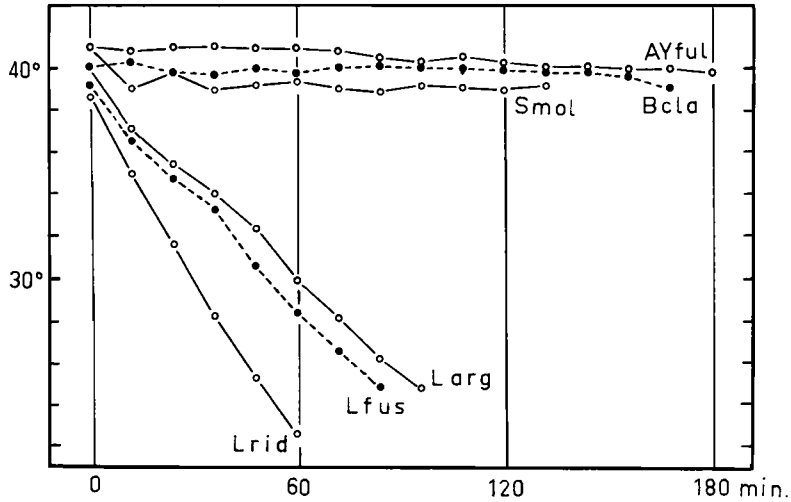


Figure 4. Changes in body temperatures of one-day-old young of various birds when exposed to temperatures of 8 to 10°C. AYful = *Aythya fuligula*; Bcla = *Bucephala clangula*; Smol = *Somateria mollissima*; Larg = *Larus argentatus*, Herring Gull; Lfus = *L. fuscus*, Lesser Black-backed Gull; Lrid = *L. ridibundus*, Black-headed Gull.

essentially continuous observation and recording of the course of the body temperature under similar and longer exposures. A flexible 0.1 mm silk-coated copper-constantan thermocouple was inserted about 30–50 mm into the proventriculus of the chick and fastened with adhesive tape at the base of the bill. The probes were left fastened to the birds for the entire period of the experiment, sometimes for as long as 24 hours. They were not found to disturb the birds to any appreciable extent. The thermocouples were connected to a Brown ElectroniK 12-point recording potentiometer calibrated to record with an accuracy of 0.2°C. The recorder sequentially printed the ambient and body temperatures from each measuring point at intervals of 72 seconds. In all other respects the birds were treated as in the experiments previously described.

In Figure 4, results are given for exposures to temperatures of 8 to 10°C in three species of diving ducks and, for comparison, three species of gulls. The ducks studied had consistently differing body temperature levels, *Aythya fuligula* (Tufted Duck) being the highest, *Somateria mollissima* the lowest, and *Bucephala clangula* having an intermediate temperature. So far, we are not able to conclude whether such differences between the species are genetically fixed and whether they are of ecological significance. All three species, however, maintained their body temperatures essentially unchanged for a period of at least two to three hours.

Figure 5 illustrates the reaction of the body temperature of three one-

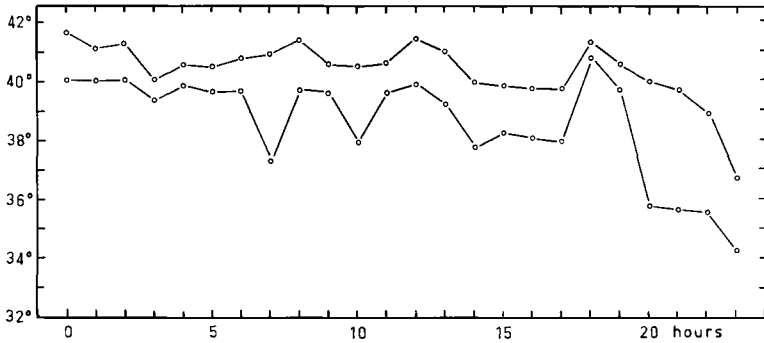


Figure 5. Maximum and minimum body temperatures of three one-day-old young of *Anas penelope* exposed to temperatures of 8 to 10°C.

day-old ducklings of the European Widgeon, *Anas penelope*, upon prolonged exposure to similar conditions (8 to 10°C). For almost 20 hours they maintained their high body temperature, but after that (in the morning, after a period of peak body temperature values probably resulting from increased muscular activity) the thermoregulation of all three ducklings broke down almost simultaneously, yet not very rapidly.

Although no strictly comparable experiments were carried out with *Anas platyrhynchos* or *A. crecca*, it appears from the 20-minute experiments that *A. penelope* is less cold-sensitive than its two relatives, and more comparable with the diving ducks in its cold-hardiness. The difference between *A. platyrhynchos* and the diving ducks (and *A. penelope*) became even more obvious in a series of severe exposures to ambient temperatures ranging from 0 to 2°C. Three one-day-old individuals of *A. platyrhynchos* were not at all able to maintain the normal body temperature (Figure 6), whereas the one-day-old young of *Melanitta fusca* (Velvet Scoter) and *Mergus merganser* (Common Merganser; Goosander) endured this stress for quite long periods. *Mergus merganser* maintained thermal balance and normal high body temperature to the end of the experiment, i.e., over 15 hours. The young of *Melanitta fusca* had apparently exhausted their energy reserves after about 5 and 14 hours, respectively; but judging from the constant high body temperature level prior to the abrupt collapse of thermoregulation, this was not the result of inadequate thermoregulation, as was clearly the case in *A. platyrhynchos*. Similarly, three one-day-old young of *Mergus serrator* (Red-breasted Merganser) were exposed to temperatures 0 to 2°C for three hours without any noticeable effect on body temperature.

