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ENERGY METABOLISM OF TWO SPECIES
OF THE GENUS EMBERIZA AS CORRELATED WITH
DISTRIBUTION AND MIGRATION

BY
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WITH 16 FIGURES AND 25 TABLES IN THE TEXT AND TWO MAPS

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CONTENTS

	Pag.
Introduction	5
I. Experimental work	7
1. The problems	7
2. Material and methods	8
A. Experimental animals	8
B. Determination of the respiratory quotient	9
C. Carbon dioxide output	10
a. Apparatus	10
b. Experimental procedure	11
D. Computation of the results; the basis of comparison	14
3. The respiratory quotient	16
A. The time required for reaching post-absorptive conditions	16
B. The R.Q. of fasting birds	18
4. Standard metabolism as a function of environmental temperature	19
A. Earlier investigations	19
B. Carbon dioxide output	22
C. Discussion	23
a. The zone of thermal neutrality and the range of tolerance	23
b. The shape of the curve	28
5. Adaptation to sudden temperature changes	29
6. Effect of average temperature	30
A. Adaptation to low temperatures	30
a. Introductory	30
b. Energy metabolism of yellow buntings acclimatized to room and to outdoor temperature during different seasons	34
c. Discussion	34
B. Adaptation to high temperatures	39
a. Introductory	39
b. Experimental device and procedure	41
c. Results	44
d. Discussion	46
7. Basal metabolism	48
8. Plumage and temperature regulation	52
A. Determination of the insulating power of the plumage	52
a. Earlier investigations	52
b. Photographic determination of the thickness of the plumage	53
B. Metabolism and plumage	55
a. The metabolism at low temperatures of birds with defective plumage	55
b. Heat resistance of birds with defective plumage	56
c. Discussion	57

9. Molt and metabolism	58
10. Energy metabolism in moist air	61
A. Material and methods	61
B. Discussion	62
11. Water evaporation	64
12. Fat deposition	66
A. Weight variations	66
a. Introductory	66
b. Weighings	67
c. Results	69
B. Energy metabolism and deposition of fat	71
a. Deposition of fat in relation to photoperiod and temperature	71
b. The carbon dioxide output of fat birds	72
C. Discussion	74
13. Summary of the results	78
II. Ecological considerations	81
1. Phenological data	81
A. Breeding range	82
a. Yellow bunting	82
b. Ortolan	82
B. Distribution during the winter	84
a. Yellow bunting	84
b. Ortolan	84
C. Migration	85
a. Yellow bunting	85
b. Ortolan	85
D. Summary	86
2. Photoperiod and average temperature within the ranges of the two species	86
3. Ecological significance of the physiological differences demonstrated	89
A. Cold tolerance, autumn migration, and wintering	89
B. Heat sensivity as correlated with spring migration and the southern boundaries of the breeding ranges	94
C. Summary	97
4. Concluding remarks	99
Acknowledgements	101
References	103

INTRODUCTION

In modern research on bird migration, there are four major lines. The fundamental problems were formulated in 1926 by THOMSON (according to WOLFSON 1948). They are: (1) the origin of migration; (2) the ends served by migration; (3) the annual stimuli for migration; and (4) the path and goal of flight. Of these, three, and especially the first and second of them, are closely connected with each other. Studies on the biological significance of migration, on its role in the balancing of species and individual between life and death, may throw light on the evolution of migration also, by elucidating the selective mechanisms.

In the middle of the 1920's, ROWAN initiated a new epoch, the experimental one, in the history of research on bird migration. His experiments have been followed by numerous others. But in spite of the great body of work involved, the literature in this field still gives a confusing picture. There is an obvious disproportion between facts and hypotheses. In the present situation, facts are badly needed: the supply of hypotheses is assured for a considerable time. There is one generalization we can safely make »in our present state of ignorance« (MAYER 1953a): that the problem seems very complicated. PHILLIPS (1951), in reviewing the difficulties involved, arrives at some pessimistic conclusions as to the possibility of clarifying the problem. They are, in a sense, sound and correct. But they should not discourage research in this field.

The experimental work has mainly been focussed on the problem of the annually recurring stimuli to migration. The literature in this field has been reviewed by FARNER (1950) and SCHÜZ (1952). In no case is the problem definitely solved. This depends partly upon the fact that many fundamental features of the physiology of birds are still too little known. During the last few years, studies on orientation during migratory flights have made admirable progress. These two are perhaps the most dramatic aspects of bird migration. Research on the biological significance of migration has gained much less attention. But for a proper understanding of the whole problem, it is of great importance.

KENDEIGH (1934) wrote »that the physiological and structural characteristics of the individuals and species are fundamental and condition all other responses; that the behavior of the species is adjusted to make the most of these inherent characteristics and avoid circumstances that are detrimental; and that the final ecological distribution, abundance, and relations of a species are the result and expression of the interplay of environmental conditions, behavior responses, and structural and physiological characteristics.» The same attitude is expressed in the following sentences of FARNER (1950): »Migration is the result of the release of a complex inherited behavior pattern stereotyped in the nervous and endocrine systems. Presumably such patterns have evolved by variation and selection as in the evolution of morphologic features. Among the selective factors may be more favorable breeding conditions in summer in the breeding area, more favorable energy intake and energy relationships in winter (as suggested by KENDEIGH), unfavorable summer temperatures in the winter area (KENDEIGH 1934), and more favorable nutritional conditions. Much more attention should be given to this aspect of migration.»

PALMGREN (personal communication) suggested that comparative studies of closely related species would make possible a systematic treatment of the problem. As a suitable pair of species he proposed the yellow bunting (*Emberiza c. citrinella* L.), and the ortolan bunting (*E. hortulana* L.). Temperature is one of the most important abiotic factors. This paper is devoted to the study of the energy relations and temperature physiology of the two species. It seemed very likely that there would be differences between the two buntings in these respects. During the course of a year they are exposed to quite different climatic conditions.

From the study of these factors, there may also emerge facts of fundamental importance in the ecology of the species, and in some aspects of the phylogenetic development of migration, too. Then there are contradictory views concerning, for instance, adaptation to various environmental temperatures, which make confirmation and verification of many points necessary.

At this point, I wish to emphasize that in my opinion nothing has emerged to justify generalizations. The conclusions must be limited to the two species studied. But in spite of my efforts to insure comparable results, there are still features which make the avoidance of perhaps undue generalization impossible. The discussion is based upon the results of experiments with some sixty birds from southwestern Finland. Nothing is known about any possible physiological differences between different populations of the species or about the wintering of the birds from this part of their range. Therefore, it is necessary to discuss the results using the whole range of the species as a background.

There may be serious mistakes in the evaluation of the absolute significance of the results. Perhaps more important than the absolute reliability of the numerical data is nevertheless a clear picture of the relation between the two species.

I. EXPERIMENTAL WORK

1. THE PROBLEMS

Scattered in the literature there are many reports of observations showing that weather may at times have a direct, easily detected influence upon bird life. Such are the many notes on catastrophes among wild birds, owing to sudden unfavourable changes in the weather conditions (see e.g. DU PALLUEL 1899, GRESCHIK 1907, CHILDS 1913, WILLFORD 1925, BERNEY 1928, PITT 1929, SMITH 1929, WITHERBY & JOURDAIN 1929, SCHÜZ 1935). But in general the effects of climate are more cryptic, and their nature can be analyzed only by careful investigation, including laboratory studies of physiological regulation in different environmental conditions.

The most detailed and perspicuous picture of the ability of a homoiothermic organism to regulate its body temperature is obtained from the graph showing its energy metabolism as a function of environmental temperature. The first part of the study, carried out in the years 1950—1951, was performed with this object in view. A summary of the main results was published in 1952. In the experiments were included determinations of the upper and lower limits of tolerance, the zone of thermal neutrality, and the basal metabolic rates. Room-adapted birds were mainly used. For technical reasons, determinations of the respiratory quotients also were made, including observations on how fast postabsorptive conditions were reached after the birds had been deprived of food.

During 1953—1954 the effect of adaptation to different environmental temperatures was especially studied. The main problems were:

1. Which are the seasonal changes in basal metabolic rates and metabolism at low temperatures occurring in (a) room-adapted birds, and (b) birds adapted to out-of-door conditions? (Studied on yellow buntings from February 1953 to March 1954.)

2. Is there any effect on metabolic rates of prolonged exposure to warmth? (Studied on both ortolans and yellow buntings from October 1953 to March 1954.)

3. The energy metabolism in warm and moist air.

Additional determinations of R.Q. were performed during August—September 1953.

Weight variations were studied in both species in connection with the respiratory experiments, and additional weighings were performed with the ortolans from July to December 1953 in order to gain information concerning their fat deposition. The energy metabolism during deposition of fat was studied on ortolans in 1953—1954.

In the second part of this paper, the correlation of the physiological findings with the distribution and migration of the two species is discussed.

2. MATERIAL AND METHODS

A. EXPERIMENTAL ANIMALS

The birds were taken as nestlings at an age of 8—10 days. Thus a homogeneous material was obtained. In addition, yellow buntings trapped as adults were used. They served, among other things, as a check upon the reliability of the results obtained with the hand-raised birds. In 1950—1951 I had 4 juvenile and 5 adult yellow buntings. Of the latter, one was used throughout the whole of the experiments, whereas two were obtained in February and two in March. There were 8 ortolans, all of them raised during the summer of 1950. These birds were all released in summer 1951.

During February 1953, 9 yellow buntings were trapped and used in experiments during the spring. 4 remained and experiments were made with them from July 1953 to March 1954. During the summer, 14 yellow buntings were raised in addition, together with 17 ortolans. Of the former, three were killed in September, of the latter one in August and two in September. Altogether, 32 yellow and 25 ortolan buntings have been used in my experiments. Each bird was banded. Tables showing the use of the birds will be given below (pp. 12—13).

During the time immediately after the young birds had been removed from the nests, they were fed by hand using blunt tweezers. They were given insects, fresh and dried ant pupae, hard-boiled egg, and fresh, crushed green vegetables. At least a small quantity of fresh insects or ant pupae every day was necessary. At the age of about 18 days, they usually began to feed themselves. From the middle of September onwards, they received almost exclusively vegetable food: canary-, hemp-, and millet seed, oats and fresh greenstuff. A few times during the course of the winter, they obtained fresh mealworms. This diet was supplemented with gravel, shells, and a vitamin preparation, containing vitamins A and D, thiamine, riboflavin, pyridoxine, nicotylc amide, PABA, pantothenol, tocopherol, and ascorbic acid. Except from the vitamin preparation, the food was available *ad libitum*, and so was drinking and bathing water. The birds seemed healthy and vigorous. They moulted normally, and nothing unusual was observed in their pigmentation. The sex of the yellow buntings could be determined after a few weeks (compare O. & M. HEINROTH 1924), whereas the males and females among the ortolans could not be distinguished until October.

In 1950, the birds were kept out of doors during the summer. The dimensions of their cage were 110 × 85 × 85 cm. In September, the birds were moved to the Zoological laboratory and from this time onwards they were kept in cages, measuring 100 × 50 × 50 cm. They were placed in a room where the temperature during the winter varied between 16 and 21°C. In the front area of the laboratory building, there is a small, unheated house where

the birds could be kept in almost natural conditions. Here, the birds obtained in February and March 1951 were placed.

In 1953 the birds were treated in the same way, but they were kept in the small house mentioned above from mid-July to the first days of October. In this house, the windows were open and thus natural conditions were approached.

Natural light is, of course, much stronger than the light in the bird room. The light variations in the bird room were not quite natural, owing to the street-lighting. The conditions were, however, more closely related to natural winter light conditions within the winter range of the yellow bunting, and the temperatures prevailing in the wintering areas of the ortolan. To secure comparable results in the experiments, it was essential that the birds were in similar conditions.

B. DETERMINATIONS OF THE RESPIRATORY QUOTIENT

Determinations of the R.Q. were made with both species from October 1950 to May 1951 and in 1953 from August to the first week of October. The same birds were used in these experiments as in the determinations of the CO_2 output at various environmental temperatures (see below tables 1 and 2, pp. 12—13).

The apparatus was a modification of the wellknown device described by HALDANE (1892). It is cheap, easy to handle, and very suitable for work at varying temperatures. When the energy metabolism in different environmental temperatures was studied, only the CO_2 output and water loss could be determined (see below, p. 10). In view of the possibility that the R.Q. may vary, CO_2 production is not alone a sufficient basis for combustion determinations. A standard procedure insuring a consistent R.Q. must be used. Experiments were carried out in order to ascertain how long the birds had to be deprived of food before they reached postabsorptive conditions, and what the R.Q. of fasting birds was.

In R.Q. determinations with this form of respiratory device, the experimental animal is weighed before and after the experiment. Its water loss and CO_2 output are added up, and from the sum its weight loss during the experiment is subtracted. The difference is the amount of oxygen consumed.

In the R.Q. determinations, a respiratory chamber of glass tubing was used. The bird was weighed within the chamber — the best method for prevention of uncontrolled weight losses — on an analytic balance.

The arrangement of the apparatus for the experiments was about the same as that described by KENDEIGH (1944). As absorption media, soda lime and silica gel were used. The air tubes were of glass or plastic, provided with short rubber connections. In some thirty model experiments, known quantities of water and CO_2 were introduced into the system. The accuracy of the determinations was ± 1 mg. The errors in the weighings of the birds were 2.5 mg. at maximum. The greatest possible error in the determinations of the R.Q. was 6 per cent.

During 24 hours before the beginning of each experiment performed in 1950—1951, the animals used were fed with canary seeds only. This was the case in the determinations of the R.Q. of fat ortolans in September 1953, too. During the time August — first week of October 1953, a study was made of the R.Q. of fasting yellow buntings which had been fed on the food mixture described above (p. 8) until they were deprived of food as the experiment commenced.

Just before a determination, the apparatus was checked, and the absorption tubes weighed. A bird, deprived of food from 0 to 10 hours, was placed in the respiration cham-

ber and weighed. Immediately afterwards, the CO_2 and water determinations were made. Then the bird was weighed a second time. Through the use of two sets of absorption-tubes, the experiments could be made successively at short intervals.

$\frac{1}{2}$ -hour periods were used. This seemed convenient, as the birds did not suffer noticeably during this short time. As a rule, the birds seemed quite tranquil after the experiments, and soon began to feed. ASHER & CURTIS (1925) showed that the R.Q. of rats rose during work. In spite of the fact that the experimental error could have been reduced in my experiments by the use of longer experimental periods, such were used only in a few determinations. The reason was that during a prolonged stay in the apparatus the birds became very restless and active, and it was thought that the muscular work involved might lead to an effect similar to that described by ASHER & CURTIS.

As a control, some determinations of the R.Q. were made with the great respiration chamber described below, with which otherwise the CO_2 output only was studied. Excreta, feathers, etc., were collected by means of plastic cloth, which made recording of the bird's movements impossible. These experiments were time-consuming and difficult to perform with sufficient accuracy. It was necessary to keep the bird within the chamber for rather a long time before the actual determinations were made, to secure the balanced conditions needed for proper determination of the water loss. The assumption was made that the bird lost weight at a constant rate throughout.

C. CARBON DIOXIDE OUTPUT

a. Apparatus. As respiration chamber, a slightly conical glass jar with a ground glass cover was used. It was sealed with vacuum grease. The diameter at the mouth was 200 mm., the depth 220 mm., and the volume about 6.8 litres. The ample space permitted the birds to sit freely in a natural posture, which is necessary when resting values are desired. The chamber was completely blacked out with rubber cloth.

The activity of the birds was registered with an electric device, constructed by PALMGREN (1943). In the chamber, there was a sitting perch and a disk of wire-netting, both on a balance. The contact was between two copper plates. One of these was fixed whilst the other moved with the bird's movements. The arrangement worked satisfactorily and was absolutely necessary for the success of the experiments. When obtainable, a pneumograph or a device of the type described by BENEDICT & FOX (1932) is presumably more handy.

The temperature was recorded with a mercury thermometer inserted in the air current just in front of the chamber. Checks with two thermometers indicated no rise of the temperature when the air passed through the chamber during experiments. Temperatures differing from room temperature were achieved by means of a water thermostat, and cold mixture. Temperature variations amounting to $\pm 0.5^\circ\text{C}$. could not be prevented. In 1953–1954, a refrigerator was at hand. Model experiments indicated the same accuracy of the CO_2 values as in the R.Q. determinations. The rate of the air current was 0.6–0.7 litres per minute. It was checked with the aid of a gas-meter.

As the sets of absorption tubes could be exchanged without disturbing the experimental animal, successive periods of arbitrary length could be used, and the results of the CO_2 determinations were very exact. Especially at temperatures below 0° and above 25°C ., however, it was difficult to achieve accuracy in determinations of the water loss. In the former case, the moisture froze in the respiration chamber, in the latter, part of it was condensed in the pipe between the chamber and the U-tubes. Furthermore, it was impossible to separate the moisture from the excreta. The necessity of recording the bird's

activity did not, for technical reasons, permit collection of the excreta, down, feathers, etc., lost during the experiment. Thus, the R.Q. could not be determined.

Dry air entered the respiration chamber. The relative humidity of the air leaving it at $+7^{\circ}\text{C}$. was 95 per cent, at still lower temperatures 100 per cent, and at temperatures above $+20^{\circ}\text{C}$. usually less than 50 per cent. As it was considered possible that the dry air at high temperatures might irritate the birds, some control experiments were performed. The air was saturated with moisture at $+20^{\circ}\text{C}$., and warmed to $+25^{\circ}\text{C}$. before entry into the chamber. Thus, the relative humidity was 73 per cent, augmented by the moisture produced by the bird. The CO_2 output was not altered. Probably the results obtained at different temperatures are comparable in spite of the different relative humidities.

In September 1953, another similar apparatus was built.

b. Experimental procedure. Resting values were obtained and the effect of the daily rhythm upon the metabolism was eliminated by performing all experiments between 7.30 p.m., and 1.30 a.m. BENEDICT & FOX (1933) observed that birds confined in a dark respiration chamber were active and slept in perfect accordance with their normal daily rhythm. According to BERGMAN (1950), the yellow bunting sleeps during the first 5—6 hours of the night. Thus the late evening until midnight was the most suitable time for the experiments. HIEBEL & REYS (1951) obtained results that confirm this conclusion.

Prior to the experiments, the birds were fasting at least 4 hours. As will be seen in the following section, the R.Q. during this time dropped to values about 0.7, indicating oxidation of fat and a postabsorptive state.

In all experiments during 1950—1951, the birds had been fed on canary seed alone during 24 hours before they had been deprived of food. From experiments performed in August–September 1953 it appeared that the R.Q. during fasting was not influenced by the food consumed (see below, p. 19). From October 1953, the birds fed freely on the mixed food described above, until the experiments were commenced by depriving them of food.

Usually, the birds fasted from 4 p.m. and were placed in the chamber at 5 o'clock in experiments performed at or below room temperature. An adaptation time of 3—4 hours before the actual determinations was thus secured. The birds were weighed before they were placed in the chamber and immediately after the experiment.

The respiration chamber had to be completely blacked out. Even the slightest glimpse of light caused an immediate rise in the CO_2 output. It also proved necessary to have the bird sitting on the perch. When the bird was sitting on the bottom of the chamber, higher and more variable results were always obtained.