In all of these cases, the ducklings were 24 to 48 hours of age at the onset of the exposure and still to a great extent dependent on the energy

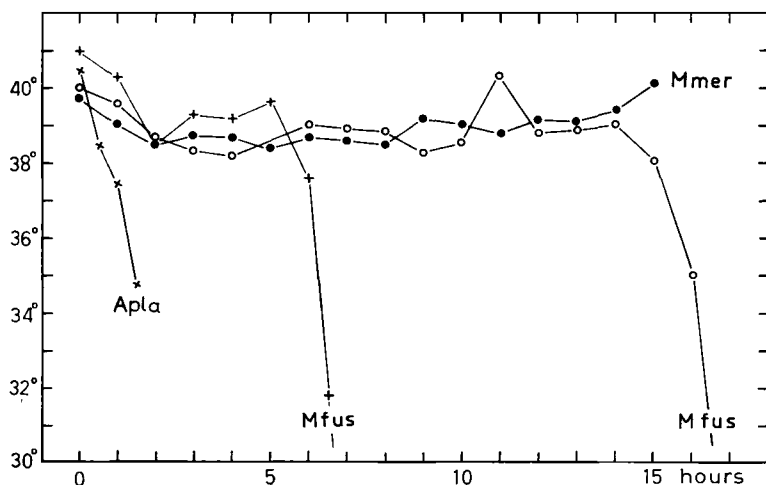


Figure 6. Body temperatures of some one-day-old young when exposed to temperatures of 0 to 2°C. Apla = *Anas platyrhynchos* (average of three individuals); Mfus = *Melanitta fusca*; Mmer = *Mergus merganser*.

reserves of the yolk sac. The results of these experiments suggest that, with adequate energy reserves, the young of the diving ducks studied, as well as of *Anas penelope*, can endure essentially any length of exposure to air temperatures as low as 10°C (and at least *Melanitta fusca* and the two species of *Mergus* even to 0°C). The collapse of their thermoregulation after prolonged exposure takes place as a result of depletion of energy reserves and not because of inadequacy of the thermoregulatory mechanisms *per se*.

Of the surface-feeding ducks, the young of at least *Anas platyrhynchos* and *A. crecca* show a cold-hardiness clearly inferior to that of the other ducklings studied. But even so, they are much more cold-hardy than any of the chicks of the other precocial bird groups so far studied, such as the gallinaceous birds (Figures 2-3) and gulls (Figure 4; see also Barth, 1951; Bartholomew and Dawson, 1952, 1954).

METABOLIC HEAT PRODUCTION AT THERMAL NEUTRALITY

In 1961 and 1962 a total of 115 runs of metabolism experiments was performed, involving the determination of the complete metabolism-ambient temperature curve of an equal number of 0- to one-day-old ducklings. The distribution of the experiments between the 10 species studied and the two age groups is shown in Table 1.

Since sufficient data were not obtained for either age class alone, and since in most species no significant differences could be established between

TABLE 1
BODY WEIGHTS AND METABOLIC CHARACTERISTICS OF DUCKS ONE DAY OLD OR LESS¹

Species	Number of young ²	Mean body weight (g)	BMR (cal/hr × g)		Theoretical wt.-specific BMR (HHP) (cal/hr × g)	Relative heat production (RHP) (per cent)
			Mean	S.E.		
<i>Anas platyrhynchos</i>	10 + 3	28.8	5.71	0.18	11.05	52
<i>Anas crecca</i>	0 + 6	16.8	8.22	0.37	13.43	61
<i>Aythya fuligula</i>	9 + 2	34.1	6.41	0.12	10.41	62
<i>Mergus serrator</i>	14 + 5	44.2	5.90	0.16	9.48	62
<i>Mergus merganser</i>	5 + 4	46.2	5.94	0.14	9.32	64
<i>Aythya ferina</i>	6 + 1	40.1	6.39	0.17	9.81	65
<i>Anas penelope</i>	5 + 4	26.4	7.62	0.38	11.40	67
<i>Somateria mollissima</i>	0 + 6	61.4	5.98	0.22	8.44	71
<i>Bucephala clangula</i>	7 + 8	32.4	7.58	0.16	10.60	72
<i>Melanitta fusca</i>	13 + 7	54.7	6.37	0.19	8.78	73

¹ For discussion of symbols and formulae see text.

² Less than one day old (left) + one day old (right).

the metabolic reactions of these age groups, the data for the two groups are combined in the following treatment, unless expressly indicated otherwise. Thus the material comprises an average of 11.5 (varying from 6 to 20) determinations of the metabolic response curve per species. For *Anas crecca* and *Somateria mollissima*, data for the older age group only are available.

Of the experiments, 93 were carried out in 1962, using the Beckman oxygen analyzer, and 23 (*Anas crecca*, 6; *Bucephala clangula*, 10; *Melanitta fusca*, 2; and *Mergus serrator*, 5) in 1961 with the Haldane technique. No difference could be found between the results obtained with the two methods. Consequently, they have been treated as homogeneous data.

Results obtained with different individuals of the same brood were generally consistent. On the other hand, the different broods of a species occasionally exhibited consistent differences in both metabolic characteristics and hatching weights. The reasons for such differences are unknown. Although the statistical error of the resulting averages was somewhat increased because of this variation, the differences between the species were not obscured, and hence all data concerning the same species have been pooled in the treatments.