BENEDICT & CARPENTER (1948) and BENEDICT (1938) discuss the advantages of long and short experimental periods respectively in measuring the respiratory exchange. They conclude that short periods are preferable, provided that the technical error can be kept within reasonable limits. In this case, it was necessary to limit the periods to the shortest possible time, as the birds often exhibited spells of activity. For technical reasons, 20 min. was about the shortest possible period. In 1950—1951, $\frac{1}{2}$ -hour periods were mainly used. As the activity of the birds was recorded, every value obtained during restlessness could be excluded. The CO_2 output of quiet birds remained at the same level throughout the experiments.

Before and immediately after the experiments at -17°C . the rectal temperature of the birds was recorded by means of a mercury thermometer. The measurements of

the birds' temperatures obtained in 1953—1954 were taken from the throats using a thermocouple. The accuracy was $\pm 0.2^{\circ}\text{C}$.

In the first experiments performed at temperatures above room temperature, a marked restlessness of the birds became apparent. KENDEIGH (1944) observed that his birds were more active after they had been some two to three hours in the apparatus. RINNE (1951) has noted the same behaviour on the part of rats. In accordance with KENDEIGH's observation, the procedure was altered as follows: At 4 o'clock, the experimental animal was placed in a cage without food. By means of electric light, it was prevented from

TABLE 1. The use of the birds in 1950—1951*).

<i>Ortolans</i>	Month							
	X	XI	XII	I	II	III	IV	V
M20	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
F13	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
F24	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
F14	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
M12	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
M 0	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
M25	RQ	RQ	RQ	C+RQ	C+RQ	C	C	RQ
F15	RQ	RQ	RQ	C+RQ	C+RQ	C	C+RQ	RQ
<i>Yellow buntings</i>								
juv. M06	RQ	RQ	RQ	C+RQ	C	C	C+RQ	RQ
» M23	RQ	RQ	RQ	C	C †			
» F22	RQ	RQ	RQ	C+RQ	C	C	C+RQ	RQ
» F21	RQ	RQ	RQ	C	C	C	C+RQ	RQ
ad. F	RQ	RQ		C+RQ	C	C	C+RQ	RQ
» F74					NA	NA	NA+RQ	RQ
» M37					NA		NA+RQ	RQ
» MN1						NA	NA+RQ	RQ
» MN2						NA	NA+RQ	RQ

*) Signs used.

The first column gives the marks of the individual birds (F = female, M = male). These marks are used throughout the text.

C = CO_2 output as a function of environmental temperature.

EF = energy metabolism during fat deposition.

D = influence of temperature and photoperiod on fat deposition.

M = metabolism during moult.

MA = metabolism in moist air.

NA = metabolism of birds adapted to natural light and temperature.

RA = metabolism of room-adapted birds.

P = effect of plumage deficiency on metabolism.

RQ = respiratory quotient.

W1, W2, and W3 = the groups in the experiments on exposure to warmth.

† = bird died.

Weighings performed in addition to those connected with the experiments are not indicated in the tables.

sleeping. About 8 p.m. it was weighed and the experiment commenced. Half an hour after the bird had been placed in the chamber, the first determination began. When twenty minute periods were used, two experiments could be performed in one evening. This method worked well: the birds were quiet. Apparently, they often slept, because as they were removed from the chamber after the experiment, they very typically exhibited the diminished alarm preparedness described by BERGMAN (1950) as characteristic of yellow buntings, etc., immediately after they have waked up.

D. COMPUTATION OF THE RESULTS: THE BASIS OF COMPARISON

The results of the experiments will usually be given as means of several measurements. In the calculations, SNEDECOR (1950) has been followed. For each group of values, the number of observations ($= n$) is given. Only a simple analysis of the significance of observed differences between groups has been necessary. The following symbols have been used:

m = the mean.

σ = the standard deviation.

C = the coefficient of variation.

The mean is given $\pm$ the standard error, and the coefficient of variation is σ as a percentage of the mean. t -values greater than 2.7 indicate a P -value greater than 0.02, and t -values greater than 3.1 a P -value greater than 0.01.

Comparisons between the energy metabolism of two species are misleading, unless the experimental results are expressed in units giving correct relative values. According to BENEDICT (1938), the comparison between two species should be based on the total energy production of individuals with the same total weight. This procedure is, however, only exceptionally practicable. Besides, there always remains the risk of different proportions between the metabolically active and inactive tissue, especially when systematically widely different forms are studied. E.g. BENEDICT (l.c.) and BRODY (1945) emphasize the »metabolically active mass» as the ideal basis. It has been impossible, however, to show even in one single case what exactly this metabolically effective weight is.

The bigger a homoiothermic animal, the less its metabolism per unit weight. This was observed as early as the beginning of the 19th century, and led to the formulation of the »surface law» (RAMEAUX & SARRUS 1837, according to BRODY 1945). This and other bases of reference are discussed by BENEDICT (1938), BRODY (1945), ZEUTHEN (1947, 1953), PROSSER (1952), EDWARDS (1953), etc.

Since the surface law was formulated, attempts have been made to calculate an empirical constant which, multiplied by the $2/3$ power of the weight, will give the surface. The surface measurements are, however, very

difficult to perform, and have given rather inconsistent results (see e.g. GIAJA 1925a and b, BRODY 1945). Besides, according to several authors (BENEDICT 1938, BRODY 1945, SCHOLANDER & AL. 1950b, ZEUTHEN 1947), the combustion is more closely correlated with the 0.7 or $3/4$ power of the weight. This applies mostly to the mammals. In birds, the correlation with the $2/3$ power is more obvious.

There was considerable variation in the weights of the birds used in my experiments, and, as will be shown later (p. 69), the ortolans were on an average 4.4 grams lighter than the yellow buntings. Only one ortolan weighed during part of the time exactly as much as a yellow bunting. A comparison based on the total weight of the birds did not seem satisfactory.

In almost all the literature, data concerning energy production of animals are given per unit of weight. BENEDICT and BRODY do not consider this method theoretically satisfying. It gives, however, a clear picture of the relation between the birds here studied. Presumably these closely related and anatomically similar species have about the same proportion of metabolically effective weight. Even rather great weight variations seemingly did not affect the energy production per unit of body weight (with one important exception: see below the section on the effect of fat deposits pp. 72—74). The metabolism is thus not strictly correlated with the $2/3$ power of the body weight. CHEVILLARD (1935) concluded that the metabolism of white mice is proportional neither to the body surface nor to the body weight.

ODUM & PERKINSON (1951) have demonstrated that variations in body lipids are not the only cause of alterations of the body weight in *Zonotrichia leucollis*. In man, relatively great variations in body weight can be observed, owing to changes of the muscles or other tissues (KEYS & BROŽEK 1953). Such modifications do not seem to affect the values of combustion per unit of weight because they are confined to metabolically active tissue. BENEDICT & CARPENTER (1918), BENEDICT (1938) and KENDEIGH (1949) discuss the possibility that body fat does not participate in the energy metabolism, but they have no data to show what is actually the case. Experiments on man (KEYS & BROŽEK 1953), the mouse (MAYER 1953b), and the ortolan (this paper) show, however, that the total energy output in basal conditions is not augmented by fat deposits. The basal metabolic rates, at least, should be calculated on the basis of unit lean weight. My experiments indicate that fat deposits do not affect the total energy metabolism at lower temperatures, either.

For these reasons, the results of the respiration experiments are given as mg. CO_2 /gm./hr. For the ortolans, the weight is corrected to «normal» lean weight, because during the migratory seasons they store large amounts of fat. In my earlier report (WALLGREN 1952) this had not been observed. Fat

birds were then used only in the experiments above room temperature, and consequently these results have been recalculated. The oxygen consumption as ml. O₂ consumed per gm. of body weight per hour is also given. These values have been calculated using an R.Q. of 0.895 for the ortolans, and 0.883 for the yellow buntings.

To facilitate comparisons with results from other investigations, there are given in connection with the tables of the results, factors that, multiplied by the CO₂ values, will give the energy production as gcal./gm./hr., and kcal./sq.m. body surface/24 hr. The calculation of these factors is based on the assumption that one ml. of oxygen consumed indicates the production of 4.69 gcal.s, i.e. the standard value for the biological oxidation of fat (BRODY 1945, PEARSON 1950). The calculation of the heat production per unit of body surface has been performed using MEEH's constant 10 and the formula $S = kw^{2/3}$, where S = surface in sq.cm., k = the constant, and w = the weight in grams. The factor given pertains to an «ideal» bunting weighing 25 grams.

Still, there is one conceivable cause of error in these calculations: the body temperature of the birds — mostly not recorded — may have varied, and this in turn may have affected the CO₂ output, as RODBARD (1950), for instance, thinks possible. Firstly, however, the birds were in standard conditions, similar to those required for the obtaining of standard temperatures (HILDÉN & STENBÄCK 1915, BALDWIN & KENDEIGH 1932). The body temperature during otherwise standardized conditions is remarkably stable in spite of variations over a wide range of the external temperature (compare e.g. BALDWIN & KENDEIGH l.c., BENEDICT 1938, KENDEIGH 1944, BRODY 1945, HARDY 1950). Secondly, it seems evident from the results obtained by HART (1951), WILLIAMS (according to HIMWICH 1945), and DONHOFFER & AL. (1953) that the metabolism of homoiotherms is not correlated with the body temperature at least within the limits of normal variation of this, and thus that they do not exhibit the VAN'T HOFF effect.

The results of all the experiments, which are to be described in the following sections, are summarized on pp. 78—81.

3. THE RESPIRATORY QUOTIENT

A. THE TIME REQUIRED FOR REACHING POST-ABSORPTIVE CONDITIONS

The results obtained by LAPIQUE (1911), BENEDICT & FOX (1933), STEVENSON (1933) and KOCH & DE BONT (1945) show that small birds when fasting very soon reach a postabsorptive state, with R.Q. values indicating

utilization of fat (about 0.7). In accordance with the standard procedure described by BENEDICT & FOX (l.c.), a fasting period of ten hours was used in my preliminary experiments. As soon as it became evident that the method gave reliable results, the period without food was reduced to 4—6 hours. The duration of the effect of the digestion was studied by successive determinations upon birds which had been feeding until the first experiment in the series was carried out. The results (table 3) indicate a portabsorptive state after as little as three hours. Appropriate control of the time of the last

TABLE 3.
The effect of digestion upon R.Q.

<i>Ortolans</i>			<i>Yellow buntings</i>		
Date	Time without food	R.Q.	Date	Time without food	R.Q.
20.1.	1 hr. 45 min.	0.84	21.4.	1 hr. 45 min.	0.82
	2 » 30 »	0.72		2 » 20 »	0.83
17.2.	30 »	0.86		3 »	0.71
	1 » 40 »	0.75		3 » 40 »	0.73
	2 » 30 »	0.73	17.5.	2 » 30 »	0.75
	3 » 15 »	0.72		3 » 15 »	0.72
23.4.	45 »	0.89			
	1 » 30 »	0.87			
	2 » 15 »	0.71			
	2 » 50 »	0.73			
18.5.	30 »	0.79			
	1 » 10 »	0.74			
	1 » 50 »	0.72			

feeding and the amount of seeds then consumed, could not be accomplished. It is therefore possible that in some instances the time may have been longer.

STEVENSON (1933), using marked seeds, studied how fast the food passes through the intestines of house sparrows. I made some complementary experiments of this kind. The birds were placed in a cage without food and water. After a few hours they were given canary seed treated with a cherry-red dye used in sweets which was unalterable by the digestive processes. The birds were hungry, and as a rule immediately accepted the coloured seeds. For the lapse of time from the moment they first fed until traces of the dye could be seen in the excreta, the following values were obtained: ortolan 2 hr. 21 min. (mean of 8 determinations); yellow bunting 2 hr. 14 min. (mean of 8 determinations).

In a few experiments, the birds were fed with flies, the remains of which were also easily detected. The results were: ortolan 1 hr. 20 min. (mean of 4 determinations); yellow bunting 1 hr. 23 min. (mean of 4 determinations).

Of these few data it would seem that the rate of digestion of the two birds is about the same. But their capacity for absorption of food per unit time — which is, as GROEBBELS (1928) and SEIBERT (1949) have pointed out, from the ecological point of view the essential aspect of the problem — cannot be judged unless calorimetric studies of food and excreta are performed.

B. THE R.Q. OF FASTING BIRDS

In calculating the mean values of the respiratory quotients, all data obtained with birds which were known to have been fasting more than 3 hours, and other data when lower than 0.75, were used. The results of the experiments carried out in 1950—1951 were as follows:

Yellow buntings	Ortolans
n = 36	n = 44
m = 0.683 ± 0.0026	m = 0.695 ± 0.033
σ = 0.0156	σ = 0.0197
C = 2.28	C = 2.84

With the great respiration chamber, the following values were obtained: yellow buntings 0.68 (5 experiments); ortolans 0.69 (6 experiments).

The slight difference is insignificant. Both values seem rather low. As pointed out for instance by KROGH (1941), one of the fundamental features of metabolism is the necessity to oxidate some carbohydrate together with fat. On the other hand with fasting birds much lower values have been obtained (see e.g. KOSKIMIES 1950). All the winter, the R.Q. was stable. The values obtained with the great respiration chamber do not deviate from the other determinations. The R.Q. apparently was not influenced by the time of day. In pigeons, it has been shown by BURCKARD, DONTCHEFF & KAYSER (1933) and HIEBEL & REYS (1951) that the R.Q. of fasting individuals is not correlated with the time of day. A possible source of error might be different mobilisation of carbohydrate at different temperatures. Fasting birds, however, consume their glycogen deposits at a very rapid rate. In experiments with pigeons it has been shown that the glycogen reserves are depleted after 24 hours, and during the same time the R.Q. is lowered to normal fasting values (HARDY 1950). In the cold, the same process may be completed in 8 hours, and the R.Q. is not altered (STREICHER & AL. 1950). LAPIQUE (1911) calculated that the glycogen stored in the body of a small bird would suffice for four hours. Then gluconeogenesis comes into play. Thus it seems that the CO_2 values provide a safe basis for the comparison of the energy metabolism of the two species at different environmental temperatures.

Before all the measurements of the respiratory exchange made in 1950—1951, the birds had been fed for 24 hours on canary seed only. BURCKARD &

AL. (1933) showed that the previous diet had no influence on the R.Q. of fasting pigeons. In September 1953, a series of R.Q. determinations were made using yellow buntings that had been feeding on the commonly used mixed food until 4—6 hours prior to the experiment. The mean value was:

$$\begin{aligned}n &= 35 \\m &= 0.688 \pm 0.0031 \\ \sigma &= 0.0185 \\C &= 2.68\end{aligned}$$

There was no difference compared with earlier experiments. Neither was the standard metabolism altered.

Ortolans accumulate fat during their migratory period. MERKEL (1937) suggested that this process might alter the R.Q. Experiments with fasting ortolans in September-October 1950 and 1953 gave the following mean:

$$\begin{aligned}n &= 52 \\m &= 0.693 \pm 0.0024 \\ \sigma &= 0.0173 \\C &= 2.50\end{aligned}$$

According to MAYER (1953b), the R.Q. of fasting fatty mice was normal, but that of non-fasting higher than normal. BENEDICT & LEE (1937, according to PROSSER 1950) found a high value in fattening geese, force-fed with carbohydrate.

4. STANDARD METABOLISM AS A FUNCTION OF ENVIRONMENTAL TEMPERATURE

A. EARLIER INVESTIGATIONS

So far as I know, there has been no physiological work done with ortolans. The yellow bunting has been used as an experimental animal only occasionally and to a limited extent. The effects of temperature on organisms are one of the classical objects of research. There are, however, only a few studies concerning the relation of energy metabolism to environmental temperature in wild birds, and in only four of these is a comparison between stationary and migrating birds attempted.

LAVOISIER (1777, according to BRODY 1945) performed the first measurements of respiratory exchange, using among other organisms house sparrows (*Passer domesticus*). In 1824, EDWARDS (according to BRODY l.c.) studied the CO₂ output and oxygen consumption of sparrows, yellow buntings, and goldfinches (*Carduelis carduelis*). As long ago as 1845 LETELLIER, using chaffinches (*Fringilla coelebs*) and greenfinches (*Chloris chloris*), etc., demonstrated

a gradually diminishing combustion when the environmental temperature was raised from 0 to 41°C., and an augmentation of the water loss between 30 and 41°C.

LARGUIER DES BANCELS (1902), RÖRIG (1905), LAPIQUE & LAPIQUE (1909a and b) and LAPIQUE (1911) studied the food intake at different temperatures of several species of small birds.

GROEBBELS (1920, 1928) published results of respiratory experiments with different species of small birds, carried out at various temperatures. In these experiments, however, the control of the activity was entirely unsatisfactory, and the results are of little value. GIAJA (1925, 1928) studied the metabolism of the goldfinch. TERROINE & TRAUTMAN (1927) studied the metabolism of the little »widow bird» (*Vidua*) from tropical Africa at temperatures ranging from +40 to +17°C.

SCHILDMACHER (1928) determined the food consumption of one species belonging to the genus *Ploceus*, and another of the genus *Quelea*. The *Ploceus* sp. could augment the energy intake per unit time better than could the *Quelea* sp., which is in harmony with the fact that *Ploceus* thrives in cooler localities than does *Quelea*.

BENEDICT & FOX (1933) have published a methodologically valuable study of the basal metabolism and temperature coefficient (viz. the rise in metabolism in relation to the basal metabolism, caused by a fall in environmental temperature of one °C.): as experimental animals, canaries and shell paroquets were used. GELINEO (1934) and GOTO (1934) have also studied the metabolism of small birds.

RIDDLE, SMITH & BENEDICT (1932) performed respiration experiments with three American doves, of which one was a migratory species. It was shown that the migratory species had a more intensive combustion than the wintering ones, and was thus less suited to endure the winter cold. LONG (according to BALDWIN & KENDEIGH 1938) found that the food consumption of *Colinus virginianus* and *Phasianus colchicus* was much greater in winter than in summer. QUIRING & BADE (1943) studied the metabolism of the house sparrow.

DE BONT (1945) determined the oxygen consumption of several species at +10°C. Two determinations with a male yellow bunting gave an average of 4.55 ml./gm./hr., and an R.Q. of 0.72.

In 1939, KENDEIGH published results of experiments with the house wren, *Troglodytes aedon*. This was the first time that the metabolism of a wild bird had been studied over the whole range of its temperature tolerance. In 1944, a similar study on the house sparrow appeared. In both birds, the CO₂ output is at a minimum at +37°C.: from this point, there is a linear rise in metabolism, both when the temperature is lowered and when it is raised.

The house wren endured temperatures from $+41$ to -5°C .; the lethal temperatures of the house sparrow were $+45^{\circ}$, and -40°C . The house wren migrates south for the winter, and the correlation of the findings with the ecology of the birds is obvious.

Later KENDEIGH (1949) studied the effect of temperature and season on the energy resources of the house sparrow. These experiments provided a basis for approximate calculation of the energy available for other than pure maintenance requirements during different seasons. The author concludes that the observed gain of »productive energy» (as opposed to energy required for maintenance) accompanying the change in thermal environment from the winter's cold to the warm summer, would make possible such activities as migration, reproduction, moulting, and fat deposition.

This latest work of KENDEIGH is supplemented in a valuable way by SEIBERT (1949). The food and water consumption of the house sparrow, the wintering species *Cyanositta cristata*, and the migratory species *Junco hyemalis*, *Spizella pusilla*, and *Zonotrichia albicollis* were determined at $+34$, $+22$, $+10$, and -13°C ., and 10- and 15-hour photoperiod. A rise in food consumption appeared when the temperature was lowered. The hourly consumption was greater during a 10-hour than during a 15-hour photoperiod. Only the house sparrow, however, was capable of as great an energy intake during the shorter as during the longer photoperiod at low temperatures.

SEIBERT's data show that it is impossible for *Zonotrichia* to maintain its energy balance during a 10-hour photoperiod when the temperature falls below 0°C . The correlation with its migration is evident. SEIBERT writes: »The change in photoperiod is, therefore, a primary factor causing southward migration in the fall. . . . The more a species can increase its hourly food intake, the farther north it can be expected during the winter.»

KOSKIMIES (1950) found some very interesting peculiarities in the metabolism of the swift (*Micropus apus*). PEARSON (1950) studied the oxygen consumption of hummingbirds.

SALT (1952) compared the energy metabolism of three American finches of the genus *Carpodacus*. In SALT's investigation, there are some regrettable limitations: the most serious weakness is perhaps that no experiments were carried out at temperatures lower than $+20^{\circ}\text{C}$. The graphs showing the metabolism are extrapolated but not on a safe basis. The comparison of the birds' regulation against overheating in dry and moist air is very interesting.

According to SCHILDMACHER (1952), the northern boundary of the range of the redstart (*Phoenicurus phoenicurus*) coincides with the $+10^{\circ}\text{C}$. isotherm for July, whereas its wintering range is entirely to the south from the $+10^{\circ}\text{C}$.

January isotherm. The redstart maintains itself at $+10^{\circ}\text{C}$. and a 9 hour photoperiod. But when the temperature sinks below $+8^{\circ}$, the energy balance cannot be maintained even at a longer photoperiod. $+10^{\circ}\text{C}$. thus seemed to be a physiologically limiting temperature for the birds used in the experiments. SCHILDMACHER performed respiratory experiments, too, but the results were inconclusive.

B. CARBON DIOXIDE OUTPUT

From January 10 to April 20, 1951, 79 respiratory experiments in all were carried out. 354 periods in 73 experiments gave resting values. These are combined as follows: in table 4, the CO_2 output of the laboratory yellow buntings, 27 experiments, 131 periods (supplemented by 4 experiments at $+37^{\circ}\text{C}$., carried out in 1954); in table 5 the combustion of the ortolans, 30 experiments, 151 periods (supplemented by 4 experiments at -11°C ., carried out in August, 1953). Wild yellow buntings, and ortolans with defective plumage were also used, but the results of these experiments will be discussed later (pp. 33 and 55).

The graphs showing the dependence of energy metabolism on environmental temperature are given in figure 1.

Fig. 1. CO_2 output of the ortolan and the yellow bunting at various environmental temperatures. Vertical stretches = double standard deviation (σ).

TABLE 4.

Carbon dioxide output (expressed as mg./gm./hr.), and oxygen consumption (expressed as ml./gm./hr.) of the *yellow buntings*.

(Multiplication of the CO₂ values by 7.02 gives the results as gcal./gm./hr., by 485 as kcal./sq.m./hr.)

Date	n (birds; periods)	Temp. °C.	CO ₂	σ	C	O ₂
8.1.54	4; 16	+37	4.78±0.170	0.702	14.69	3.50
17.4.	1; 5	+36	4.94			3.69
6.—7.4.	2; 9	+34	5.00±0.148	0.444	8.89	3.74
8.—14.4.	4; 21	+32.5	4.40±0.054	0.250	5.70	3.29
29.—30.3.	2; 8	+30	4.62±0.068	0.192	4.12	3.45
17.3.—3.4.	3; 14	+25	4.42±0.066	0.244	5.53	3.30
5.—9.2.	3; 15	+20	4.82±0.074	0.274	5.68	3.60
18.—23.1.	3; 14	+14	5.64±0.082	0.310	5.50	4.10
13.—27.2.	3; 15	+ 7	6.50±0.120	0.464	7.13	4.85
29.1.—2.2.	3; 15	— 1	7.66±0.158	0.612	7.98	5.72
24.1.	1; 5	— 7	8.56			6.32
15.—16.3.	2; 10	—17	10.06±0.178	0.566	5.63	7.52

TABLE 5.

Carbon dioxide output (expressed as mg./gm./hr.), and oxygen consumption (expressed as ml./gm./hr.) of the *ortolans*.

(Multiplication of the CO₂ values by 6.97 gives the results as gcal./gm./hr., by 480 as kcal./sq.m./hr.)

Date	n (birds; periods).	Temp. °C.	CO ₂	σ	C	O ₂
17.—18.4.	2; 9	+42	4.88±0.268	0.802	16.40	3.59
16.4.	2; 9	+40	4.88±0.142	0.426	8.70	3.56
14.—15.4.	3; 14	+38	4.56±0.080	0.304	6.66	6.56
4.—5.4.	2; 9	+35	4.36±0.082	0.248	5.69	3.14
27.—28.3.	2; 9	+30	4.56±0.094	0.282	6.20	3.28
18.—31.3.	3; 15	+25	4.96±0.058	0.218	4.40	3.64
4.—8.2.	3; 15	+20	5.84±0.084	0.328	5.61	4.28
10.—17.1.	3; 13	+14	7.32±0.126	0.456	6.22	5.38
12.—2.—4.3. ...	3; 14	+ 7	8.64±0.166	0.616	7.14	6.34
25.—30.1.	3; 16	— 1	10.30±0.122	0.484	4.70	7.55
21.1., 12.3.	2; 10	— 5	11.28±0.178	0.566	5.02	8.20
10.—11.8.53. ...	4; 26	—11	13.06±0.133	0.683	5.21	9.57
13.—14.3.	2; 18	—17	12.80±0.224	0.956	7.46	9.40

C. DISCUSSION

a. *The zone of thermal neutrality and the range of tolerance.* In the graph, fig. 1., the CO₂ output is indicated on the ordinate and the temperatures

on the abscissa. The difference in the reaction of the yellow buntings and the ortolans to heat and cold is evident. The material is not very great. The experiments at various temperatures, however, supplement each other, and the similarity in the main features of the curves for both of the species indicates that the results give a fairly correct picture of the metabolic reaction upon changes in environmental temperature. This conclusion is amply supported by the results obtained in 1953—1954.

The small coefficients of variation lend support to the method adopted. RINNE (1951) in determinations of the basal metabolism of rats, showed that the coefficients of variation decreased parallel with reduction of the activity. For animals, active 53, 16, and 0 per cent of the time (the last group was anaesthetized), the coefficients of variation in RINNE's experiments were 20, 9.8 and 4.9. Within the limits of tolerance, the variation is not much altered. The procedure used seems to have secured resting values.

In all comparative studies of energy metabolism, the zone of thermal neutrality — i.e. the temperature range within which standard metabolism is at a minimum — must be known. Thus it becomes possible to determine the temperature coefficient and the cold sensitivity.

The zone of thermal neutrality extends approximately from +25 to +33°C. for the yellow bunting, and from +32 to +38°C. for the ortolan. There is thus a difference of some 6°C. Considering the usually narrow limits within which temperatures above this zone can be endured by small birds (compare e.g. KENDEIGH 1939 and 1944, BRODY 1945), this seems important. As will be shown later (p. 34), there may be a small seasonal change in the upper limit of thermal neutrality. This possibility was suggested by BENEDICT & FOX (1932), RIDDLE & AL. (1934), BENEDICT (1938) and HERTER (1941), and it was supposed that the cause would be the gradual wearing off of the feather or fur covering. In the yellow bunting, only a very small change could be detected. Even if there are similar changes in the yearly cycle of the ortolan, it need not alter the relation between the two species, which I am inclined to regard as virtually constant throughout the year.

The zone of thermal neutrality is ecologically and physiologically important, and interesting from the comparative point of view. In table 6, some values for other species are given. As a rule, small birds have high values.

An attempt was made to determine at exactly what temperature physical regulation against overheating begins. In birds, water evaporation is chiefly procured through increasing ventilation of the airsac-system. The breathing frequency rises sharply — from 56/min. at rest at +30°C. to about 200 at +40° in the house sparrow (KENDEIGH 1944) — and the bird pants with the mouth open.

Observations were made by placing the bird in a cupboard provided

TABLE 6.
Zone of thermal neutrality of various homoiotherms.

Species	Zone of thermal neutrality	Author
Homo (female)	about 30°C.	BRODY 1945
Chimpanzee	20—29	BENEDICT 1938
Dog	25—29	» »
Bullock	12—28	» »
Goat	13—21	BRODY 1945
Rabbit	15—20	» »
Rat	28	BENEDICT 1938
Normal mice	28.5	BENEDICT & FOX 1932
Hairless mice	34	» & » »
Albino mice	28—35	BENEDICT 1938
»Fat mouse»	28—35	» »
Dwarf and wild mice	34—35	» »
Chaffinch	30—31	BRODY 1945
Canary	34—36	» »
House sparrow	37	KENDEIGH 1944
<i>Mariposa</i> (East India)	39	LAPIQUE 1909b
<i>Vidua</i> sp. (trop. Afr.)	37	TERROINE & TRAUTMAN 1927
House wren	37	KENDEIGH 1939
Goose (domestic)	18—25	BRODY 1945
Hen	26	TERROINE & TRAUTMAN 1927
Turkey	20—28	BRODY 1945
<i>Streptopelia risoria</i>	30—35	LAPIQUE 1909b
Pigeon (domestic)	29	TERROINE & TRAUTMAN 1927
Tippler pigeon (dom. race) ..	about 28	BENEDICT 1938
<i>Geopelia</i> (trop.)	39	LAPIQUE 1909b
<i>Chamaepelia</i> (trop.)	39	» »

with a pane of glass. The temperature was gradually raised, some 1°C./10 minutes, until the bird was panting continuously. These observations were duplicated with all the birds available, viz., 4 yellow buntings and 5 ortolans. The result was always the same: the yellow buntings began to pant at 34—35°C. and the ortolans at 40—41°C. The difference is 6°, as in the zones of thermal neutrality.

The »critical» temperature, i.e. the temperature at which a rise in metabolism caused by overheating becomes apparent, is some 33°C. in the yellow bunting, and 38—39° in the ortolan. It is thus ca. two degrees lower than the temperature at which panting becomes continuous. GROEBBELS (1927) gives some corresponding values for other birds, and points out that the panting comes into play when the rise of body temperature has already begun. This was also observed by SEATH & MILLER (according to LEE 1948).

Perhaps this fact could be useful for rapid approximate determinations of the zone of thermal neutrality of small birds.

Above the zone of thermal neutrality, 7 experiments were done with yellow buntings, viz., 2 at $+34^{\circ}$, 1 at $+36^{\circ}$, and 4 at $+37^{\circ}\text{C.}$: with the ortolans, 2 were made at $+40^{\circ}$, and 2 at $+42^{\circ}\text{C.}$ The values obtained are higher than those obtained at 32.5 and 38°C. respectively. Moreover, the dispersion is greater, as was the case in experiments with the house sparrow (KENDEIGH 1944). The yellow bunting used in the experiment at $+36^{\circ}\text{C.}$ was very enfeebled after the experiment, and so were two of the birds used in determinations at $+37^{\circ}\text{C.}$ One of the ortolans was apparently near death from heat-stroke after 100 minutes at $+42^{\circ}\text{C.}$, whereas the other, though it panted vigorously, seemed otherwise relatively little fatigued. The latter had a considerably lower metabolism. The birds that were most exhausted when the experiments were stopped, were sitting quiet with the head lowered, and the plumage tightly pressed against the body: they breathed convulsively, and when they were removed from the apparatus there was no sign of the normal escape reaction. After some 10 minutes in coolness, they had recovered. Similar individual differences in the reaction to heat were found by KENDEIGH (l.c.) in the house sparrow.

The curve showing the metabolism of the ortolan rises when the temperature drops below $+25^{\circ}\text{C.}$, and the heat production is augmented by 0.7 gcal./gm./hr. for each degree that the temperature falls. The corresponding values of the yellow bunting are $+20^{\circ}\text{C.}$ and 0.49 gcal. The ortolan's temperature coefficient between $+25$ and -11°C. is 5.25 per cent; that of the yellow bunting between $+20$ and -17° is 3.2 per cent. At all temperatures between $+20$ and -15°C. the metabolism of the yellow bunting is about 75 per cent of that of the ortolan. The differences are significant. Already at $+25^{\circ}\text{C.}$, $t = 6.37$. From $+20^{\circ}$ downwards, t -values about 9 are obtained, i.e., P is greater than 0.001.

Down to -5°C. , the ortolans seemed quite indifferent even after a long stay in the cold. At -17°C. , it became evident that the lethal temperature had been passed. At the beginning of the experiments, the metabolism rose to almost 3.5 times the minimum standard metabolism, but thereupon there was a falling tendency. TERROINE & TRAUTMAN (1927), GIAJA (1925 a and b, 1932), and KENDEIGH (1939, 1944) in experiments with various small birds have found that the resting metabolism can usually be raised to some three or four times the minimum value. In pigeons, the same observation has been made (STREICHER & AL. 1950).

The rectal temperatures of the birds confirm the assumption that limiting temperatures had been reached. One of the birds was 2 hr. 30 min. only at -17°C. Its rectal temperature was $+41^{\circ}$ before, and $+39.2^{\circ}\text{C.}$ after the

experiment. The slight fall in temperature was perhaps insignificant. In the other experiment, the temperature of the bird fell from $+41.1$ to $+34.6^{\circ}\text{C}$. during the 6 hours for which the experiment lasted. When the experiment was stopped its condition resembled the description given by HUXLEY & AL. (1939) of »partial torpidity» in birds. After twenty min. at room temperature, the bird seemed to have recovered, but the plumage was still fluffed out, and occasionally the body shivered.

The exact cause of death from hypothermy is not known. There is probably no immediate danger until the body temperature has dropped below 30°C . Thus it seems that a rectal temperature of 34.6°C . would be well out of the danger zone. A homoiotherm, however, keeps its body temperature normal as long as possible: when the mechanism controlling temperature breaks down, there is a sudden fall in body temperature which continues until death (BALDWIN & KENDEIGH 1932, GIAJA 1932, KENDEIGH 1939, 1944, BRODY 1945, STREICHER & AL. 1950).

At -11°C . the ortolans had a metabolism higher than at -17°C . The birds were at least 5 hr. in the apparatus. After the measurements, the plumage was fluffed out, and they were all shivering violently. The body temperature, however, (recorded from the throat by means of a thermocouple) did not fall below $+39.5^{\circ}\text{C}$. Apparently, the lethal temperature is about -15°C . Naturally, because of the often considerable individual variations it cannot be exactly determined, any more than the time during which it can be endured (compare e.g. GIAJA & GELINEO 1933, KENDEIGH 1944, STREICHER & AL. 1950). There must also be a distinction between death owing to depletion of the energy reserves, and death directly caused by cold. Pigeons maintain a normal body temperature for one hour at -80° , and for 80 hours at -40°C . (STREICHER & AL. l.c.).

The rectal temperature of the yellow buntings before and after the experiments at -17° were: F ad. 15.3. $+41.2^{\circ}$, and $+40.7^{\circ}$; M 06 17.3. $+41.5^{\circ}$, and $+40.6^{\circ}\text{C}$. These figures and the small dispersion of the values of the CO_2 output, indicate that the yellow buntings were quite indifferent at this temperature. The curve for the metabolism of the yellow bunting can presumably be safely extrapolated, because it seems plausible that it will not deviate much from a straight line. Assuming an equal metabolic quotient for both of the species, the yellow bunting would be forced to maximal combustion (3.5 times the minimum value) at ca. -36°C .

According to these results, the zone of thermal adjustment would be between -36 and $+34^{\circ}\text{C}$. in the yellow bunting, and between -15 and $+40^{\circ}\text{C}$. in the ortolan. Thus, the yellow bunting would tolerate temperatures some 20 degrees lower than that endured by the ortolan, whereas the latter would have 6 degrees in its favour at high temperatures. The corresponding

zones of accommodation are 130—140° in geese and ducks, 125° in pigeons, 85° in larks, 70—90° in hens, 70° in small Passerines, 65° in rats, and 55° in guinea pigs (BRODY 1945). The value given for Passerines corresponds well with that obtained in this study for the yellow bunting, and with that of the house sparrow (KENDEIGH 1944). KENDEIGH's experiments with the house wren (1939), and the value for the ortolan indicate that a common value cannot be given for small birds. The values for geese, ducks, and pigeons, quoted by BRODY, are too great (compare STREICHER & AL. 1950).

b. The shape of the curve. The only complete curves for the metabolism of small birds as a function of environmental temperature known to me are those given by TERROINE & TRAUTMAN (1927), and by KENDEIGH (1939, 1944). My results correspond to those achieved by TERROINE & TRAUTMAN; between the rectilinear rise at high and low temperatures, part of the curve runs more horizontally. The same is the case with the curves obtained by SALT (1952). There seems to exist a transitional zone between the temperatures at which regulation against high and low temperatures comes into play. In the curves given by KENDEIGH there is a sharp angle. Of course, the width of the transitional zone may be widely different in different species. It does not, however, seem likely that it could be represented on the temperature scale by only a single point. This implies a schematization of a process, in actual fact more complicated. KENDEIGH (l.c.) writes himself: »Although there is a sharp break at 37°C. in the curve showing rate of heat production this does not indicate a similar abrupt change from chemical to physical regulation. . . . The transition is, therefore, a gradual one.»

How are KENDEIGH's curves to be explained? The combustion values are high. In part this depends on the fact that the experiments were carried out in daytime (compare BURCKARD & al. 1933). But partly, there may have been a direct influence of the technique. As respiration chambers, KENDEIGH used glass tubes 8 cm. in diameter. Even at night, he got values considerably above those obtained in my experiments with the two buntings. Obviously, an effect of the confining of the birds in the narrow tubes came into play.

In my determinations of the R.Q., the glass tube used was even narrower than those used by KENDEIGH, having a diameter of 4.6 cm. only. The values for the oxygen consumption were great and very variable in comparison with those obtained with the great respiration chamber. KENDEIGH's figures exhibit great variability: but as the experimental temperature approaches +37°C. the dispersion is radically diminished. The explanation of the sharp break in the curve could be a gradually increasing relaxation of the birds which lessened the risk of overheating. Thus, their metabolism could be lowered to the minimum possible in the prevailing conditions.

5. ADAPTATION TO SUDDEN TEMPERATURE CHANGES

The adaptation accompanying changes of the environmental temperature must presumably be especially rapid in small animals. The relation of surface to body volume is less favourable, the smaller the animal, and a greater sensitivity probably makes a greater agility of the thermostatic mechanism necessary. The physical elements of temperature regulation as a rule very soon become apparent when an animal is exposed to extreme temperatures. It is more difficult to demonstrate by actual experiments how fast chemical regulation, and thus metabolism, is affected. The experimental animals need time for adjusting themselves to the experimental conditions: the temperature effect is often hidden by muscular activity during the critical time of adaptation.