Figure 7 illustrates mean basal metabolic rate in relation to mean body weight in the ducklings of each species. The center of each rectangle indicates the arithmetic mean of both basal metabolic rate and body weight (the latter taken immediately after the experiment). An area proportional to twice the standard error of the mean has been depicted on both sides of the mean. The total range is indicated by a line connecting the extreme values.

There are significant differences between the metabolic rates of the

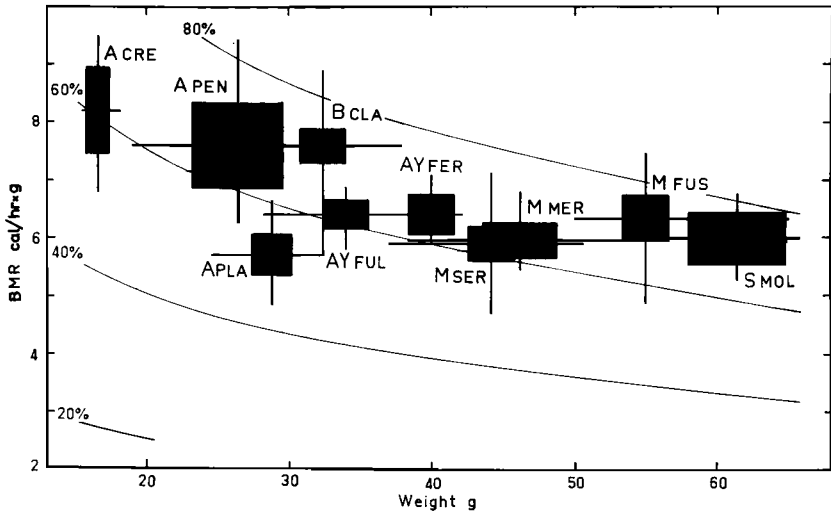


Figure 7. Basal metabolic rate as related to body weight (for both, means \pm two standard errors, and ranges are shown) of 0- to one-day-old young of 10 species of ducks. The 20, 40, 60, and 80 per cent levels of RHP (see text) are shown for reference. Acre = *Anas crecca*, Apen = *A. penelope*, Apla = *A. platyrhynchos*, Bcla = *Bucephala clangula*, AYful = *Aythya fuligula*, AYfer = *A. ferina* ([Common] Pochard), Mser = *Mergus serrator*, Mmer = *M. merganser*, Mfus = *Melanitta fusca*, Smol = *Somateria mollissima*.

species studied. The means range from 5.71 ± 0.18 (*Anas platyrhynchos*) to 8.22 ± 0.37 (*A. crecca*) cal/hr \times g (Table 1). It can be seen from Figure 7 that the young with a smaller body weight have, on the average, a higher basal metabolic rate than the larger ones. Thus, as in the adults, the metabolic rate of the young to some extent shows a quantitative relationship to body weight. The basal heat production of an adult homeotherm is known to be an exponential function of body weight (see Brody and Procter, 1932; Brody, 1945; Kleiber, 1947), and follows the general form:

$$\text{BMR} = K \times W^a$$

where W is body weight and K a constant denoting units of measurement. The exact numerical value of the exponent "a" has been subject to some disagreement (see King and Farner, 1961). Until more quantitative data on avian metabolic rates have been accumulated, the value 0.64 proposed by Brody and Procter (*op. cit.*) seems as good as any for birds of less than 100 g body weight, and has been accepted for the purposes of the present paper. Thus the theoretical predicted basal metabolic rate, which we have (Koskimies, 1962) termed the "homeothermic heat production" (HHP), of an adult bird weighing 28.8 g (which is the mean weight of the ducklings

of *Anas platyrhynchos* of this study) is $371/28.8 \times 28.8^{0.64}$ cal/hr \times g = 11.05 cal/hr \times g. As our *A. platyrhynchos* chicks have an observed BMR of only 5.71 cal/hr \times g, they produce only $5.71/11.05 \times 100$ per cent or 51.7 per cent of the amount of heat that would be produced by an adult of the same body weight. This relation of the observed to the theoretical value of the metabolic rate, expressed as a percentage, we have called the "relative heat production" (RHP).

The concept of relative heat production has proved useful in studies on the ontogeny of thermoregulation and thermogenesis in homeotherms (Koskimies, 1962). It has been found that the thermogenic deficit indicated by low RHP values characteristic of young gallinaceous chicks manifests itself in a corresponding inadequacy of thermoregulatory efficiency and cold-hardiness. In *Gallus domesticus* (domestic fowl), *Phasianus colchicus* (Ring-necked Pheasant), and *Lophortyx californicus* (California Quail) the ontogenetic development of the RHP and that of thermoregulation are in close correlation (Koskimies, *op. cit.*).

The 20, 40, 60, and 80 per cent levels of the RHP have been drawn for reference in Figure 7. It is evident that the relative heat production differs distinctly from species to species. The numerical RHP values and the data underlying them are given in Table 1, in which the species have been arranged in order of increasing RHP.

The RHP of ducklings of the 10 species studied varied from 52 per cent (*Anas platyrhynchos*) to 73 per cent (*Melanitta fusca*), thus indicating relatively wide deviations from a rigid pattern of quantitative relationship between basal metabolic rate and body size.

The RHP values obtained in this study are on the average clearly higher than those found in 9 species of European and North American gallinaceous chicks (from 20 per cent to 55 per cent; Koskimies, 1962, and later unpub. data) and 7 species of European larid chicks (from 35 per cent to 60 per cent; unpub. data).

METABOLIC HEAT PRODUCTION DURING COLD STRESS

The curves illustrating the average metabolic response to temperature in the one-day-old young of three species of ducks are shown in Figure 8.

The metabolic rates at each full degree centigrade were read from curves drawn for each individual experiment. From these values the average caloric output for each full degree and a total average curve of the metabolic response for each species and for the two age groups were derived. The lowest points of these curves are thus not exactly identical with the species averages of the BMR given in Table 1 and Figure 7, which are the means of the lowest readings of all individual experiments in both 0- and one-day-old chicks.

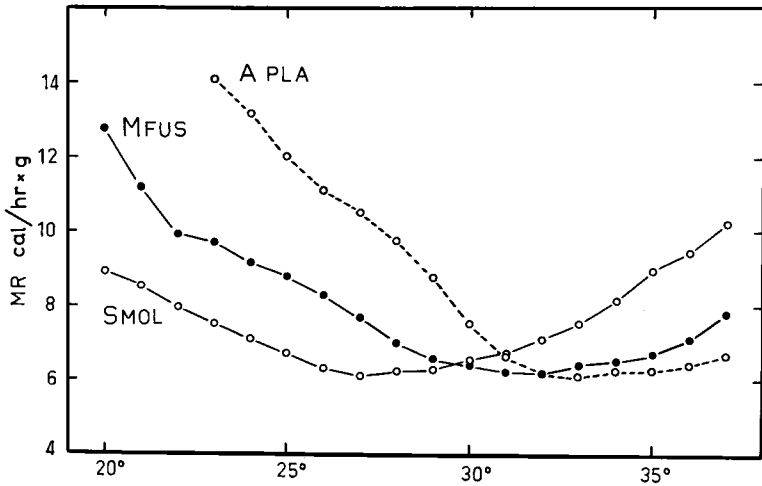


Figure 8. Metabolic rates at different ambient temperatures of one-day-old young of *Anas platyrhynchos* (Apla), *Melanitta fusca* (Mfus), and *Somateria mollissima* (Smol).

The metabolic responses to temperature in *Anas platyrhynchos*, *Melanitta fusca*, and *Somateria mollissima* differ considerably. As the basal metabolic rates of these species are almost the same, the differences in the critical temperature (32–33°C in *Anas*, 30–31°C in *Melanitta*, and 26–27°C in *Somateria*) and, consequently, in the slope of the ascending limb of the curve, are an expression of corresponding differences in cold-hardiness as a result of differences in insulation.

It is obvious that, of the three species involved, *Anas platyrhynchos* is the one least adequately adapted to live in cool environments, whereas *Somateria mollissima* shows a metabolic response typical of a bird adapted to relatively low temperatures. The zones of thermal neutrality of these species differ in a corresponding manner. Thus, for instance, an environmental temperature of 31 to 32°C is a little low for *A. platyrhynchos*, thermally comfortable for *Melanitta*, and uncomfortably warm for *Somateria*. At 25°C the young *Anas* must produce heat at a rate of over 12 cal/hr × g, *Melanitta* at less than 9 cal/hr × g, and *Somateria* at less than 7 cal/hr × g (i.e., about half the heat needed by *A. platyrhynchos* to maintain its heat balance).

For a comparison of the degrees of cold-hardiness in the 10 species of ducks studied, the method proposed by Scholander *et al.* (1950b) and explained earlier was used. The metabolic curves of the one-day-old birds, for which data were available for all 10 species, were rendered comparable by giving the basal metabolic rate the value 100 and simplified as shown

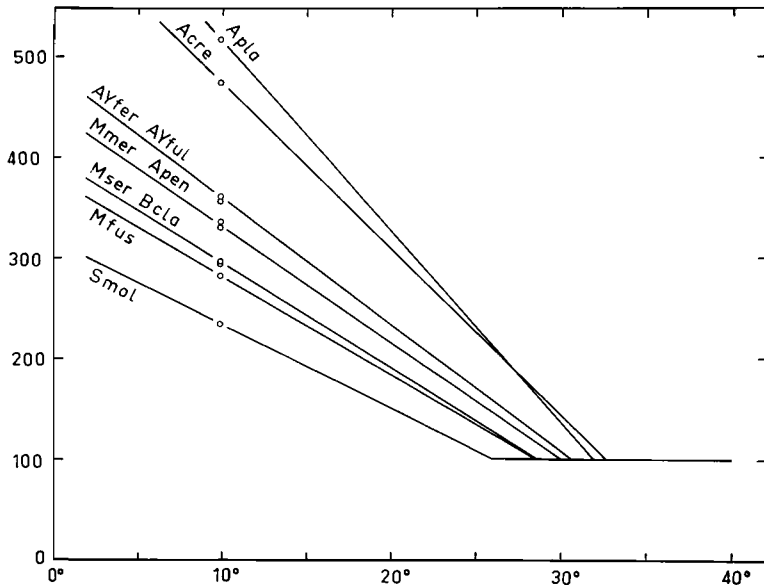


Figure 9. Simplified curves of metabolic responses to changing ambient temperatures, showing the relative cold-hardiness of the one-day-old young of the 10 species studied. A high degree of cold-hardiness is indicated by low metabolic effort (metabolic rate in relation to the basal level set at 100, vertical axis) at low ambient temperatures, e.g., 10°C. See legend to Figure 7 for key to abbreviations.

in Figure 9. The basal values were taken from the average curves to the nearest 0.1 cal/hr \times g. The slope of the curve toward the lower temperatures was determined by a visually fitted line through the empirical values of metabolic rate, and the mean actual body temperature (at the level of MR = 0) after the metabolism experiments. The critical gradient was in each case determined as the difference of the true mean body temperature and the temperature at which the line indicating the slope crossed the level of BMR. An index of insulation was obtained by rearranging the formula given on p. 282:

$$I = \frac{\Delta CT (^{\circ}C)}{BMR \text{ (cal/hr } \times \text{ g)}}$$

To illustrate quantitatively the degree of cold-hardiness resulting from the interplay of basal metabolic rate and insulation, the relative metabolic effort at 10°C was computed as the percentage ratio of the metabolic rate at 10°C to the BMR. The relevant data involved in this calculation are given in Table 2, in which the species are arranged in order of increasing cold-hardiness.