In experiments at temperatures near to or beyond the limit of tolerance to heat or cold, however, complete rest is usually soon achieved. This is quite a natural part of the process of adaptation: in extreme cold muscular work speeds up the use of the energy reserves, and exhaustion lessens the resistance of the organism; consequently it succumbs more rapidly when working than when resting (GIAJA 1932, HART 1950b). Moreover, the mobility of the air around the animal is greater when it is active, and thus heat loss faster. In heat, cessation of muscular activity diminishes the danger of hyperthermy. From the experiments with two ortolans at -17° , it is possible to conclude something about the speed of adaptation. In the first experiment, the bird (F13) was put into the chamber at 7.20 p.m. At 8.04 the temperature had fallen to -14° (from $+17^{\circ}\text{C.}$). During the first period 8.02—8.32, the CO_2 output was 12.86 mg./gm./hr. In the following period, from 8.32 to 9.02, the maximum value, 14.0 mg., was obtained. Then there was a fall in the CO_2 output, perhaps indicating the start of a break-down of the regulation. The bird was quiet all the time. The second experiment with M12 was commenced at 7.05 p.m. (room temp. $+17^{\circ}\text{C.}$). One hour later, the temperature in the respiration chamber was -15°C. The first period lasted from 8.13 to 8.43: the CO_2 output was 11.32 mg./gm./hr. During the following periods it was 13.18 and 13.92. The latter was the maximum value, and there was no marked drop in metabolism until $3\frac{1}{2}$ hours later. F13 thus seems to have raised its energy production to the maximum level after only 50—60 minutes' exposure to temperatures below -10°C. , whereas M12 needed 80—90 minutes for the corresponding procedure. KENDEIGH (1944) found that the house sparrow also needs 1 to 1.5 hours for adaptation to extreme cold.

The corresponding adaptation to heat — observations at $+38^{\circ}\text{C.}$ with the ortolans, and $+32.5^{\circ}\text{C.}$ with the yellow buntings — was achieved in

30—40 minutes. This value, too, is about the same as that found by KENDEIGH for the house sparrow. The adaptation to heat is apparently sooner completed than the adaptation to cold, but both of them are performed within a short time.

6. EFFECT OF AVERAGE TEMPERATURE

A. ADAPTATION TO LOW TEMPERATURES

a. Introductory. It is supposed that homoiothermic organisms exhibit slow seasonal changes of adaptive value in accordance with changing climatic conditions. Adjustment of the metabolic rate to the general requirements of the season are involved. These changes, however, are poorly understood both as regards nature and extent.

Some problems in this connection are important both for the experimental technique, and from the ecological point of view. They may be formulated as follows: (1) Does the zone of thermal neutrality shift? (2) Is there any change in the minimum standard metabolism? (3) Is there an effect on the percentage change in metabolism caused by a drop in temperature? (4) Is the metabolic quotient different during different seasons?

Now, question (1) is to be answered before (2) can be solved. In ecology, the answers to questions (3) and (4) are the most interesting ones, because they would show how metabolic adaptation influences the temperature tolerance of animals during changing seasons. But of course they cannot be obtained unless (1) and (2) are known. Thus these two questions are the fundamental ones and constitute the chief problems when experiments on energy metabolism are planned. Experiments at one single temperature are of little value unless the temperature characteristics and the basal metabolic rate of the experimental animal are known. Two examples may illustrate these points.

GESSLER (according to DONTCHEFF & AL. 1935) propounded a hypothesis, according to which the reaction capacity of the thermoregulatory centres should be decreased during the night. It was based on the observation that the metabolism of diurnal animals at a given temperature is lower during the night than during the day. The hypothesis was put to the test by KAYSER (1929a and b), BURCKARD & AL. (1933) and DONTCHEFF & AL. (1935). Common pigeons were used. Their metabolism was measured at four different temperatures by day and night. The oxygen consumption was 15 per cent greater during the day-time. This fact was interpreted as being due to different muscle tone. The relative increase of metabolism caused by the

same fall of temperature, however, was identical. Thus there was apparently no difference in the activity of the thermoregulatory centres during day-time and night.

When the energy metabolism is to be studied, the effect of thermal adaptation must apparently be taken into consideration, (compare e.g. HERRINGTON 1940). But sometimes important factors have been neglected in attempts to eliminate the influence of thermal adaptation. This applies, for instance, to the work of DE BONT (1945) on the energy metabolism of several species of birds. The experimental animals were kept for months at $+10^{\circ}\text{C}$., and then the respiratory exchange was measured at the same temperature. Systematically and ecologically widely different birds were used. It is not surprising, however, that, as DE BONT writes, «ni le régime alimentaire ni le comportement sédentaire ou migrateur ne se reflètent dans les valeurs absolues du métabolisme». The value of this investigation would have been greater, had the zone of thermal neutrality and the temperature coefficient been determined. And GESSLER's hypothesis would probably never have been put forward, had these factors been taken into consideration.

GIAJA and GELINEO have studied the effect on metabolic rates of a prolonged stay in constant temperatures. GIAJA (1925b) was the first to emphasize the importance of this factor. GIAJA & GELINEO (1936) claim to have demonstrated that the limits of tolerance are greatly affected by the temperature to which the animal has previously been acclimatized. According to these authors, the metabolic quotient also depends on this factor.

As an example, GELINEO's (1934) determinations of the oxygen consumption at $+31^{\circ}\text{C}$. of a female brambling (*Fringilla montifringilla*) may be quoted. After 30 days at $0-+8^{\circ}\text{C}$. it was 9.458 ccm./gm./hr. after 16 days at $+16-+21^{\circ}\text{C}$. it was 8.507 ccm.; and after 22 days at $+29-+31^{\circ}\text{C}$. it was 4.431 ccm. It seems, however, that the experimental procedure — which is, indeed, but briefly described — was inadequate. True, the birds were in a post-absorptive condition, but so far as I am aware, the measurements were limited to one hour immediately following removal from the constant temperature of adaptation. It seems likely that the experiment took place during the period of adaptation to the experimental temperature, and the results probably were influenced by the birds' activity.

In 1936, GIAJA & GELINEO published what they called «la courbe réelle de la thermogénèse». The metabolism of individuals adapted to different environmental temperatures was determined at the temperature of adaptation. The curve showing the dependence of metabolism on environmental temperature was based on the values thus obtained. According to GIAJA & GELINEO, the curve of the metabolism is shifted as a result of adaptation, every single point of the curve being higher when the animal has been

adapted to low temperatures than when it has been kept in a warm environment.

This «courbe réelle» seems to be a rather fictive conception. The average temperature varies, indeed, from season to season in temperate and cold regions: but it is not usually constant for a long continuous period. In nature, the organisms are usually exposed to great variations of temperature even within short spells of time. From the ecological point of view, a more real curve is obtained, when KENDEIGH's (1944) principle is adopted. He kept his experimental animals in outdoor temperatures, limited the experiments to one season, and investigated the effect of temperature within the whole range of tolerance of the species. In my work, however, this was not possible, owing to the different wintering habits of the ortolan and the yellow bunting.

The values obtained by GELINEO and GIAJA indicate only a minute effect of adaptation to various temperatures between 0 and +25°C. There is also a comparatively good correspondence in the percentage change of metabolic rates. The zone of thermal neutrality and the minimum metabolism were not known in all species and individuals used by GELINEO and GIAJA, and as these two fundamental quantities do vary from species to species, the interpretation of their results is difficult.

MILLER (1939) measured the metabolic rates of house sparrows at +28°C. There were three groups of birds: one group in cold, one in the laboratory at room temperature, and wild, freshly trapped winter birds. The caged birds exposed to cold still had a greater oxygen consumption when they had been 5—8 hours in the laboratory, whereas the wild birds exhibited higher values than the laboratory birds after 1—3 days in the laboratory.

RIDDLE, SMITH & BENEDICT (1934) reported that the percentage change of metabolism in tuppier pigeons decreased during autumn and winter (metabolism measured at +20 and +15°C.), and that basal metabolic rates were highest in summer and autumn. Both these findings differ from those communicated by GIAJA, GELINEO, and MILLER. MAYER & NICHITA (according to KENDEIGH 1934) found a lower percentage change in metabolism in cold-adapted than in warm-adapted rabbits. The finding of KENDEIGH (l.c.) that house sparrows endure starvation at low temperatures better during the winter than during the summer indicates that the metabolism at the corresponding temperature is lower during the cold than during the warm season.

For the laboratory worker, the question of the application of the results to natural conditions often arises. The mechanism for regulation of the body temperature of homoiothermic animals seems, however, to be one of the most tenacious elements of their constitution (compare for instance BENEDICT & FOX 1933, PFLEIDERER 1935). KENDEIGH (1944) did not find any difference in the energy metabolism of house sparrows kept for months in cages, and

wild recently captured birds. According to KENDEIGH, the lethal temperature of the house sparrow is -40°C . There is a striking conformity with some observations in nature. Thus MONTELL, an experienced ornithologist, has reported to PALMGREN (personal communication) that in the valley of the river Torneå the house sparrows disappeared in winters with temperatures lower than -40°C .

TABLE 7.

Carbon dioxide output (expressed as mg./gm./hr.) and oxygen consumption (expressed as ml./gm./hr.) of the *wild yellow buntings*.

Date	n (birds; periods)	Temp. $^{\circ}\text{C}$.	CO_2	σ	C	O_2
19.—20.4.	4; 20	+ 32.5	4.34 ± 0.044	0.196	4.51	3.24
26.2.—1.3.	2; 10	+ 18	4.90 ± 0.078	0.246	5.02	3.66
5.—7.3.	2; 8	+ 14	5.28 ± 0.110	0.308	6.28	3.94
28.2.—2.3.	2; 8	+ 7	6.74 ± 0.132	0.372	5.58	5.03

Still, the possibility that the conditions in captivity may affect the results must be taken into consideration. From this point of view, it would be most correct to use only newly captured, wild animals in the experiments. In many cases, however, reliable results cannot be obtained with such material, owing to the alarm reaction of the animals.

Both from this point of view and in the light of the somewhat contradictory results reported in the investigations quoted in this section, the results of the control experiments with the «wild» yellow buntings were interesting (see table 7). These birds were visited only once a day and thus were not used to people. During all the time until the days in late April when the last experiments were performed, they had not been exposed to warmer daily means of temperature than $+4$ — $+5^{\circ}\text{C}$. In spite of this, their metabolism was higher than that of the laboratory birds only at $+7^{\circ}\text{C}$. The material from the three lower temperatures, however, is small: the results may be affected by chance. But the value obtained at $+32.5^{\circ}$ seems convincing. Thus it seems that the birds had not been unfavourably influenced by the conditions in captivity.

Questions 1, 2, and 3 (mentioned above, p. 30) were studied in 1953—1954 using yellow buntings. The metabolic quotient could not be determined, because sufficiently low temperatures could not be produced in the laboratory. For the determinations of the minimum standard metabolism $+32.5^{\circ}\text{C}$. was chosen as experimental temperature. Thus it was considered possible to detect shifts in the upper limit of the zone of thermal neutrality. The percentage change of metabolism was studied by performing experiments at -11°C ., a sufficiently low temperature to produce a marked rise in metabo-

lism, and high enough not to be detrimental. It was supposed that the changes in metabolic rates during different seasons could be caused both by thermal adaptation, and by physiological adjustment, not directly linked with the temperature effect. Therefore, it was planned to study the changes in CO_2 output of individuals kept in the laboratory and outdoors.

b. Energy metabolism of yellow buntings acclimatized to room and to outdoor temperature during different seasons. In February 1953, 9 yellow buntings were trapped. 5 were kept in the laboratory, 4 in the unheated building previously mentioned. The cages, the diet, and the experimental procedure were as usual: in cold experiments, the birds kept in the cold were placed in the respiration chamber immediately after they were brought into the laboratory, whereas in determinations of the minimum metabolic rate, they were without food in the laboratory from 4 p.m.

During the summer, 5 of these birds were lost. The 4 remaining were incorporated as a control group in the experimental series described in the following section. On January 12, 1954, these birds were moved out of doors. In late February, their metabolism was determined after a cold spell with temperatures falling below -20°C ., and during two weeks hardly rising above -10°C . Both in 1953 and 1954, the birds endured three consecutive nights in early February with temperatures below -20°C . without weight loss, in spite of the fact that they slept on perches without shelter.

In table 8, the minimum standard metabolism of the yellow buntings is given, in table 9 the metabolism at -11°C .

c. Discussion. From the results, there appears to be no change in the minimum standard metabolism during different seasons. The first experiments were carried out immediately after the birds had been trapped in February 1953. The birds were very restless, and the few resting values obtained exhibit an average and dispersion greater than normal. This was certainly in part due to the fact that the birds had yet to grow accustomed to the procedure. The same observation was made earlier too, and applies to other animals (see RINNE 1951). In part, the result might also depend on a slight downward shift of the upper limit of the zone of thermal neutrality. Anyway, the results of the following experiments at $+31^\circ\text{C}$. exhibit nothing unusual. The last experiments in February with birds that had been in a very cold environment also suggest the possibility that a shift may occur. The difference between the results obtained at $+31$ and $+32.5^\circ\text{C}$. is not significant, but both the mean and the dispersion show a tendency to rise at the higher temperature. Within the zone of thermal neutrality, the standard metabolism of the yellow buntings in these experiments was not altered by the temperature at which the birds had lived prior to the determinations.

TABLE 8.

Minimum standard metabolism of the *yellow buntings* at different seasons. (CO₂ output expressed as mg./gm./hr.).

Experimental temperature +32.5°C. when not otherwise indicated.

Room-adapted birds.		Birds kept outdoors.	
5 birds.	22.—25.2.53.	4 birds.	27.2.—1.3.53.
n = 10		n = 11	
m = 4.78 ± 0.164		m = 4.74 ± 0.150	
σ = 0.528		σ = 0.500	
C = 11.02		C = 10.56	
5 birds.	2.—4.3.53.	4 birds.	5.—10.3.53.
temp. +31		temp. +31	
n = 21		n = 18	
m = 4.42 ± 0.062		m = 4.40 ± 0.074	
σ = 0.286		σ = 0.314	
C = 6.78		C = 7.14	
4 birds.	27.—29.4.53.	3 birds.	4.—6.5.53.
n = 20		n = 20	
m = 4.38 ± 0.056		m = 4.30 ± 0.074	
σ = 0.250		σ = 0.292	
C = 5.71		C = 6.79	
		4 birds.	23.—25.7.53.
		n = 20	
		m = 4.30 ± 0.070	
		σ = 0.298	
		C = 7.10	
4 birds.	1.—12.11.53.	4 birds.	21.—22.9.53.
n = 20		n = 20	
m = 4.34 ± 0.076		m = 4.34 ± 0.074	
σ = 0.322		σ = 0.328	
C = 7.8		C = 7.56	
3 birds.	6.—7.1.54.	3 birds.	20.2.54.
n = 16		temp. +31	
m = 4.44 ± 0.062		n = 20	
σ = 0.256		m = 4.38 ± 0.056	
C = 5.76		σ = 0.244	
		C = 5.57	
		3 birds.	23.2.54.
		n = 21	
		m = 4.50 ± 0.084	
		σ = 0.386	
		C = 8.56	

TABLE 9.

Carbon dioxide output of *yellow buntings* in cold ($-11^{\circ}\text{C}.$) at different seasons (expressed as mg./gm./hr.).

Room-adapted birds.		Birds kept outdoors.	
4 birds.	26.3.—9.4.54.	4 birds.	23.—26.3.53.
n	= 20	n	= 20
m	= 8.66 ± 0.088	m	= 8.08 ± 0.076
σ	= 0.390	σ	= 0.326
C	= 4.50	C	= 4.31
4 birds.	13.—16.5.54.	3 birds.	7.—11.5.53.
n	= 20	n	= 20
m	= 8.92 ± 0.104	m	= 9.00 ± 0.094
σ	= 0.462	σ	= 0.424
C	= 5.18	C	= 4.71
		4 birds.	27.—30.7.53.
		n	= 20
		m	= 9.76 ± 0.116
		σ	= 0.424
		C	= 4.86
		4 birds.	24.9.—1.10.53.
		n	= 20
		m	= 8.04 ± 0.072
		σ	= 0.320
		C	= 6.98
3 birds.	8.—10.1.54.	3 birds.	22.—23.2.54.
n	= 16	n	= 21
m	= 8.48 ± 0.086	m	= 7.22 ± 0.112
σ	= 0.328	σ	= 0.504
C	= 8.10	C	= 6.98

Significance of differences between the groups.

Groups	Time	t
indoors—out	late March	5.03
out— »	March—May	7.51
» — »	May—July	5.34
» — »	July—Sept.	12.76
» — »	Sept.—Feb.	5.84
indoors— »	Jan.— »	7.68
» —indoors	Jan.—May	2.07
» —out	Sept.—Jan.	4.58
» — »	May—Sept.	6.63

There is no sign of an effect of sexual maturity in spring, a factor supposed to cause a rise in metabolism (KENDEIGH 1934, 1944, BENEDICT 1938). As long ago as 1916, KROGH pointed out the marked stability of the metabolic rates of the same individual during different seasons. BENEDICT & FOX (1933) and KOCH & DE BONT (1945) found no change in the metabolism of sexually maturing small birds. SCHILDMACHER (1952) claims to have obtained such a result in experiments with male redstarts (*Phoenicurus phoenicurus*). The material, however, is small. The birds were in a postabsorptive condition, and the respiration chamber was blacked out during the experiments, which were performed in late evening. The determinations, however, were confined to one 5-hour period with several birds together. The activity was not recorded, and from the information published, it does not appear whether the birds were sitting on the perch or not. As mentioned above (p. 11), even such a factor may influence the results.

There is an apparent misconception in SCHILDMACHER's report. According to him, GROEBBELS has shown »dass beim Vogel eine erhebliche Steigerung des Umsatzes durch Temperatursenkung nur dann stattfindet, wenn man den Vogel rupft». Owing to an inadequate experimental technique, GROEBBELS has not, however, proved such a finding. SCHILDMACHER's experiments were carried out at room temperature, which presumably caused a slight rise in the metabolism of the redstarts. — The results, and especially the suitability of the experimental temperatures used in my determinations of the minimum standard metabolism, will be further discussed in the section on basal metabolism, pp. 48—52.

The experiments at -11°C . indicate the great importance of acclimatization for the percentage change in metabolism, and thus for the cold tolerance. The metabolism of the outdoor group rises steadily from March to July. In August, the yellow buntings moulted, and in late September their metabolism at -11°C . had diminished radically. Thus, an important factor must be the gradual wearing off of the feathers. The condition of the plumage is at its best in September, and poorest in July.

The birds kept indoors during the winter are comparable with those placed outdoors during the time May-October as to thermal environment. The results with the groups out September; indoors January; indoors March; out May; out July (table 9) exhibit a gradual rise of the combustion values, presumably in connection with changing insulating power of the plumage. The importance of this factor has been emphasized by KENDEIGH (1934) and BALDWIN & KENDEIGH (1938).

There are, however, other factors involved, too. This appears from comparisons between the birds kept out of doors during September and February, and between the groups kept indoors and outdoors during late winter and

early spring. The same individuals had a lower metabolism in February when kept outdoors than they had in September: but the plumage must have been in better condition in September, immediately after the moult. In late March, there was an obvious difference between the laboratory and the outdoor birds. In May, the outdoor temperature had become comparatively high, and the difference disappeared, but it returned, and became more conspicuous in the experiments which were performed in January (indoors) and February (outdoors) using the same individuals.

The comparison may be facilitated by the *t*-values given in table 9 (below). From them, there appear significant differences between all the groups compared, except those kept indoors during January and May. Even in this case, the metabolism shows a tendency to rise in warmth.