The cold sensitivity of *Anas platyrhynchos*, which was found in the ex-

posure experiments, is rationally explained by its low degree of insulation ($I = 0.91$) and its very low relative rate of thermogenesis (RHP = 47 per cent), which together make it less able to cope with low temperatures such as are easily tolerated by the young of most species of ducks. Similarly, *A. crecca*, which was found to be a poor thermoregulator, has the lowest insulation value of all 10 species ($I = 0.70$) and the second to lowest heat production relative to its size (RHP = 61 per cent).

In conformity with the results of the exposure experiments, in which *Anas platyrhynchos* and *A. crecca* were found to lack the capacity for successful thermoregulation at 10°C, it is seen from Figure 9 that the high metabolic effort (about 500 per cent) required from these two species for the maintenance of heat balance at this ambient temperature is beyond the normal capabilities of homeotherms. Similarly, at 20°C the metabolic effort in the case of these two species is still higher than that required from most of the other ducklings at a temperature of 10°C.

Mergus merganser, which was able to maintain its thermal balance when exposed to 0 to 2°C, seems consequently able to exhibit a metabolic effort of over 400 per cent for prolonged periods of time. An equal metabolic effort would enable the one-day-old duckling of *Somateria mollissima* to endure air temperatures lower than -10°C! In *Anas platyrhynchos* and *A. crecca* the same effort would be sufficient only to maintain the heat balance at about 15°C. Thus, at this level of metabolic effort, the difference between a cold-sensitive (*A. platyrhynchos*) and a cold-hardy (*Somateria mollissima*) species means a difference of about 25°C in the air temperatures tolerated by the one-day-old ducklings.

The relative order of cold-hardiness within the group of diving ducks could not be established from the exposure experiments, and hence a comparison with theoretical degrees of cold-hardiness found in the metabolism experiments cannot yet be made. It should be noted, however, that the good thermoregulatory capabilities of *Anas penelope*, which were in contrast to the two other *Anas* species studied, are correlated with high metabolic cold-hardiness values, in which *A. penelope* was comparable with the diving ducks, as it also was in the ability to endure exposure.

Somateria mollissima, as expected from its high degree of over-all insulation ($I = 1.94$) and its high metabolic heat production (RHP = 71 per cent), is known to be an excellent thermoregulator, capable of maintaining its body temperature at the age of two to seven hours in environmental temperatures of 5 to 10°C (Rolnik, 1948; see also the exposure experiments of the present study).

The efficiency of insulation (Table 2) is probably to a large extent correlated with the total body size. An efficient surface insulation seems achievable only in species in which the ducklings are relatively large on

TABLE 2
CHARACTERISTICS RELATED TO COLD-HARDINESS IN ONE-DAY-OLD DUCKS¹

Species	Body temperature (°C)	Critical gradient (ΔCT) (°C)	Basal metabolic rate (BMR) (cal/hr \times g)	Index of insulation (I)	Relative heat production (RHP) (per cent)	Metabolic effort at 10°C (BMR = 100)
<i>Anas platyrhynchos</i>	37.2	5.3	5.8	0.91	47	515
<i>Anas crecca</i>	38.7	6.1	8.7	0.70	61	470
<i>Aythya ferina</i>	38.9	8.1	6.9	1.17	67	360
<i>Aythya fuligula</i>	38.0	7.9	6.7	1.18	62	355
<i>Mergus merganser</i>	38.2	8.4	6.3	1.33	62	335
<i>Anas penelope</i>	39.3	8.9	8.8	1.01	72	330
<i>Mergus serrator</i>	38.4	9.6	7.1	1.35	69	295
<i>Bucephala clangula</i>	38.3	9.6	8.6	1.12	73	295
<i>Melanitta fusca</i>	38.8	10.2	7.4	1.38	82	280
<i>Somateria mollissima</i>	38.0	11.8	6.1	1.94	71	235

¹ For discussion of symbols and formulae see text.

hatching. The three *Anas* species with the lowest hatching weights in the series also have the lowest insulation values (which fact does not prevent *A. penelope* from being a fairly cold-hardy species, because of its high relative heat production), whereas the largest young (*Somateria*, *Melanitta*, *Mergus*) also have the highest insulation values.

DISCUSSION

It can logically be assumed that the degree of cold-hardiness of ducklings is not a random functional trait but must be correlated with the species-specific patterns of behavior and ecology of the young and the broods. Beyond, an attempt is made to correlate the bioenergetic characteristics found in this study with aspects of the life history of the species and groups of species in question.

EFFECT OF COLD-HARDINESS ON BEHAVIOR

The low degree of cold-hardiness found in the young of some species, notably *Anas platyrhynchos* and *A. crecca*, can be expected to restrict the independence of these ducklings. Low cold-hardiness in the young implies the necessity to be brooded by the duck under adverse weather conditions and, generally, under conditions where species with greater cold-hardiness would require no extra heat. In the northern parts of the range of both of these species, temperatures exceeding the capabilities of independent thermoregulation of the chicks (about 10°C) occur regularly in the brood season of these species, particularly at night. Thus, in southern Finland, broods of *A. platyrhynchos* regularly spend the night under the duck until the age of at least three weeks (M. Pirkola, pers. comm.).