The acclimatization of the birds to cold apparently involves a decrease in heat loss, probably brought about, among other factors, by diminished peripheral circulation, and improved exploitation of the insulating power of the plumage. The demonstrated difference in percentage change in the metabolism caused by the same temperature fall indicates a marked improvement in the cold tolerance of the yellow buntings during natural winter conditions. Theoretically the lower lethal temperature of room-adapted birds is about -36°C . The corresponding value for cold-adapted yellow buntings, calculated on the basis of the same assumed metabolic quotient, is -75°C . There is only a slight downward shift of the upper critical temperature, and thus the zone of accommodation has been augmented by almost 40°C . The extrapolation, however, is extremely uncertain, owing to the slow rise of the curve. On the other hand, the cold-sensitivity of the birds is much greater during the summer than in laboratory conditions during the winter. In any case it is evident that winter adaptation improves the tolerance of cold even without a rise in the metabolic quotient, the latter possibility being suggested by KENDEIGH (1934) and GIAJA & GELINEO (e.g. 1936).

In all the experiments, the ortolan has exhibited reactions similar to those of the yellow bunting, and I am thus inclined to assume that it would behave in a similar way in this respect, also. This would still mean that it is a comparatively cold-sensitive species, because ecologically limiting temperatures are always less extreme than those demonstrated in respiratory experiments of the type here described.

Here a mechanism is demonstrated resulting in a lower metabolism in cold in cold-adapted birds than in those adapted to a warm environment. It saves energy and thus seems biologically more favourable than the rise in metabolic rates in cold, supposed for instance by GIAJA, GELINEO and MILLER. The results obtained by RIDDLE & AL. (1934) and KENDEIGH (1934) are supported. In claiming that the range of tolerance is increased when an animal

is acclimatized to a cold environment, GIAJA and GELINEO seem to be perfectly right. Whether the metabolic quotient is altered or not, remains unknown.

B. ADAPTATION TO HIGH TEMPERATURES

a. Introductory. The regulation of body temperature is accomplished in a similar way both in mammals and birds (see for instance GRANT 1951, RODBARD & AL. 1951). Therefore in the following account I shall refer to conclusions from experiments with birds and mammals as comparable.

When homoiotherms are exposed to cold, they exhibit a rise in metabolism which is not connected with muscular activity (compare e.g. CRAMER 1916; MILLS 1917; BARBOUR 1921; CANNON & AL. 1927; and HARTMAN & HARTMAN 1925, according to BAZETT 1927.) Thyroxine and adrenaline are important in this «chemical» regulation against cold. When the importance of the thyroid gland in temperature regulation was realized, its yearly cycle gained attention: in birds it has been studied by RIDDLE & FISHER (1925), HAECKER (1926, according to KENDEIGH 1934), RIDDLE & AL. (1932), KÜCHLER (1935, including the yellow bunting), and MILLER (1939). In some instances, but not in all, an increase in thyroid activity during the cold part of the year has been observed. The results are still contradictory. From the reviews of BRODY (1945) and HARDY (1950), it appears that a synthesis of the immediate or seasonal reactions to cold is not yet possible. And still less is known about regulation against heat.

The generally accepted concept of regulation against heat involves physical reactions only. A rise in temperature level above the zone of thermal neutrality induces a vasomotor response increasing heat radiation, and brings water evaporation into play. Theoretically, there is another possibility besides augmentation of heat loss: the organism should be able to decrease the metabolism («second zone for chemical temperature regulation»). The first sign of such a zone was reported by PLAUT & WILBRAND (1922). Studies of this phenomenon have been combined with research on the thyroid cycle.

MANSFELD (1949) assumed that the thyroid gland secretes two active principles, the «thermothyrones», which are thyroxine antagonists and diminish the cellular combustion. Later investigations (BALOGH & AL. 1951, 1952a, 1952b, DONHOFFER & AL. 1953) have revealed that the rôle of the thyroid gland in regulation against heat is at the most of secondary importance, and possibly of none. It seems, however, proved that serum from hyperthermal animals diminishes the metabolism of normal animals, and that there is often, if not always, a drop in metabolism as compared with normal basal values in the beginning of exposure to a hot environment. Especially in view of the observation that a decrease in metabolism occurs in warm-

adapted, but not hyperthermal animals, it seems worth while to summarize what is known concerning the reactions of homoiotherms in a warm environment.

There are some generally known negative reactions of man combined with a stay in a warm, and especially a warm and humid climate. Corresponding phenomena have been observed in all animals studied, and, as would be supposed, they are most conspicuous in non-sweating animals. The practical difficulty of adapting to a hot climate high-yielding farm animals from stocks bred and improved in a temperate climate has been the stimulus to investigations, important also from a more general ecological point of view. BRODY (1946) and HAMMOND (1947) review these studies.

I wish again to stress that many effects of warmth, not dependent on hyperthermy, have been demonstrated. Thus productivity decreases: growth, muscular work, production of milk, eggs and wool are all affected. Fertility is diminished, owing to disturbances in spermatogenesis and foetal development. Such disturbances have been observed in rats, too (OGLE 1934a and b). Further support to the view that high temperatures are unfavourable for spermatogenesis is put forward in studies on mammals, for instance by MOORE (1926) and WISLOCKI (1933): on birds by COWLES & NORDSTROM (1946), COWLES (1947) and RILEY (according to COWLES l.c.).

MILLS (1943, 1944), MILLS & COTTINGHAM (1944) and MILLS, COTTINGHAM & MILLS (1944) have demonstrated in rats an increased requirement of vitamin K (apparently this pertains also to new-born infants), thiamine, methionine, and choline when the animals have been exposed to warm environmental temperatures, corresponding to a tropical climate.

Every homoiothermic organism has an energetically optimal temperature, i.e. a temperature allowing the greatest productivity per calory consumed. For pullets, it is $+32^{\circ}\text{C}$. (KLEIBERT & DOHERTY 1934). This temperature, however, depends not only on the thermophysiological characteristics of the animal, but on the kind of activity required, too. The temperature optimum for growth is certainly higher than that for muscular work, for in the latter much more heat is evolved which must be promptly dissipated or else the body temperature would rise. HART (1951) showed that in mice there was very little difference in body temperature during rest and activity at $+10^{\circ}\text{C}$.: at $+30^{\circ}\text{C}$., however, there was a rise of 4.0°C . in rectal, and 3.5°C . in average body temperature during activity compared with the resting values. In nature, the demands for activity may vary from season to season, and thus change the optimal temperature.

Of all the facts mentioned above, it is evident that there is at least one temperature zone, lower than the upper critical temperature, at which detrimental effects of insufficient heat dissipation become apparent. The problem

is: how could such a temperature zone be demonstrated? BRODY (1946) writes: »One of the major problems in agriculture is to map the influence of temperature and other climatic factors on growth and other productive processes». This problem is of interest in general ecology, too. Is there some easily detected physiological change, which is sufficiently well correlated with such a limiting temperature? BRODY (l.c.) believes that the secretion of thyroxine diminishes. I do not think, however, that this change is suitable for an exact determination of the effect in question. Opinions as to the thyroidal cycle are too divergent.

GELINEO (1934a and b) and GIAJA & GELINEO (1931, 1936) demonstrated the greatest effect of temperature-adaptation — a marked decrease in metabolism — in animals acclimatized to warmth. Results pointing in the same direction have been reported by DE ALMEIDA (1920, 1924, according to BAZETT 1927), KNIPPING (1923), SUNDSTROEM (1926, according to RIDDLE & AL. 1934), KAYSER (1929b), CHEVILLARD (1935), BENEDICT & FOX (1933), ORSINI, and BROCH (according to RINNE 1951), VIANJIC, MORSCHAK, and BENEDICT & MC LEOD (according to BALOGH & AL. 1951). These findings were the foundation for the procedure adopted in this investigation.

b. Experimental device and procedure. Table 14 (p. 49) shows the basal metabolism of some small birds. The results obtained by BENEDICT & FOX with warm-adapted birds are clearly lower than the other values, except that reported by PEARSON. Intermediary results have, as far as I know, not been reported. It therefore seemed worth while to perform a series of experiments in order to find out whether there is a temperature with a distinct lowering effect on basal metabolic rates.

A cupboard, having room for two cages measuring $100 \times 50 \times 50$ cm., was provided with a 500 W heater, a regulator, a fan and a safety switch, the latter preventing a rise in temperature in case the regulator would stop working. Above the fan and the heater, there was space for a little cage, intended for birds fasting before experiments. The cupboard was lighted through the glassdoors, which were opened twice a day when the cages were cleaned out or moved and food and water put in. The temperature was regulated with an accuracy of 0.5°C . Of course, there was a drop in temperature when the doors were opened, but it lasted only some ten to fifteen minutes. The relative humidity (determined gravimetrically using a gas-meter) varied between 51 and 77 per cent, but usually was between 60 and 65 per cent.

The birds were separated into three groups: group I (5 yellow buntings and 5 ortolans) in the warm cupboard; group II (5 yellow buntings and 4 ortolans) 16 hours of the day in the warmth, and 8 hours in a cool room with temperatures varying from some $+14^{\circ}\text{C}$. during October—November to $+10$ — $+11^{\circ}\text{C}$. during the winter; group III (4 yellow buntings and 4 ortolans) serving as controls and kept at room temperature, or some $+17$ — $+18^{\circ}\text{C}$. As previously (p. 34) mentioned, the yellow buntings in this group were moved out on January 12.

TABLE 10.

The minimum standard metabolism of group I, expressed as mg. CO₂ produced/gm./hr.

<i>Yellow buntings.</i> (exp. temp. +32.5°C.)		<i>Ortolans.</i> (exp. temp. +36°C.)	
Initial.		Initial.	
5 birds.	21.—23.10.53.	5 birds.	21.—24.10.53.
n	= 19	n	= 20
m	= 4.40 ± 0.078	m	= 4.36 ± 0.072
σ	= 0.352	σ	= 0.322
C	= 8.0	C	= 7.4
After +25°C.		After +25°C.	
5 birds.	24.—26.11.53.	5 birds.	25.—27.11.53.
n	= 20	n	= 24
m	= 4.36 ± 0.064	m	= 4.28 ± 0.074
σ	= 0.288	σ	= 0.334
C	= 6.6	C	= 7.8
After +27.5°C.		After +30°C.	
5 birds.	27.—28.12.53.	5 birds.	9.—10.2.53.
n	= 23	n	= 28
m	= 3.76 ± 0.070	m	= 4.28 ± 0.074
σ	= 0.222	σ	= 0.306
C	= 5.9	C	= 7.2
After prolonged stay at +27.5°C.		After one week at +32.5°C.	
4 birds.	17.1.54.	4 birds.	14.—15.2.54.
n	= 18	n	= 20
m	= 3.84 ± 0.070	m	= 4.46 ± 0.048
σ	= 0.298	σ	= 0.212
C	= 7.8	C	= 4.76
After +30°C.: fan rattling.		F 51	
5 birds.	3.—4.2.54.	n	= 4
n	= 23	m	= 3.38
m	= 4.64 ± 0.126	After two weeks at +32.5°C.	
σ	= 0.644	4 birds.	25.2.54.
C	= 13.04	n	= 17
After +30°C.		m	= 3.86 ± 0.048
4 birds.	8.2.54.	σ	= 0.196
n	= 24	C	= 5.06
m	= 3.68 ± 0.060	After +32.5°C.	
σ	= 0.290	4 birds.	1.3.54.
C	= 7.9	n	= 22
After 8 days at room temp.		m	= 3.56 ± 0.056
4 birds.	16.2.54.	σ	= 0.276
n	= 14	C	= 7.45
m	= 4.50 ± 0.070		
σ	= 0.250		
C	= 5.89		

TABLE 11.

The minimum standard metabolism of group II, expressed as mg. CO₂ produced /gm./hr.

<i>Yellow buntings.</i> (exp. temp. +32.5°C.)		<i>Ortolans.</i> (exp. temp. +36°C.)	
Initial.		Initial.	
5 birds.	26.—30.10.53.	4 birds.	27.—30.10.53.
n = 20		n = 20	
m = 4.34 ± 0.076		m = 4.28 ± 0.084	
σ = 0.338		σ = 0.374	
C = 7.7		C = 8.7	
After +27.5°C.		After +25°C.	
5 birds.	29.11.—1.12.53.	2 birds.	28.11.—1.12.53.
n = 20		n = 12	
m = 4.46 ± 0.035		m = 4.38 ± 0.088	
σ = 0.148		σ = 0.304	
C = 3.2		C = 6.9	
After +30°C. 11.—12.2.54.		After +30°C.	
M66 and M82.	M80, M92, and F84.	4 birds.	12.—14.2.54.
n = 8	n = 15	n = 22	
m = 3.94	m = 4.38 ± 0.092	m = 4.42 ± 0.086	
	σ = 0.338	σ = 0.386	
	C = 8.18	C = 8.7	
After +32.5°C.		After +32.5°C.	
M66 and M82.	M80, M92, and F84.	4 birds.	28.2.54.
n = 8	n = 15	n = 19	
m = 3.96	m = 4.46 ± 0.080	m = 4.44 ± 0.068	
	σ = 0.306	σ = 0.286	
	C = 6.87	C = 6.7	

Group II was taken out in the morning and put in in the afternoon. In spite of the glassdoors, the cupboard was darkish and hence it was lighted with an electric bulb during these 8 hours.

The experiment was commenced on October 20, when groups I and II were placed in +22.5°C. On November 3, the temperature was raised to 25°C., and on December 2 to 27.5°C. As it became evident that the yellow buntings had been influenced by this temperature, the sojourn was prolonged to January 17. The temperature was then raised to 30°C., and on February 8 to 32.5°C. On March 1, the ortolans exhibited a clear drop in metabolism, and the experiment was stopped one week later.

The dividing of the birds into three groups as described above was directly based on the experiments by OGLE & MILLS (1933). They studied the effect of environmental temperatures on rabbits. Part of the animals were adapted to +12°C., part to +32°C. and part were kept 8 hours at +12°C. and 16 hours at +32°C. Varying temperature proved to be favourable for the maintenance of temperature tolerance. During a prolonged stay in the warmth, the cold-sensitivity markedly increased.

c. *Results.* In this experimental series, 92 experiments were performed with yellow buntings, and 84 with ortolans, including 498 periods with the former, and 474 with the latter. The data obtained are presented in tables 10—13. The ortolans moulted during December and January, and the results of the experiments performed during this time are discussed later.

After a good three weeks at $+27.5^{\circ}\text{C}.$, the minimum metabolism of the yellow buntings in group I was lowered by 13.6 per cent. The difference was significant ($t = 7.68$). The stay was prolonged but there was no further decrease: the value obtained on January 17 was 3.84 ± 0.070 mg. $\text{CO}_2/\text{gm.}/\text{hr.}$ In these experiments, however, the birds for some unaccountable reason were restless. After almost three weeks at $+30^{\circ}\text{C.}$ (on February 2 and 3) the CO_2 output was 4.64 ± 0.126 , this high value being combined with a great dispersion. It is to be observed that the birds were quiet during the measurements. It appeared that the blower in the warm cupboard was loose and had begun to rattle; the birds reacted on removal to the silent respiration chamber. The fan was exchanged for a new less noisy one, and on February 8 the metabolism was 16 per cent lower than normal. This incident shows the importance of nervous factors in experiments with birds, which has been stressed for instance by ROWAN (1946).

TABLE 12.

The minimum standard metabolism of group III, expressed as mg. CO_2 produced /gm./hr.

<i>Yellow buntings.</i>		<i>Ortolans.</i>	
(exp. temp. $+32.5^{\circ}\text{C.}$)		(exp. temp. $+36^{\circ}\text{C.}$)	
4 birds.	1.—2.11.53.	4 birds.	30.10.—1.11.53.
n	= 20	n	= 20
m	= 4.34 ± 0.076	m	= 4.32 ± 0.070
σ	= 0.342	σ	= 0.318
C	= 7.80	C	= 7.30
3 birds.	6.—7.1.54.	3 birds.	6.—7.1.54.
n	= 16	n	= 13
m	= 4.44 ± 0.062	m	= 4.32 ± 0.080
σ	= 0.256	σ	= 0.286
C	= 6.47	C	= 6.7
3 birds.	23.2.54.	3 birds.	14.2.54.
n	= 21	n	= 13
m	= 4.50 ± 0.084	m	= 4.44 ± 0.096
σ	= 0.386	σ	= 0.354
C	= 8.56	C	= 8.00
Same at $+31^{\circ}\text{C.}$ 20.2.54.			
n	= 20		
m	= 4.38 ± 0.056		
σ	= 0.244		
C	= 5.57		

As it became evident that a temperature effect was to be expected, intermediary experiments were performed with ortolans in order to determine at how fast a rate the change appeared. After the stay at $+30^{\circ}\text{C}$. a value still within the limits of normal variation was obtained. After one week at $+32.5^{\circ}\text{C}$. the female 51 had seemingly reacted, whereas the others were normal. After one week more the metabolism of these four birds was significantly lowered ($t = 5.11$). After three weeks, the metabolism was 18.3 per cent lower than normal ($t = 8.45$). The experiment was terminated.

TABLE 13.

The cold metabolism of yellow buntings (exp. temp. -11°C .), and ortolans (exp. temp. -1°C .), expressed as mg. CO_2 produced /gm./hr.

	<i>Yellow buntings</i>	<i>Ortolans.</i>
Group I.	11.—13.1.54.	4 birds. 8.—9.3.54.
	M57 (weight 25.9 gms)	$n = 21$
	F63 » 24.8 »	$m = 11.68 \pm 0.128$
	$n = 11$	$\sigma = 0.576$
	$m = 11.22 \pm 0.172$	$C = 4.94$
	$\sigma = 0.570$	
	$C = 5.07$	
	M52 (weight 29.0 gms)	
	F81 » 28.4 »	
	M61 » 26.8 »	
Group II.	4 birds. 14.—15.1.54.	3 birds. 18.—19.2.54.
	$n = 20$	$n = 15$
	$m = 8.70 \pm 0.104$	$m = 10.14 \pm 0.220$
	$\sigma = 0.468$	$\sigma = 0.860$
	$C = 4.96$	$C = 8.5$
	M66 and M82 after their minimum metabolism had diminished (27.2.54.).	
	$n = 13$	
	$m = 10.10 \pm 0.136$	
	$\sigma = 0.502$	
	$C = 4.96$	
Group III.	3 birds. 8.—10.1.54.	3 birds. 17.—18.2.54.
	$n = 16$	$n = 21$
	$m = 8.58 \pm 0.086$	$m = 10.36 \pm 0.148$
	$\sigma = 0.348$	$\sigma = 0.668$
	$C = 4.05$	$C = 6.45$

According to TAYLOR & AL. (1943) complete acclimatization to heat in man is achieved in three weeks. This corresponds to the time needed for lowering the metabolism of the ortolans in these experiments. The effect of warmth seems to disappear relatively soon: only 8 days after the yellow buntings had been removed from the warm chamber and placed at room temperature their metabolism was normal. HENSCHER & AL. (1943) have demonstrated that some cardiovascular adjustments of man reacting to warmth still persist after three weeks in a cool environment.

The experiments with the yellow buntings of group II show that in spite of a cool period during the day a sign of an unfavourable effect of high temperature may become apparent. Two of the birds exhibited a metabolism clearly below the normal variation of the population after a stay at +30 and +32.5°C. The result is further supported by the experiments in the cold with the same birds.

The results of the respiratory determinations in the cold are presented in table 13. As soon as a reaction to warmth of the birds in group I was detected, the metabolism at low temperature of all the three groups was determined. The CO₂ output of the birds in group I was significantly higher than that of the other. The yellow buntings in group I could be separated into two groups: two lean birds had a higher metabolism at -11°C. than that of the three fatter individuals. The three latter, however, already had a metabolism high enough to give a t-value of 8.75 in comparison with the metabolism of the control birds in early January. The corresponding t-value for the ortolans is 5.11.

In one cold experiment with ortolans a still unexplained result was obtained. When it appeared from the determinations of the minimum metabolism that the CO₂ output was diminishing, some experiments at -1°C. were performed on February 19 and 21. Two of the birds used had a metabolism higher than normal, but the other two gave during 8 periods the average values 7.40, and 8.12 mg. CO₂/gm./hr. respectively. No technical disturbances could be detected, and the birds seemed to be perfectly normal. It was at first thought that the result obtained with the yellow buntings during January was faulty. The yellow buntings in group II, however, that had reacted to warmth, exhibited a rise in metabolism with cold (compare table 13). Later experiments with the same ortolans gave an identical result with that obtained with the seven yellow buntings.

d. Discussion. In the experiments described above a sign of an effect of temperatures not leading to hyperthermy was demonstrated, viz., the decrease of the minimum standard metabolism that accompanied a stay in warmth. It presumably indicates an unfavourable effect on the organism.

This appears at a distinct temperature, and exposure to temperatures lower than the limiting one has not resulted in lowering of the metabolism to some intermediary value. The confinement in the warm cupboard has apparently not caused the diminution because the reactions of the two species appear at distinct and different temperatures. For the yellow bunting, the limit is between $+25$ and $+27.5^{\circ}\text{C}$., and for the ortolan between $+30$ and $+32.5^{\circ}\text{C}$.. The difference is thus at least 3.5 , and at most 6.5°C ., or of the same order of magnitude as the differences between the upper lethal temperatures, the upper critical temperatures, and the average temperatures during July on the southern boundaries of the breeding range of the two species (see p. 96).

BROCH & AL. (according to RINNE 1951) found that rabbits adapted to $+28$ — $+30^{\circ}\text{C}$. had a lower metabolism in basal conditions than rabbits adapted to $+25$ — $+26^{\circ}\text{C}$.. This is the only case I know in which signs of such a distinct limiting temperature have been reported.

KENDEIGH (1944) demonstrated considerable individual variation in the reaction to heat of house sparrows. When the temperature was raised as high as $+43^{\circ}\text{C}$., the CO_2 output of some of the birds was depressed to a level lower than that at $+37^{\circ}\text{C}$.. The same phenomenon appeared in some of my birds during hyperthermy. Could such cases be considered as proof of the existence of a secondary zone of chemical temperature regulation in birds? According to KENDEIGH (l.c.) »there is no evidence for a secondary zone of chemical regulation above the critical temperature as GELINEO ('36) has postulated.»

Could such a zone exist below the critical temperature? The mechanism of diminution of the metabolism has been studied in hyperthermic animals only. GIÁJA & GELINEO (1936), and later e.g. BALOGH & AL. (1951) point out that such an effect as that described above could be interpreted as due to a hormonal mechanism. The sole cause might even be simply the weakening, enervating effect of warmth, as supposed, for instance by BENEDICT (1938). There is, however, no conclusive evidence for the correctness of this solution of the problem. On the contrary, the papers by BALOGH and coworkers and other Hungarian investigators published during recent years (see above p. 39) support the view of there being a secondary zone of chemical temperature regulation. If such a mechanism is involved in the lowering of metabolism which accompanies a prolonged exposure to moderately high temperature this phenomenon would apparently be a suitable basis for the study of it, because a relatively stable physiological state is developed that apparently does not harm the animals.

DONNER and the present author (unpublished data) have recorded the heart rates of undisturbed yellow buntings and ortolans. *Inter alia*, the ortolans in groups I and III were compared after the metabolism of the former had decreased as a result of the stay in the warmth. The determinations were

made at the temperature, $+32.5^{\circ}\text{C}$., to which group I was acclimatized. The birds of group III were kept two hours at $+32.5^{\circ}\text{C}$. before the actual recording of the heart rates, thus allowing ample time for adjustment to the high temperature. The room-adapted birds exhibited a very marked decrease of the heart frequency, which apparently was an immediate effect of the warmth. In spite of the lower metabolism of the birds in group I, their heart rates were higher, approaching those of the room-adapted birds at room-temperature. This apparently supports the hypothesis of chemical regulation against heat.

GELINEO (1934a and b) and GIAJA & GELINEO (1936) postulated that acclimatization to a warm environment would result in a lowering of the metabolic curve, and a decrease of the metabolic quotient. The results of the cold experiments with the birds from group I do not support these views. On the contrary, there was a marked increase of the metabolism as compared with that of room-adapted birds. The result obtained with the ortolans at -1°C . and with the lean yellow buntings in group I indicates that the metabolic quotient was at least not diminished, and could well be higher than normal. What is evident is that the warm-adapted birds resisted cold less well than the room-adapted ones. The birds that had been at varying temperature maintained a normal tolerance against cold. These findings are in harmony with those of OGLE & MILLS (1933).

7. BASAL METABOLISM

There is a need for a stable foundation for comparison of the metabolism of different individuals and species. In comparative investigations, the concept of basal metabolism has been very useful. It could be defined as the metabolism needed for the fundamental hormonal and enzymic processes of the body, augmented by the inevitable need of energy for respiratory movements, circulation, and maintenance of the muscle tone. In the previous sections, the term »minimum standard metabolism» has been mainly used. The reason has been that there is involved in the concept of »basal» metabolism an implication of something fundamental — of something constant and unalterable — whereas in reality, though well defined, it is not a fixed quantity. As ZEUTHEN (1948, 1951) points out, it applies only to homoiothermic animals. But even within this group it is not easy to secure comparable conditions for the measuring of the basal metabolism of all species.

There was earlier an *a priori* inclination to suppose that the basal metabolic rates of small birds would be high. Reliable determinations have been difficult to achieve because of the restlessness of these animals. BENEDICT & FOX

(1933) review the results obtained up to then. The values are high almost throughout, indicating failure in the elimination of muscular activity. In table 14, some seemingly well-founded values for small birds are given, combined with the results obtained in this investigation.

TABLE 14.

The basal metabolism of some small birds, expressed as kcal./sq.m./24 hours.

Species	Temp. °C.	Basal met.	Author
Greenfinch	30	1225	GIAJA & MALES 1928
Brambling	31	1360	GELINEO 1934a
Canary	28	762	BENEDICT & FOX 1933
Goldfinch	30	1099	GIAJA & MALES 1928
House sparrow	30	924	» » »
» »	28	1000 (summer)	MILLER 1939
» »	28	1350 (winter)	» »
» »	28	652	BENEDICT & FOX 1933
Barn-swallow	35	1200	GIAJA & MALES 1928
Hummingbird		680	PEARSON 1950
Shell paroquet	28	688	BENEDICT & FOX 1933
Yellow bunting	32.5	1058	This investigation
Ortolan bunting	36	1058	» »

It is evident that the basal metabolism of small birds is not greater than that of other homoiotherms. The values obtained by BENEDICT & FOX, and PEARSON constitute, however, a group definitely lower than the others. In the hummingbird *Selasphorus s. sasin* the phenomenon depends upon the bird's peculiar metabolism. The determinations performed by BENEDICT & FOX were included in a great series of corresponding measurements on other species, ranging from the mouse to the elephant, in which low values were usually obtained with small animals.

What circumstances can account for the difference between the values obtained by BENEDICT & FOX, and in this investigation? BENEDICT (1938) summarizes in 8 points the ideal conditions for obtaining comparable measurements of basal metabolism. Of these, all but one — that the birds should be adapted to the zone of thermal neutrality during a long time prior to the measurements — have been adhered to. Another, viz., the demand for sexual quiescence, seems not relevant for the two species here investigated.

BENEDICT & FOX (1933) did secure experimental conditions that in the main corresponded to these demands. If one accepts KENDEIGH's (1944) view that the zone of thermal neutrality in the house sparrow is limited to +37°C., it may seem strange that such a low value as 652 kcal. could be obtained at

+28°C. It is quite possible, however, that this zone is wider, as it seems to be, for instance, in the yellow bunting and the ortolan. It is not very likely that the values would have been lower if BENEDICT & FOX had performed their experiments at a higher temperature.

The birds of BENEDICT & FOX fasted 10 hours before the experiments, which were performed between 7 and 12 p.m. After a night without food, the birds had very little time to feed in the morning. The consequence may have been an accumulated effect of starvation for considerably more than ten hours. According to BALDWIN & KENDEIGH (1932) the body temperature of the house wren commences to drop below the standard level after 7 hours without food. A similar effect of starvation, combined with a decreasing basal metabolism, was demonstrated by BENEDICT & RIDDLE (according to BALDWIN & KENDEIGH l.c.) and BENEDICT & FOX (1927). BRODY (1945) also mentions that fasting causes a drop in body temperature and basal metabolism.

The main reason for the low values obtained by BENEDICT & FOX seems, however, to be that the experimental animals were kept at a constant environmental temperature as high as +28°C. It might be claimed that the »basal» metabolism should always be determined by means of a procedure which results in the lowest possible values, taking values thus obtained as the natural foundation for all comparisons. But BENEDICT himself expresses (in 1938) the opinion that determination at the critical temperature could result in low and perhaps variable values. He does not, however, discuss the effect of prolonged exposure to warmth.

As already mentioned in the previous section, it is not known whether the »enervating» effect alone or a more complicated neurohumoral chain of events causes the lowering of the metabolism. But one thing seems obvious: the basal metabolism of homoiotherms is altered during a long stay at high temperature, even if this is considerably lower than the critical temperature. Thus it seems important that prior to the determinations of basal metabolic rates the experimental animals should be kept at a temperature which does not affect their metabolism. When the experimental temperature is the same as that used in this investigation, the yellow bunting and the ortolan can be kept practically within the whole of their range of tolerance, provided that the temperature does not rise above an upper limit, at which a decrease in metabolism appears.

The choice of a suitable experimental temperature constitutes a separate problem. BENEDICT (1938) discusses various temperatures and concludes that it is most practicable to base comparisons on measurements performed within the zone of thermal neutrality. The conclusion is in my opinion sound, because it does not seem logical to determine the basal metabolism at tempera-

tures which bring chemical temperature regulation into play. But when the zone of thermal neutrality extends over several degrees on the temperature scale, should the experimental temperature be chosen at the upper or the lower limit of this zone? Some inconsistencies in the available information could perhaps be explained on this basis. MILLER's (1939) determinations showed different winter and summer values in house sparrows, the basal metabolism being determined at $+28^{\circ}\text{C}$. (critical temp. $+37^{\circ}\text{C}$.). RIDDLE & AL. (1934) found differences in the yearly changes of metabolism in the tippler pigeon when it was determined at $+30^{\circ}\text{C}$. (critical temperature), and at $+20^{\circ}\text{C}$. (lower limit of zone of thermal neutrality). They suppose that some of the changes in metabolism connected with the yearly cycle may be obscured when the determinations are performed at the critical temperature. In their work there is, however, an obvious weakness: determinations at $+15$ and $+30^{\circ}\text{C}$. are not considered reliable, because they do not exhibit the yearly fluctuations that the authors had expected to find, whereas determinations at $+20^{\circ}\text{C}$. are accepted as valid because they come up to expectation. In any case, the problem is not solved.

SCHILDMACHER's (1952) experiments with redstarts were performed at room-temperature. Such a procedure may be very suitable: but the motivation seemingly depends on a misinterpretation. SCHILDMACHER writes: »RIDDLE und Mitarbeiter (u.A. 1926) haben mehrfach darauf hingewiesen, dass Versuche bei Neutraltemperatur infolge unnatürlicher Versuchsbedingungen zu abweichenden Werten führen können. Es lag mir bei meinen Versuchen daran, solche Abweichungen nach Möglichkeit zu vermeiden.» RIDDLE and coworkers (e.g. 1926, and in two reports 1932) point out several times, however, that basal metabolic rates are obtained only within the zone of thermal neutrality. The paradoxical values obtained by RIDDLE & AL. (1926), and mentioned by SCHILDMACHER, were reported in connection with experiments involving injection of prolactin and thyreotropic hormone. RIDDLE & AL. (1934) point out that a temperature lower than the critical one may be suitable, but they do not claim that the *basal* metabolism should be determined at temperatures below the zone of thermal neutrality.

My experiments were planned in order to gain information concerning some ecologically important problems, viz., among other things, any changes occurring in the zone of thermal neutrality and the percentage change in metabolism. Some other variations might have been obscured by the high experimental temperatures. The interpretation of the results in the field is, however, difficult. The exact reason for some of the supposed changes in basal metabolic rates is not known. It seems possible that uncontrollable chance variation may occur more easily at the lower than at the upper limit of the zone of thermal neutrality.

With the ortolans, 12 series of respiratory measurements in basal conditions have been performed, and with the yellow buntings 16. The means for the ortolans vary between 4.28 and 4.46 mg. CO₂/gm./hr., for the yellow buntings between 4.24 and 4.50. The mean for all the periods — 214 with ortolans and 299 with yellow buntings — is 4.36 for both of the species. This is thus a good intermediary value. The means and the dispersions of the groups of determinations, giving this value for the basal metabolism of both species, are given below:

Ortolan	Yellow bunting
n = 20	n = 20
m = 4.36 ± 0.072	m = 4.36 ± 0.064
$\sigma = 0.322$	$\sigma = 0.288$
C = 7.40	C = 6.60
s.r. = 1.04	s.r. = 0.94
s.r.m. = 0.234	s.r.m. = 0.208

S.r. (= standard range = the range of normal variation within the natural population = $3.24 \times \sigma$) has been computed in accordance with SIMPSON's method. It is for the ortolan 23.8, and for the yellow bunting 21.6 per cent of the mean. All the values obtained have been within these limits. As is generally known, a deviation from the normal basal value amounting to more than 20 per cent is considered pathological in human medicine.

S.r.m. ($= 3.24 \times$ the standard error of the mean) indicates the limits within which the mean of different series of determinations are to be expected. All the values obtained during this investigation lie well within these limits.

8. PLUMAGE AND TEMPERATURE REGULATION

A. DETERMINATION OF THE INSULATING POWER OF THE PLUMAGE

a. Earlier investigations. One of the most powerful physical factors influencing the heat loss of birds is the insulating capacity of their plumage. It affects both the tolerance against cold, and as pointed out by BENEDICT (1938) and others, against heat, and it may influence the situation of the zone of thermal neutrality, as previously mentioned (p. 37).

Reliable measurements of the insulating capacity of the plumage are not, however, readily performed. Up to now, almost all efforts in this direction have been limited to weighing of the feathers and comparing of their weight with total body weight. TIEDEMANN (according to HOLLAND 1861) and MAGNAN (1911) have performed such weighings. KENDEIGH (1934) studied the house sparrow, and excluded the feathers which do not participate in the insulation.

The weight of the remaining feathers varies during different seasons, being greatest in the autumn immediately after the moult, and then gradually sinking. WETMORE (1936) reports that birds belonging to the same species have fewer feathers during the summer than during the winter.

Usually, wintering birds have a heavier plumage than migrating ones. PALMGREN (1944) reports a surprisingly low value (4.1 per cent of body weight) for the plumage of a yellow bunting obtained in December. He points out that the relative weight of the plumage cannot be a comprehensive indicator of its insulating power, which also depends on the quality of the down, the structure of the feathers, and the thickness of the plumage. The thickness and the mobility of the air layer between the contour feathers and the skin are decisive. These factors depend on the features mentioned by PALMGREN.

SCHOLANDER & AL. (1950) have performed measurements of the insulation capacity of the skin of birds. The evidence thus obtained cannot, however, give a complete understanding of how this factor works during natural conditions, when the position of the feathers can be altered through muscular movements which have great importance in temperature regulation.

b. Photographic determination of the thickness of the plumage. It was not possible to secure as many ortolans as required for a reliable determination of the relative weight of the plumage. Another method was to be used. It is plain to see that a yellow bunting seems much chubbier than an ortolan of identical weight. Presumably an ortolan and a yellow bunting have about the same specific gravity. Even if the absolute weight of the plumage differs much, its importance relative to the total body weight is so small that it does not need to be taken in consideration. Supposing that these assumptions hold true, differences in the thickness of the plumage would appear in different dimensions of the silhouettes of two birds of identical weight.

The photographs needed for the comparison were taken by Mr. F. HACKMAN. The following method was adopted: a box, measuring $24 \times 18 \times 5$ cm. was manufactured and provided with one long and one short wall of glass. In the middle of the box, a perch was fixed. The back wall was covered with a coordinate-system forming 1 cm. squares. Thus it was possible to reduce the pictures obtained to natural size.

The birds were within the box when they were photographed. As the box was only 5 cm. broad, the birds could not move sideways, and the photographs could be taken from an exactly known distance. Pictures from the front were taken only when the birds were sitting on the perch.

The photographs were taken on January 25, 1951. The birds used were the yellow bunting F22 and the ortolan M12, both weighing 25.5 gm. Of both of them, two side and two front views were taken inside the laboratory building at $+20^{\circ}\text{C.}$, and outside it at -5.5°C. The silhouettes were projected from the negatives on millimeter paper with the area enlarged by two, in order to reduce the error in drawing and measuring. Even

Fig. 2. Silhouettes of yellow bunting (full line) and ortolan (broken line) of identical weight, drawn from photographs taken at $+20^{\circ}\text{C}$.

Fig. 3. Same as fig. 2, but the photographs taken at -5.5°C .

from the contour drawings (fig. 2 and 3) the great difference between the two species appears.

The computation of the differences in plumage thickness of the two birds and of the same bird at room temperature and in the cold were performed as follows: the contour length of the silhouettes was measured, omitting the bill, tail, legs, and projecting parts of the wings. The area was determined by means of a planimeter. The difference between the areas was divided by the greater circumference, and so the average difference in thickness was obtained. The figures from one such comparison are given as an example:

Yellow bunting outdoors	4. Circ.	298 mm.
	Area	5398 sq.mm.
» » indoors	2. Circ.	295 mm.
	Area	4719 sq.mm.
$\frac{5398-4719}{298} = 2.29 \text{ mm.}$		

Reduction of all the computed values to natural size revealed that the plumage was fluffed out about equally by both of the birds: F22 on an average 1.64 mm., and M12 1.50 mm. The plumage of the yellow bunting was, however, much thicker than that of the ortolan: the difference was 2.64 mm. at $+20^{\circ}$, and 2.78 mm. at -5.5°C . (cf. p. 55).

The birds were needed for respiration experiments, and it was thus not possible to kill them in order to secure an accurate measurement of the thick-

ness of the plumage. Later, the specific gravity of an ortolan was determined and found to be 0.8. On the basis of this somewhat hypothetical value (the bird was extremely lean and perhaps not normal), and subtracting the weight of the plumage (8 per cent of the total weight), the bill, and the legs and feet, the volume was approximately computed. If the assumptions made were correct, it would have been 28.8 cc. As the cross-section of a bird is nearly circular, the computation of the volume was based on SIMPSON's formula. The result is given below:

		Thickness of plumage	Volume of plumage
Yellow bunting —	5.5°C.	6.02 mm.	54.8 ccm.
»	+ 20°	4.38 »	38.7 »
Ortolan —	5.5°C.	3.24 »	30.7 »
»	+ 20°C.	1.74 »	16.7 »

As earlier mentioned (WALLGREN 1952), these figures cannot be presented with any claim to exactitude. Even if this were the case the insulating capacity need not be directly dependent on the thickness of the plumage. It is also affected by the mobility of the air layer kept within the plumage, and the surface density of the feather covering, factors depending on the structure and position of the down and feathers. All these complexities make an exact evaluation of the rôle of the plumage in temperature regulation impossible in the present situation. The values obtained here show, however, the order of magnitude of the differences. It is evident that the insulation of the yellow bunting is much better than that of the ortolan and thus may largely account both for its greater resistance to cold, and its greater heat sensitivity.