Little is known about the thermal requirements under natural conditions

of the young of the other duck species. However, the poorer thermoregulators (probably most surface-feeding ducks) seem to differ from the species with hardier ducklings in general family organization and, particularly, in the degree of independence normally enjoyed by the young. The family bonds in the diving ducks are on the whole much looser than in the surface-feeding ducks (see Hochbaum, 1944; Mendall, 1958). Combined broods, which are generally an expression of loose family bonds (see Koskimies, 1957) are common in most genera of diving ducks, such as *Aythya* (Munro, 1941; Hochbaum, 1944), *Bucephala* (Sirén, 1952, 1957; Mendall, 1958), *Melanitta* (Hochbaum, 1944; Koskimies, 1957; Grenquist, 1959), and *Mergus* (Nordberg, 1950; Bergman, 1956; Koskimies, 1957; Mendall, 1958), but are hardly ever encountered in the genus *Anas*. Such abnormally large broods, which frequently contain over 50 young, cannot be adequately brooded by one duck and must be relatively independent in their thermal economy to survive at all. From the present results it is obvious that *Anas platyrhynchos* and *A. crecca*, for instance, would hardly be physiologically capable of maintaining such combined broods as are found in the species with more cold-hardy ducklings. It is of interest that in *Somateria mollissima*, the young of which are thermally the most independent, entire families, including females, merge into large groups (e.g., Hoogerheide, 1950; Bergman, 1956; Paavolainen, 1957). The same seems to be the case with two other truly arctic, and consequently probably cold-hardy, ducks, *Somateria spectabilis* (King Eider) and *Clangula hyemalis* (Oldsquaw; Long-tailed Duck) (Witherby *et al.*, 1948).

The thermal independence characteristic of the young of most diving ducks thus renders them relatively free to devote their time to searching for food and to other necessary activities, whereas the gallinaceous chicks, for instance, have to spend much time being brooded. Such independence, however, also means decreased social cooperation between the chicks and their mother, which, in the event of danger, may prove fatal (Hochbaum, 1944; Koskimies, 1957).

In the less cold-hardy precocial chicks, such as gallinaceous birds, the dependence of the young on the parents for their thermal economy is far stricter. In these birds the capacity for independent activity can be maintained by means of frequent brooding only (see Lehmann, 1941; Pynnönen, 1954; Ryser and Morrison, 1954; Höglund, 1955; Salminen, 1957; Rajala, 1962; also pers. observations). The young of the semi-precocial groups (gulls, terns, skuas, many alcids, etc.) stay at the nest or in its vicinity and are fed by the parents; consequently more energy can be used for more rapid growth and in some cases (*Puffinus*, Farner and Serventy, 1959; larger species of *Larus*, Rolnik, 1948; Barth, 1951; Bartholomew and Dawson, 1952, 1954; pers. experiments; *Cephus*, pers. experiments;

other alcids, Rolnik, *op. cit.*) for the more rapid development of an efficient thermoregulatory mechanism than in many true precocials.

Correlated with the closeness of family bonds in ducks is the time of breaking up of the family ties. In some diving ducks, such as *Aythya fuligula* (Gillham, 1957, 1958), *Melanitta fusca* (Koskimies, 1957), *Bucephala clangula* (Sirén, 1952, 1957; Grenquist, 1962; pers. observations), and *Oxyura jamaicensis* (Ruddy Duck) (Nice, 1962) single ducklings or entire broods may separate from the mother at a very early age and lead more or less independent lives. The cold-sensitive ducklings of the surface-feeding ducks could hardly survive such an orphaned existence. The final abandonment of the entire brood in the diving ducks regularly takes place before the young have reached flying age (Hochbaum, 1944; Mendall, 1958; Nice, 1962). In the surface-feeding ducks, however, the mother accompanies the brood until, and often for a long time after, the young have attained flight (see Nice, 1962).

THE ECOLOGICAL SIGNIFICANCE OF COLD-HARDINESS

The cold-hardiness of the young of the diving ducks is without doubt an important feature of definite survival value. Compared with the more cold-sensitive surface-feeding ducks, they must spend more of their time surrounded on all sides by cool waters, in which the thermal conductivity, and consequently the cooling power, is much higher than in air of equal temperature. For the same reason, the experiments described in this study illustrate but poorly the operation of thermoregulation in these ducks in their natural surroundings. Except when on land, at least the entire ventral surface and the naked legs of the ducklings are constantly exposed to water. However, the downy plumage of the ducklings is particularly heavy on the ventral surface, and their legs are normally kept cool. Both these important properties tend to decrease to some extent the effect of the strong cooling power of water.

However, the character of cold-hardiness is not maintained without cost. As most of the cold-hardiness in the ducklings seems to be effected by means of a high rate of metabolism relative to size, i.e., high energy expenditure, any use of this capability requires a correspondingly greater utilization of food. Cold-hardiness of primarily metabolic origin is thus an expensive feature which is useful only if enough food of the required quality is available.

The heavy mortality among the newly hatched young of *Melanitta fusca* in the Finnish outer archipelago (see Koskimies, 1957) is presumably an example of the energetic stress handicapping a cold-hardy species. As the scoter ducklings have been found to possess a relatively high cold-hardiness, their mortality during spells of cold weather can be explained

only by assuming that these chicks die of malnutrition and depletion of energy reserves while taking advantage of their high but uneconomical cold-hardiness.