B. METABOLISM AND PLUMAGE

a. The metabolism at low temperatures of birds with defective plumage. In February 1951, three ortolans lost part of their plumage, apparently as an effect of vitamin A deficiency. The feathers were rapidly regenerated after the birds had been fed with a vitamin preparation with a high concentration of vitamin A. Before that, however, 6 respiration experiments were performed with these birds. The results are presented in table 15.

As it was impossible to decide whether the condition of the birds was comparable or not, an average of several measurements with all the three individuals at the same temperature was not attempted. The state of F15 was worst; the whole back, and part of the sides were naked. The hind part of the back, the lower half of the chest, and the crown of F14 were bare. M25 had the most complete insulation of the three. Especially at low tem-

TABLE 15.

Carbon dioxide output of *ortolans* with *defective plumage*, expressed as mg./gm./hr.

Bird	Temp. °C.	Number of periods	CO ₂ output	O ₂ consumption
F14	+17	4	7.34	5.16
M25	+14	4	8.18	6.00
F15	+13	5	8.70	6.37
M25	+ 7	5	9.88	7.24
F15	+ 7	4	10.62	7.80
F14	— 1	4	12.02	8.81

peratures the metabolism of these birds was much higher than that of normal individuals. Presumably the result is due to the diminished insulation, and not to the vitamin A deficiency.

b. Heat resistance of birds with defective plumage. In the experiments described above it was not possible to study whether any shift of the zone of thermal neutrality had occurred because a suitable thermostat was not then available. As shown above (p. 35) the normal wearing off of the plumage apparently does not influence the upper critical temperature of these birds to any appreciable degree, whereas adaptation to severe cold causes a slight downward shift of it. The problem was studied in 1953 using some moulting juvenile yellow buntings. The condition of the plumage of all these individuals was poor; for instance, the back was naked in all of them. Owing to the moult the metabolism in basal conditions was somewhat higher and more variable than normally. The results appear from table 16.

TABLE 16.

Carbon dioxide output in heat of *yellow buntings* with *defective plumage*, expressed as mg./gm./hr.

Temp. °C.	+35	+37	+39
Number of birds	4	4	4
» » periods	20	20	19
CO ₂ output	4.90 ± 0.066	5.14 ± 0.118	4.98 ± 0.138
Standard deviation	0.296	0.526	0.602
Coefficient of variation	6.05	10.21	12.10

The dispersion is great, owing in part to the moult, in part to the high experimental temperature. Of greater importance in this connection than the absolute combustion values, however, is the fact that the birds did not seem to suffer during the experiments at +37°C., and that they were alive after more than two hours exposure to +39°C. This is a marked improvement in tolerance of heat compared with that of yellow buntings with the plumage

intact. It presumably depends directly on the light feather covering, but the endocrinological changes in connection with the moult may also improve the heat tolerance.

c. Discussion. There are many reports showing that the tolerance of cold diminishes as the insulation of the body deteriorates (compare VOIT 1904, according to BALDWIN & KENDEIGH 1932; BARBOUR 1921, GIAJA 1931, BENEDICT & FOX 1932, BALDWIN & KENDEIGH 1932, BURCKARD & AL. 1934, KENDEIGH 1934, BENEDICT 1938 and STREICHER & AL. 1950). Only BENEDICT & FOX, however, determined the zone of thermal neutrality in animals with defective insulation. They found a shift upwards. In this investigation, a similar change was demonstrated. In several cases, the value of the results reported would be greater if attention had been paid to the possible shift of the critical temperature. As an example, GIAJA's (1931) investigation may be quoted. He studied the metabolism of geese, cocks, and ducks, and demonstrated a rise in oxygen consumption when the birds were plucked. The increase in the different species was 73, 45, and 92 per cent at the zone of thermal neutrality, and 124, 165, and 133 per cent at 0°C. This does not, however, mean that there was a rise in the basal metabolic rate. The upper critical temperatures of these species are low (see table 6, p. 25). As the feathers were plucked, it certainly shifted upwards, but GIAJA does not discuss this possibility.

SCHOLANDER & coworkers (1950) performed an extensive investigation on the relation between insulation, metabolism, and body temperature of some arctic and tropical birds and mammals. They arrived at the following conclusions: »There is, as would be expected, a good correlation between the thickness of the fur and the insulation». »The basal metabolic rate of terrestrial mammals from tropics to arctic — — is phylogenetically non-adaptive to external temperature conditions. Equally non-adaptive is the body temperature, and the phylogenetic adaptation to cold therefore rests entirely upon the plasticity of the factors which determine the heat loss, mainly the fur insulation».

The results of the experiments with yellow buntings and ortolans are in perfect harmony with these conclusions. The basal metabolism is of equal magnitude in the two species. With each of the species, 30 measurements of standard body temperature were performed (three times with 10 individuals of each, using a thermocouple, and recording from the throat). The result was: yellow bunting $+41.0 \pm 0.085$ °C., ortolan $+41.1 \pm 0.088$ °C., or no difference. The difference in the thickness of the plumage is, however, great. Presumably this is the main reason for the observed difference in reaction of the birds to cold and heat.

SCHOLANDER & AL. (1950), starting from a simple physical model, discuss a plausible but, as the authors admit, simplified mechanism for the temperature-regulation of homoiotherms exposed to falling temperature. According to this hypothesis, the first reaction would be improvement of the insulation. A rise of metabolism would only become apparent when the body temperature could not be maintained by physical means.

It seems that the mechanism is most probably much more complicated. The improvement of the insulation apparently proceeds parallel with the rise in metabolism. Such an impression is given by the photographs used for determination of the plumage volume of the yellow bunting and the ortolan. In both of the birds, the thickness of the feather covering increases very markedly when the temperature falls from $+20$ to -5.5°C . (see fig. 2 and 3, p. 54). The CO_2 output begins to increase already above $+20^{\circ}\text{C}$., and it thus seems that maximum insulation capacity is evolved at a temperature much lower than that causing a rise in metabolism. Seemingly a balance between insulation and metabolism is maintained, as the slope of the curves (fig. 1 p. 22) is rectilinear.

That thickening of the plumage is important for the temperature regulation in connection with a rise in metabolism appears from GIAJA's (1931) results, too. There is a relatively much greater augmentation in the metabolism of plucked than of normal birds when the environmental temperature is lowered from the zone of thermal neutrality to 0°C . BURCKARD & AL. (1933) demonstrated that if a pigeon is prevented from fluffing out its feathers the stress put on its metabolism by low temperatures increases.

9. MOULT AND METABOLISM

KOCH & DE BONT (1945) studied the effect of the moult on the energy metabolism of the chaffinch. To eliminate the effect of thermal adaptation postulated by GIAJA and GELINEO, the birds were kept at $+10^{\circ}\text{C}$. The measurements of the respiratory exchange were performed at the same temperature, which — as pointed out by the authors — caused a rise in metabolism. This circumstance would be of no importance if a possible deterioration of the insulation had not to be taken into account. At as high a temperature as $+10^{\circ}\text{C}$. defects of the plumage cause a considerable rise in metabolism above the normal values.

KOCH & DE BONT suppose that such a factor had not affected the results on the basis of the finding that there was a maximal rise in metabolism (25 per cent) when only the tail quills were moulted. The heat loss may, however, increase through the blood circulation in the developing quills. In any case,

it seems unlikely that such a factor could wholly obscure the effect of a moult on the metabolism: one is inclined to suppose an increase in basal metabolism also, owing to greater thyroxine secretion. At least in part such factors seem to have caused the metabolic rise observed by KOCH & DE BONT.

Yellow buntings moult in August, both in the wild state and in cages (WALLGREN, unpublished). My ortolans, all of which were juvenile individuals, moulted from the latter part of November to early January. Moulting was complete in both species.

The statements in the literature as to the moult of the ortolan are contradictory. According to BREHM (1856) the bird has a winter moult. NESTEROV (1911) reports that the moult occurs in late July—early August. According to NATORP (1925) ortolans on autumn migration through Silesia have finished their moult. WITHERBY (1929) records complete moult in the autumn: according to him, however, juvenile birds do not moult the tail. The feathers of the body are moulted in spring, but whether this is a regular phenomenon or not, the author does not know.

My birds did moult during the same time both in 1950—1951, and 1953—1954. Perhaps there is a difference in this respect between juvenile and adult ortolans. The moult in these caged birds may have been abnormal, but this seems not very likely, as it began in all individuals at about the same time. Perhaps the different statements can be explained as due to the ortolan having two moults, a phenomenon reported by GÖTZ (according to KIPP 1936) for many migrating species.

The metabolism of moulting yellow buntings and ortolans was determined. The results are presented in tables 17—19. The mean values indicate a signifi-

TABLE 17.

Carbon dioxide output of *moulting yellow buntings*, expressed as mg. CO₂/gm./hr.

Adult		Juvenile	
4 birds.	12.—20.8.53.	4 birds.	21.—27.8.53.
n	= 37	n	= 20
m	= 4.98 ± 0.068	m	= 4.46 ± 0.124
σ	= 0.408	σ	= 0.550
C	= 8.2	C	= 12.3

TABLE 18.

Carbon dioxide output of *moulting ortolans*, expressed as mg. CO₂/gm./hr.

Group I		Group II	
5 birds.	29.12.53—6.1.54.	4 birds.	29.12.53—5.1.54.
n	= 24	n	= 20
m	= 5.48 ± 0.284	m	= 4.82 ± 0.124
σ	= 0.822	σ	= 0.584
C	= 15	C	= 12.1

cantly higher metabolism than that normally prevailing, except in the juvenile yellow buntings. The increased dispersion in all the groups is very conspicuous. Only the adult yellow buntings do not exhibit a variation significantly

TABLE 19.

Carbon dioxide output of *moulting adult yellow buntings*, average results for individual birds.

Individual	M93		F99	
Date	12.8.	20.8.	12.8.	20.8.
Number of periods	5	5	5	5
Av. CO ₂ output	5.52	5.40	5.44	5.02
Individual	M95		F97	
Date	13.8.	19.8.	13.8.	19.8.
Number of periods	4	3	5	5
Av. CO ₂ output	4.52	4.80	4.56	5.18

greater than normal. This increase of the dispersion is mainly due to individual differences. During the moult the metabolism of the same individual may seemingly vary considerably during short periods of time (compare table 19). The low value obtained with the yellow buntings may depend on the fact that the experiments happened to be performed during periods of low metabolic activity. KOCH & DE BONT (1945) also found variation in the oxygen consumption of the same moulting individual. SCHILDMACHER (1952) reports an increase in metabolism during moulting.

KOCH & DE BONT (l.c.) assume that the rise of metabolism in the zone of thermal neutrality might be markedly greater than what they found at +10°C. In my experiments, however, the rise has been found to be of the same order of magnitude as that reported of KOCH & DE BONT, the highest value being 26.6 per cent above the basal metabolism. It is evident, too, that a metabolic level as low as, and even lower than the normal one, may occur during the moult, indicating an unusual variability in the physiological state.

From the evolutionary point of view, the present moulting time of the yellow bunting seems to be the only possible one. It is interposed very elegantly between the exhausting reproductive activities and the cooler autumn, and the selective factors in favour of such an arrangement are easily imagined.

10. ENERGY METABOLISM IN MOIST AIR

A. MATERIAL AND METHODS

It is generally known that heat is more dangerous in moist than in dry air. At temperatures from room temperature downward the humidity does not seem to affect the temperature regulation and metabolic level of homoiotherms from temperate regions. HART (1950a) has shown that the relative humidity of the air does not influence heat transmission through the fur of mice.

The effect of moist air at high temperatures naturally depends on failure in securing effective heat dissipation, owing to blockade of water evaporation. This effect was studied by determination of the CO_2 output of the yellow buntings and the ortolans at about 95 per cent relative humidity. The birds in the control group (see p. 4 and table 2 p. 13), four individuals of both species, were used. The experiments were performed in December 1953 with the yellow buntings, and in late January and early February 1954 with the ortolans.

The same respiration apparatus was used as in other experiments. The air was passed into the apparatus through a tube provided with soda lime for removing the carbon dioxide. It was then pumped through a bottle of water, and another one containing a saturated solution of K_2SO_4 . Both these bottles were submerged in the water bath containing the respiration chamber, and thus a relative humidity of 92—95 per cent was secured in the air entering the chamber (see SWEETMAN 1933). When the experiments were commenced, no water bottle was used. It soon appeared, however, that the cool air entering the tube which passed into the solution in the first flask, caused a deposition of the salt on the walls of the pipe.

TABLE 20.

Carbon dioxide output of yellow buntings and ortolans in moist air, expressed as mg. $\text{CO}_2/\text{gm.}/\text{hr.}$

Temp. °C.	<i>Yellow buntings</i>	<i>Ortolans</i>
+20	4 birds. 23.11., 2.12. n = 21 m = 4.84 ± 0.076 $\sigma = 0.350$ C = 7.25	
+25	4 birds. 2.—4.12. n = 15 m = 4.70 ± 0.080 $\sigma = 0.310$ C = 6.59	4 birds. 18.—22.1. n = 21 m = 5.16 ± 0.096 $\sigma = 0.440$ C = 8.53

Temp. C°.	<i>Yellow buntings</i>	<i>Ortolans</i>	
+30	4 birds. 4.—10.12. n = 32 m = 4.10 ± 0.072 σ = 0.404 C = 9.8	4 birds. 24.—25.1. n = 21 m = 4.16 ± 0.058 σ = 0.268 C = 6.5	
+32.5	4 birds. 11.—14.12. n = 17 m = 4.32 ± 0.106 σ = 0.436 C = 10.1	4 birds. 2.2. n = 20 m = 4.22 ± 0.082 σ = 0.366 C = 8.7	
+35	4 birds. 15.12. n = 18 m = 4.44 ± 0.132 σ = 0.544 C = 12.23	4 birds. 25.—29.1. n = 23 m = 5.72 ± 0.592 σ = 1.360 C = 24	
+37	4 birds. 17.12. n = 19 m = 5.12 ± 0.140 σ = 0.608 C = 11.88	2 birds. 29.1.* M53 F58 6.32 8.98 5.50 7.60 5.40 7.60 8.90	
+39	2 birds. 22.12.* M95 F97 7.68 5.92 8.70 6.88 died 5.00	*) Single values obtained.	

The results are combined in table 20. Experiments were not performed at higher temperatures than +39°C. with yellow buntings (two birds, of which one died in 65 minutes), and at +37°C. with ortolans (two birds, both of them very exhausted after the experiments). Experimental temperatures lower than +20 and +25°C. were not used, because quite normal values were obtained at these temperatures, indicating no effect of humidity

B. DISCUSSION

SALT (1952) is the only investigator known to me who has compared the metabolism of small birds in moist and dry air. In the three species studied, he demonstrated differences in tolerance of moist heat, and these findings proved to be correlated with ecological dissimilarities. In all the birds, the metabolism in moist air fell steadily as the temperature was raised. SALT concludes that the limiting factor is the difference in vapour pressure between the environ-

ment and the respiratory system of the birds, and that the upper lethal limit may be modified through differences in efficiency of the evaporating organs. The latter conclusion is based solely on theoretical considerations.

In my measurements, the CO_2 output at $+20$ and $+25^\circ\text{C}$. was normal. At $+30^\circ\text{C}$. it was lower than the normal basal metabolism in both species, and at $+32.5^\circ\text{C}$. again within the standard range of the mean of the basal values. There was, however, a tendency to increased dispersion. At $+35^\circ\text{C}$. the metabolism of the ortolans rose high above the basal level, and there was a huge dispersion. In the yellow buntings, metabolism was still rather low, but the dispersion was significantly increased. Strangely enough, the yellow buntings seemed less exhausted than the ortolans after the experiments at $+37^\circ\text{C}$., but at $+39^\circ\text{C}$. the lethal limit had been passed.

It appeared that the ortolans tolerated heat in moist air almost less well than did the yellow buntings. The efficiency of the evaporating system must be important. Differences in insulation do not seem to affect the capacity to resist moist heat, although in dry air heat is less detrimental when the plumage is light. As SALT (l.c.) has pointed out, the decisive factor must be the vapour pressure. At a given, and, in moist air, comparatively low, temperature, the difference in vapour pressure between the respiratory-evaporating system

Fig. 4. The vapour pressure of air of 95 per cent rel. humidity (curve) as compared with that within the respiratory system of a bird (straight line) assuming a temp. of $+41^\circ\text{C}$. within the latter.

of the bird and the air becomes too small to permit sufficient heat dissipation through water evaporation, and hence the body temperature rises.

The graph (fig. 4) shows the pressure of saturated water vapour at $+41^{\circ}\text{C}$. (the temperature assumed to prevail in the lungs and air sacs of the birds), and the vapour pressure of air of 95 per cent relative humidity at different temperatures. At $+33^{\circ}\text{C}$., approximately the critical temperature for both groups of birds in air of this relative humidity, the difference is about 22 mm Hg. Then it declines rapidly, and simultaneously the need for effective evaporation rises. As will be demonstrated in the following section, water evaporation is important in the heat dissipation of both the yellow bunting and the ortolan when the temperature rises above $+30^{\circ}\text{C}$. When it is blocked, a critical situation is evolved in which the greater heat radiation and convection through the plumage of the ortolan does not suffice to place it in a better position than the yellow bunting.

11. WATER EVAPORATION

Determination of the water loss of the birds was of considerable interest, owing to its importance in the regulation of body temperature. It was, however, difficult to perform. In the literature, data on the water evaporation of birds are scarce: the same difficulties, indeed, have been experienced by all investigators studying the reaction of birds to heat.

1 mg. of water evaporated from the air-sacs of a bird binds some 0.58 gcal. On this basis the importance of water evaporation in heat dissipation may be calculated. HÁRI (1917) reports that in the goose 20 per cent of the heat loss at $+16^{\circ}\text{C}$. is due to water evaporation, whereas at $+27.2^{\circ}\text{C}$. the corresponding percentage is 50.5. I have computed some values for the pigeon on the basis of the water loss at various temperatures reported by KAYSER (1930). The result is: at $+2.5^{\circ}\text{C}$. 8 per cent; at $+25^{\circ}\text{C}$. 20 per cent; at $+30^{\circ}\text{C}$. 22 per cent; at $+36.5^{\circ}\text{C}$. 43 per cent. DONTCHEFF & KAYSER (1933), in experiments with pigeons, were able to separate moisture from the excrements, and evaporated moisture, and thus obtained lower values: at $+5^{\circ}\text{C}$. 4.5 per cent; at $+21^{\circ}\text{C}$. 9 per cent; and at $+29^{\circ}\text{C}$. 16 per cent. In the house sparrow, KENDEIGH (1944) reports the following values (including water from faeces) at $+5^{\circ}\text{C}$. 9.2 per cent; at $+25^{\circ}\text{C}$. 16 per cent; at $+35^{\circ}\text{C}$. 31 per cent; and at $+43^{\circ}\text{C}$. 47 per cent. BRODY (1946) points out that non-sweating animals can dissipate by vaporization only a little over half of the heat produced by the body. According to him, maximum evaporation in panting birds accounts for about 40 per cent of the heat produced.