It was earlier assumed, it is true, that the high mortality of scoter young during spells of bad weather was in part caused directly by exposure, and in part by predators, and that food supply was not necessarily a critical factor (Koskimies, 1957). In view of the present findings, however, the role of inadequate food supply in these marginal habitats appears more important than was previously believed. But no food studies on these or practically any other northern European ducklings have been carried out so far. This seems now to be a line of research where detailed work is urgently needed.

In contrast to the inevitably high energy demands of the young of the scoters and other cold-hardy ducks, the less cold-tolerant species seem to enjoy the advantages of a more economical energy balance in the young. In suitable climatic conditions the ducklings of the "mallard" type (characterized by a low metabolic rate relative to their size) are able to maintain themselves with low energy expenditure and food intake, in spite of lower over-all insulation. This feature may be assumed to make the low-metabolism type more successful than the species with inherently high energy expenditures in moderately warm environments approaching the thermoneutral conditions. However, at low environmental temperatures the less cold-hardy types are exposed to much higher metabolic stress than the cold-hardy ones. The greater economy of the thermoregulation of the former can thus be realized only in relatively warm environments.

A cold-hardiness based primarily on high basal heat production is particularly valuable in relatively short exposures to very low temperatures. Generally, a homeothermic organism is able to increase its metabolic heat production only a few (three to four) fold above the basal level. Other things being equal, a duckling with a high basal metabolic level, a characteristic of most of the cold-hardy species, is able to produce a greater absolute "maximum metabolic effort" to compensate for sudden extreme energy losses than one with a lower basal rate of heat production (see Hart, 1957).

COLD-HARDINESS IN RELATION TO GEOGRAPHIC DISTRIBUTION

Since cold-hardiness can be assumed to be an aspect of climatic adaptation, it can be expected to exhibit some correlation with distribution. Maps showing the breeding range of the 10 species studied are given in Figure 10, arranged in order of increasing cold-hardiness of the ducklings as found in the present experiments.

The correlation between the distribution of these 10 species and their cold-hardiness appears almost perfect. When they are arranged in order

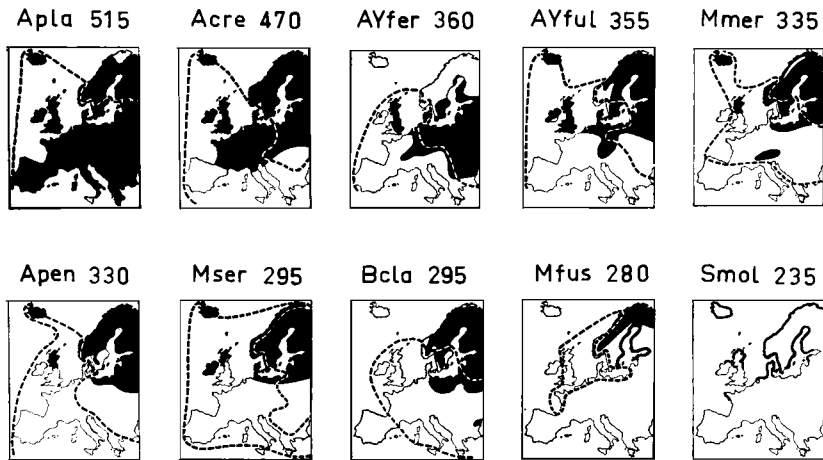


Figure 10. Breeding ranges (black) in Europe of the 10 species of ducks studied, arranged in order of increasing cold-hardiness of the one-day-old ducklings (from *Anas platyrhynchos* to *Somateria mollissima*) as assessed from their metabolic characteristics. Numbers indicate relative metabolic effort required to maintain heat balance at 10°C (see Figure 9 and Table 2). See legend to Figure 7 for key to abbreviations. Maps from Peterson, Mountfort, and Hollom (1954).

of the cold-hardiness of the young, two trends in the distributional pattern are seen. The centers of their European distributions become increasingly northern, and at the same time their ranges become increasingly restricted. One might infer that these species are, in the same sequence, to an increasing extent specialized to live in the climatic conditions of northern Europe. Specialization in this case, as always, conveys the advantage of superiority over the non-specialized (less cold-hardy) forms within a limited set of environmental conditions, here the cool northern waters. But it may also confer the disadvantage of less adequate ability to cope with conditions outside this particular environment.

It seems safe to assume that the cold-hardiness of the young of northern ducks is a feature of vital importance and one that makes their northern distribution possible. But without knowing the other factors possibly involved, we do not want to argue that characteristics of temperature-sensitivity of the ducklings also tend to restrict their distribution southwards. To be sure, a high degree of cold-hardiness generally means low heat-tolerance and it is possible that high breeding season temperatures may become critical at the southern limits of the range of the northern species. Furthermore, extreme cold-hardiness is an uneconomical property, which is useful only in a relatively narrow zone of environmental conditions, whereas it may become an energetic burden rather than an advantage

in conditions rather different from those for which it was evolved. Some evidence suggesting that northern species may have a critically low heat-tolerance and that their distribution southward may be limited by maximum temperatures of the breeding season has been presented by, among others, Ekman (1922), Kendeigh (1934), and Udvardy (1951). None of these authors specifically refers, however, to an adverse effect of temperature upon young precocial birds.

The bioenergetic differences in the species examined are primarily due to different patterns of compromise between two conflicting and, to a large extent, mutually exclusive types of adaptation: (1) cold-hardiness and thermal independence of the young with their inherently high energy expenditure, and (2) an economical energy balance which implies low cold-hardiness and greater dependence of the young upon their parents. For the northern species a relatively high degree of cold-hardiness of the young, however costly it may be, has proved necessary. For the southern ones it has been possible to dispense with cold-hardiness as a permanent character of the young; therefore they can enjoy the advantages of a more economical energy balance than their northern relatives. These two systems, in spite of their contrasting emphasis on the two mutually opposing ecological situations, are each suited to their respective environmental conditions.

Judging from their distributions, however, it seems possible that the ducks with basically low energy-expending, cold-sensitive young are ecologically more plastic and generally more successful. The survival of the offspring of such species in environments too cold for their young to cope with independently is secured, without a heavy energetic stress upon the young themselves, by means of increased frequency of brooding by the parents. *Anas platyrhynchos* is perhaps the most typical example of a species which, in spite of its low metabolic heat production and poor insulation, is, as far as range is concerned, the most successful duck of the European continent. The high survival rate of its young, given enough external heat, makes them easy to rear in captivity, and so the species has been widely successful as a domestic form. The same is true of the gallinaceous species with the lowest relative heat production values of the group, namely *Gallus domesticus*, *Phasianus colchicus*, and *Lophortyx californicus* (pers. data), whereas the more cold-tolerant, high energy-expending young (the tetraonids and the northern ducks, for instance) are much more difficult to rear in captivity.

The success of the types characterized by low thermogenic efficiency of the young and by increased dependence of young upon parents seems to parallel the general evolutionary success of systems of parental care in

which an increasing share of the burden of supplying energy is transferred from the young to the parents (e.g., Kendeigh, 1952).

So far, we have no direct evidence to indicate whether the supposedly adaptive differences in cold-hardiness of young ducks are relatively fixed characters typical of all populations within each species or whether there are also similar intraspecific adaptive differences within the range. The differences shown in the present study between the species studied, which all came from the same general area (southern Finland) may, however, be taken as an indirect indication that the cold-hardiness and other bioenergetic properties of the newly hatched young are in general fairly well fixed within the species, and that they do reflect the distributional character of the species as a whole. This would be expected *a priori* and parallels the results of Pearson (1962), for instance, who did not find appreciable differences in the metabolic responses between populations of voles (*Clethrionomys*) from localities almost 800 km apart in a south-north direction in Finland. In fact, the freedom of adaptive changes in the different populations within a species must obviously be somewhat restricted, so that the variation of adaptive properties between the populations of a species tends to be smaller than between different species. Therefore it is only natural that the climatic tolerances and faunal affinities of the species should, to some extent at least, be reflected in the innate bioenergetic properties of the young, no matter what part of the range they come from.

SUMMARY

Unfed young, one day old or less, of several species of wild ducks were exposed for various lengths of time to relatively low temperatures of 20, 8 to 10, and 0 to 2°C.

Ducklings exposed for 20 minutes to 20 and 10°C exhibited much higher cold-hardiness than gallinaceous birds and gulls of the same age (Figures 2 and 3).

The young of *Aythya fuligula*, *Bucephala clangula*, *Somateria mollissima*, and *Anas penelope* endured prolonged exposure to air temperatures of 8 to 10°C, some of them maintaining their normal high body temperature for as much as 18 hours (Figures 4 and 5).

At 0 to 2°C one duckling of *Mergus merganser* maintained complete thermoregulation during an exposure of 15 hours, and three young of *M. serrator* for at least 3 hours. Two young of *Melanitta fusca* lost control of their body temperature after 5 and 14 hours respectively (Figure 6). In all three young of *Anas platyrhynchos* exposed to this temperature, thermoregulation collapsed instantly. In general, the young of *A. platyrhynchos* and *A. crecca* exhibited a distinctly lower capability to tolerate low temperatures than those of the diving ducks and *A. penelope*.

Determinations of metabolic rates of 115 ducklings one day old or less, by means of indirect calorimetry indicated distinct differences in the relative heat production level of the 10 species studied (Figure 7). The duckling of *Anas platyrhynchos* produced only 52 per cent of the heat theoretically predicted for a bird of its weight. In *Somateria mollissima* this "relative heat production" was highest, 73 per cent. Corresponding figures for all species studied are given in Table 1.

Similarly, metabolic responses to low temperatures indicated distinct differences in the over-all insulation between the species, with indexes ranging from 0.70 in *Anas crecca* to 1.94 in *Somateria mollissima* (Table 2).

As a result of the differences in relative heat production levels and in body insulation, newly-hatched young of the 10 species studied exhibited wide differences in cold-hardiness and in the metabolic effort required at a given low ambient temperature.

The young of the most cold-sensitive species (*Anas platyrhynchos* and *A. crecca*) have been calculated to require relative metabolic rates of about five-fold the basal level to maintain their heat balance at air temperatures of 10°C. Such a high metabolic effort is generally beyond the capabilities of homeotherms. Therefore these species are unable to maintain their normal body temperature at air temperatures of 10°C or less. The most cold-hardy young were those of *Somateria mollissima*, which theoretically could endure air temperatures of -10°C with the same relative metabolic effort as *A. platyrhynchos* would have needed to expend at a temperature 25°C higher.

The correlation between the cold-hardiness of the ducklings and the behavior, ecology, and distribution of the species is discussed. There is an almost perfect correlation between the cold-hardiness of the young and the range of the species. The more cold-hardy the young, the more northern and the more restricted are the ranges of the species (Figure 10). The species with the cold-hardy young are probably specialized to live in the cool northern waters. The young of the less northern species are more cold-sensitive but at the same time may be able to survive with lower energy expenditures and seem to exhibit a greater over-all success in terms of distribution.

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