Corresponding data for the yellow bunting and the ortolan are presented in tables 21 and 22. Only values obtained in experiments when defaecation was not observed are included. Owing to technical difficulties, there may still be considerable errors, especially in the determinations performed at the highest and the lowest temperatures. The general tendency, however, corresponds well with earlier findings. In these birds, too, the absolute values diminish only slightly between $+25$ and $+7^{\circ}\text{C}$. When the temperature rises above the former value, the yellow bunting increases the vaporization profusely. In the ortolan, the increment is less pronounced. At $+30^{\circ}\text{C}$. in the yellow bunting, and $+35^{\circ}\text{C}$. in the ortolan, evaporation amounts to more than 40 per cent of total heat loss. All the available evidence indicates that even vigorous panting does not suffice to provide more efficient vaporization. Thus a rise in environmental temperature above a certain upper limit is bound to cause hyperthermy, because water evaporation cannot compensate for the diminished heat loss through radiation and convection.

TABLE 21.

Water loss of the *yellow buntings*, expressed as $\text{mg./gm.}/\frac{1}{2}\text{ hr.}$

Temp. $^{\circ}\text{C}$.	Number of periods	Water loss	Per cent of total heat loss
+ 7	10	3.70	9.2
+14	14	4.40	13.8
+20	10	5.36	18.4
+25	14	5.56	20.9
+30	8	11.92	42.9
+32.5	10	10.12	38.1
+34	8	11.34	
+36	5	10.22	

TABLE 22.

Water loss of the *ortolans*, expressed as $\text{mg./gm.}/\frac{1}{2}\text{ hr.}$

Temp. $^{\circ}\text{C}$.	Number of periods	Water loss	Per cent of total heat loss.
+ 7	10	6.00	11.7
+14	10	4.48	10.4
+20	9	5.94	17.2
+25	9	6.98	18.8
+30	7	8.94	35.5
+35	4	9.44	40.6
+38	4	9.32	39.8
+40	9	11.28	39.2
+42	5	9.82	

Neither in absolute nor in percentage values does there seem to be any appreciable differences between the water loss of the yellow buntings and the ortolans in these experiments. The most pronounced increase in vaporization occurred at a somewhat higher temperature in the ortolans than in the yellow buntings.

12. FAT DEPOSITION

A. WEIGHT VARIATIONS

a. Introductory. It has long been known that migratory birds exhibit a rise in weight during the period of migration. The ortolan happens to be the bird on which the earliest records have been made. TERENTIUS VARRO (in *De lingua latina* 5, § 76, and *De re rustica* 3, 5: 1—2) tells that the ancient Romans trapped and fattened ortolans in masses. The birds were then regarded as great delicacies. This form of purely practical interest in the matter survived in some parts of Central Europe to the middle of the 19th century (e.g. in Silesia as reported by LEIPELT, according to KAYSER 1925), and to the present days in some Mediterranean countries.

The connection of the phenomenon with migration was discussed as long ago as 1822 by NAUMANN (according to WACHS 1926). Systematic investigations have only commenced lately. A great material on bird weights has been published by BALDWIN & KENDEIGH (1938) and NICE (1937). In both papers, a slight increase in weight during the winter is reported. No significant difference between migratory and non-migratory birds was observed, a finding differing from most of the results obtained in studies on the weights of migratory birds.

Altogether, some fifteen species of small migratory birds have been found to exhibit a distinct peak in weight in spring or autumn or both (see the reports by: ZEDLITZ 1926; GROEBBELS 1928, 1932; LINSDALE & SUMNER 1934, according to WOLFSON 1945; MERKEL 1937; PUTZIG 1939; BAUMGARTNER 1938; SHAW 1939, according to DE BONT 1947; BLANCHARD 1941; WOLFSON 1945; DE BONT 1947; ODUM 1949; ODUM & PERKINSON 1951; MARSHALL 1952; SCHILDMACHER 1952; and SCHILDMACHER & STEUBING 1952). Such a peak has not been demonstrated in non-migratory species, but in several cases there is an indication of weight increment during the cold season. The close connection between rise in weight and migration becomes still more apparent from the observation that there is a difference in this respect within the species, migrating individuals gaining in weight, and non-migrating individuals showing no change (compare the findings on the robin by PUTZIG 1939, and on the chaffinch by DE BONT 1947). There is a similar difference

between migratory and non-migratory races, too, as in *Zonotrichia leucophrys nuttalli* and *Z. l. pugetensis* (BLANCHARD 1941), and the different races of *Junco oreganus* (WOLFSON 1945).

There are several possible causes for weight changes, such as, for instance, development of the muscles during periods of strenuous exercise. Dissection of migrating birds often reveals deposition of fat. PUTZIG (1939), WOLFSON (1945) and ODUM & PERKINSON (1951) showed by actual analysis that the weight increment in migrating birds was due to accumulation of fat. In this way an energy reserve is obtained which is apparently important in migration.

As mentioned already, it was known long ago that caged ortolans become extremely fat. No systematic study of the phenomenon has been carried out. There are some data on weights of wild specimens obtained on migration. SPAEPEN (1952) and WEIGOLD and KROHN (both according to SPAEPEN l.c.) present information indicating that some individuals may be fat and others normal during both the spring and autumn migrations. JOUARD (1933), PALUDAN (1938) and MAKATSCH (according to SPAEPEN 1952) have also weighed ortolans during migration, but they found no sign of weight increment. BATES & PHILBY (1936) report that ortolans shot on spring migration at Jidda were »extremely fat».

b. Weighings. When the investigation was commenced in 1950, observations on weight variations were not included in the programme. In the measurements of the respiratory exchange, weighings were necessary, and by December 1950 it was evident that the ortolans had been very fat at the beginning of the experiments. In 1953, attempts were made to observe the weights especially of the ortolans during the autumn migration.

Small birds exhibit rather great daily variations in weight, owing to their tiny bodies and intense metabolism. It might be claimed that their normal physiological daily rhythm includes energy storage during the daytime, and consumption of the deposits during the night. Minimum weight occurs in the morning before they start feeding, and maximum during late afternoon. According to NICE (1937) and BALDWIN & KENDEIGH (1938) the normal daily variation amounts to 4—5 per cent. SCHILDMACHER (1952) reports changes of 10 per cent. Fasting small birds lose weight at a rate of some 0.1 gm./hr. (NICE l.c., SCHILDMACHER l.c.). The reports cited, and the findings by KENDEIGH (1944, 1945) and the present author indicate considerable variation in these values, depending on species and environmental temperature. In small, poorly insulated species weight loss proceeds at a relatively much faster rate than in birds with greater bulk and heavy plumage. In basal conditions, the yellow buntings and the ortolans lose some 0.1 gm./hr.

Fig. 5. Weight variations of the birds expressed as deviations from the observed minimum weight, the mean of which is given in the text. The numeral by each circle indicates the number of observations. Vertical stretches = double standard deviation.

During experiments in the cold, the weight loss was ca. 0.2 gm./hr.: it was as great in the ortolans at +7°C. as in the yellow buntings at -11°C. SCHILDMACHER (1952) concludes that the value of observations on weights of small birds depends on proper recording of nutritional state and time of the day.

The bulk of my weighings were performed immediately after respiration experiments. The main part of the data thus pertains to birds deprived of food after 4 p.m., and weighed between 9.30 p.m. and 00.30 a.m. From August 15 to September 31, 1953, all the ortolans not being used in the experiments were weighed every other day. They were then kept for three hours without food. The weighings were performed between 11 and 12 o'clock. The data obtained in this way dominate the values given for the ortolans during the

period from July to October. They are not strictly comparable with the other data, but this circumstance does not obscure the general tendency in the material.

The birds were confined in cardboard tubes and weighed to the nearest tenth of a gram.

c. Results. The material consists of 521 weight observations on ortolans and 326 on yellow buntings. 24 individuals of the former species and 26 of the latter were used. Comparisons are based on the minimum weight observed (mean minimum weight in grams given below).

Ortolans	Yellow buntings
$n = 24$	$n = 26$
$m = 22.0 \pm 0.25$	$m = 26.4 \pm 0.25$
$\sigma = 1.24$	$\sigma = 1.34$
$C = 5.65$	$C = 5.10$

The yellow buntings thus weighed 16.5 per cent more than the ortolans.

In the graph, fig. 5, the observed weights are presented as deviations in grams from the observed minimum weights, (values for the ortolans below,

Fig. 6. The weight variations of four ortolans.

for the yellow buntings above). The figures by the circles indicate the number of observations, the vertical stretches represent double standard deviation. As a rule, the results have been computed as monthly means. In the graph for the weights of the ortolans, however, the values for the period July 15—August 15 are combined in one point, whereas the results from the period August 16—October 31 are given as bi-monthly means because of the numerous observations made.

The ortolans exhibit a huge weight increment. In late October they reach the maximum level. The mean deviation from the minimum weight is 14.5 gm: the fat deposits amount to 40 per cent of the total weight. Such a great increase in weight presumably does not occur in the wild state, but seems to be in some way connected with captivity. When the bird is in a state to accumulate fat, captivity apparently offers suitable conditions for a marked gain in weight. Food abounds but activity is limited, and stores are not as readily depleted as in nature.

The graph (fig. 5) gives the impression that the weight of the ortolans increases and decreases gradually. But the dispersion diminishes towards the tip of the peak. At the beginning and the end of the period of fattening, the individual differences must be great. The individuals in fact gain 30 per cent or more in weight in ca. ten days: after the first sudden rise the weight is usually rather stable until the turn of the month November—December; then it falls off steeply. The graphs in fig. 6 show the situation in four of the ortolans. It appears that the period of fat storage is of about the same length in different individuals. Generally the fatness lasted to the latest date in the birds which were late in beginning to gain weight.

One is apt to expect a similar peak in the weight of the ortolans in the spring, too, especially as there are published reports indicating that they store fat during the northward migration. But only in April did a slight rise occur: it was, however, only one quarter of the birds that fattened excessively during this period, the others remaining in a normal state as to weight. In no individual did the fat deposition in spring amount to a bulk comparable with that stored in autumn. Until data on the actual weight variations of ortolans in the wintering localities and during the spring migration are obtainable, it seems inadvisable to speculate on the causes of this phenomenon.

The weights of the yellow buntings are on the whole steady. If there are seasonal changes, they are presumably directly influenced by external factors such as temperature. There are, however, apparently differences in the reaction of different individuals. Of the nine birds trapped in February 1953, four were kept in natural temperature and light conditions, whereas five were placed in the laboratory. The birds kept out of doors maintained a relatively constant weight. Of the birds indoors, three lost some 6—7 per

cent of their weight, whereas in two of them no change was observed. When three birds were moved out of doors in January 1954, two of them had soon gained some two grams in weight, whereas the weight of the third remained unchanged.

B. ENERGY METABOLISM AND DEPOSITION OF FAT

a. Deposition of fat in relation to photoperiod and temperature. When the temperature is falling and the photoperiod grows shorter, maintenance of the energy balance becomes more and more difficult. At a certain limiting value it will be impossible to procure an adequate supply of food, and consequently the weight will start dropping. The importance of this factor in the ecology of small birds especially has been emphasized by KENDEIGH (e.g. 1934). It can, of course, be applied to the storage of fat. During September 1954 experiments were performed to find out at how short a photoperiod the deposition of fat is rendered impossible for the ortolan at certain low temperatures.

Preliminary experiments revealed that starving ortolans lost some 3.5 gm. in 24 hours. During the following day, the gain in weight amounted to ca. 2.5 gm., and complete recovery was achieved in two days. In actual experiments, the birds were kept in a refrigerator, in which the small space only permitted the use of a cage measuring $40 \times 65 \times 55$ cm. It was considered possible that this might be a disturbing factor. In control experiments, the cage was covered with white paper. The birds gained weight at the same rate as in a larger cage with a free outlook. All these preliminary experiments were performed in natural conditions as regards light and temperature.

The refrigerator was lighted with a 40 W electric bulb provided with a cooler. One further control was made with 4 birds placed in the refrigerator at room temperature and a 14 hr. photoperiod. After one day without food, two days were required for recovery as in the earlier experiments. It thus seemed clear that the birds were not seriously disturbed by being confined in the refrigerator, and that fat was rapidly accumulated.

12 ortolans were used in the experiments. They were separated into three groups with four birds in each. For elimination of individual irregularities, the sum of the weight changes of all birds in a group was used as a basis of reference. When an experiment was commenced, the birds were weighed at 6 o'clock in the morning and then deprived of food for 24 hours. They were weighed and placed in the refrigerator at 6 o'clock on the following morning. All groups were allowed a 14-hour photoperiod (6 a.m. to 8 p.m.), but they were kept at different temperatures ($+8$ — $+9^{\circ}\text{C}$., $+5$ — $+6^{\circ}\text{C}$., and $+2$ — $+3^{\circ}\text{C}$.). There was a weight increment in all groups, but it was least in the group kept at the lowest temperature. All weighings were performed in the

morning, before the light was turned on. The refrigerator was completely dark during the night and the food was removed from the cage in the evening to insure that the birds could not feed during the night.

After the experiment described above, the birds were allowed to recover their weight completely. Then the hunger treatment was repeated. The three groups were placed in the refrigerator at the different temperatures mentioned above. The experiment was started with a twelve-hour photoperiod. This was reduced by one hour a day, until the weights of the birds ceased to increase or began to drop. When this was the case, the same photoperiod was maintained for one day more. It thus became evident whether the decrease or standstill in weight was only accidental or not. The results are shown in table 23.

TABLE 23.

Photoperiods (hrs.) limiting the ability of the ortolan to accumulate fat at different temperatures.

Temp. °C.		Shortest photoperiod with gain in weight.	Longest photoperiod with weight loss.
Group I	+8—+9	9	8
Group II	+5—+6	10	9
Group III	+2—+3	11	10

There was an immediate increase in weight in the birds in group I as the photoperiod was extended from 8 hours to 9 hours. The same was the case with group III when the 10-hour photoperiod was maintained, but the temperature was raised to +7°C. The connection between the length of the photoperiod, the temperature level, and the ability to store fat seems evident.

b. The carbon dioxide output of fat birds. GROEBBELS (e.g. 1928b and 1930), and MERKEL (1937) suppose that the deposition of fat is due to a decrease in the catabolic and an increase in the anabolic functions of the body. Their hypothesis is based on their observation that only a small increase in food consumption occurs in fattening migratory birds. The possibility of lowered basal metabolism is suggested.

If this hypothesis is correct, there should be a decrease in metabolism prior to the accumulation of fat. To put this assumption to the test, 5 birds with weights still unchanged were chosen in late August. It was intended to perform respiration determinations on these birds immediately before the increase in weight began — the date for the experiments could, of course, only be chosen at random — when it was rising, after maximum weight had been achieved, during resorption of the fat, and after the fat deposits had disappeared. Unfortunately two of the birds were killed when only three

Fig. 7—11. The accumulation of fat in relation to the energy metabolism in five ortolans. Open circles = weight variation; circles with black centre = total CO₂ output expressed as mg./hr.; black circles = CO₂ output expressed as mg./gm./hr. Each point showing the CO₂ output represents the mean of five determinations.

experiments had been performed with them. With one of the birds (M87) the first determination was made when it was already fattening. On August 27 it weighed 20.7 gm., on 29th 23.4 gm., and on 31st 24.8 gm.

Ordinary determinations of the minimum standard metabolism were made. The results are presented in figs. 7—11. In addition, several similar experiments were performed with both fat and lean birds in connection with the study of the adaptation to high temperature. The results have been given above (tables 10—12, pp. 42—44), recalculated for normal weight level. As they do not differ from the data given here, they need not be further considered in this connection.

All the time before the onset of fattening the basal metabolism remains unchanged. It can be seen from the graphs that during the increase in weight the metabolism per unit weight decreases. In all the birds except M89 there is a slight increase in total energy production during the period when weight is rising. In the other determinations, this quantity remains virtually unchanged. The fatty tissues thus seem to be metabolically almost completely inactive.

In addition, experiments were performed in the cold ($-1^{\circ}\text{C}.$) with the three birds surviving after F86 and F88 had been killed. The results are given in table 24.

TABLE 24.

Carbon dioxide output of *fat ortolans* at $-1^{\circ}\text{C}.$ expressed as mg./gm./hr., and total CO_2 as mg./hr., means of 5 determinations.

Bird	M87		M89		F58	
Date	14.10.	18.2.	15.10.	17.2.	16.10.	17.2.
Weight gm.	33.6	21.5	35.1	21.4	28.3	21.6
$\text{CO}_2/\text{gm}.$	7.42	9.90	7.64	10.78	8.24	10.68
» total	249.6	213.0	268.2	230.2	234.4	230.2

The same tendency is apparent: the fat is inert. The total CO_2 output is, however, slightly greater when the birds are fat than when they are normal. The difference is significant ($t = 3.61$) as shown below (table 25).

TABLE 25.

Total carbon dioxide output (mg./hr.) of *fat* and *normal ortolans*.

Fat	Normal
$n = 15$	$n = 19$
$m = 250.2 \pm 5.2$	$m = 226.0 \pm 3.84$
$\sigma = 20.4$	$\sigma = 16.70$
$C = 8.03$	$C = 7.37$

This difference can be interpreted in different ways. It could depend, for instance, on differences in the insulating power of the plumage. It may also imply maintenance of the temperature of the fat tissues at the expense of energy. Doubtless the matter cannot be settled without extensive and thoroughgoing studies.

C. DISCUSSION

By many authors fattening is considered to play a very central rôle in the mechanism of bird migration. WOLFSON (1945) and ODUM & PERKINSON (1951) assume deposits of fat to be an essential prerequisite for migration. There is,

however, probably no absolute need for weight increment. According to PUTZIG (1939) in the robin a good nutritional state promotes, and a poor one inhibits migration, but it may occur without stored fat. NICE (1946) reports no significant change in the weights of migrating song sparrows. MERKEL (1937, 1938), PUTZIG (l.c.), and FARNER (1950) pay attention mainly to supposed changes in the »energy utilization».

In many birds there is clearly a disposition to storage of fat during the migratory seasons combined with an ability for rapid mobilisation of this energy reserve. This seems to be the important feature, not the accumulation of fat as such. It enables the birds rapidly to regain reserves consumed. My ortolans could feed at will. In some instances the weight increased by 2.5 gm. in 24 hours. Perhaps the restricted activity caused the abnormal fattening. SPAEPEN (1952) has recorded the weight of 118 ortolans on migration. They averaged 23.2 gm. the extremes being 19.8 and 27.8 gm. Not a single observation on wild specimens has yielded higher values than 30 gm. The inconsistency of the data obtained with wild birds is not surprising. Stored fat is bound to be consumed during flight at a fast rate, and the deposits are presumably renewed during rest in suitable localities. The state of a bird trapped and weighed depends on chance.

The storing of 14.5 gm. of fat in a bird weighing 22 gm., as was the case with my ortolans, does not seem energetically appropriate. In such a way a heavy ballast is formed. PEARSON (1950) speculates on the energetic aspects of migration. Such considerations may elucidate the situation a little. The rate of oxygen consumption during flight is, however, not known. PEARSON (l.c.) performed actual determinations on flying hummingbirds, finding values amounting to 6 times the consumption at rest. In mammals work can raise the oxygen consumption 10 times above the basal level. Flight is heavy muscular work, at least in such a bird as the ortolan. Assuming a metabolic intensity 6 times the basal rate in a flying ortolan weighing 25 gm., it would evolve 2200 gcal. per hour. In such a hypothetical case, 10 gm. of fat would last for forty hours. A nonstop flight of this length does not seem likely. Other physiological factors than the depletion of energy resources would presumably put a limit earlier. Pure muscular exhaustion could well be one such factor.

GROEBBELS' (1928, 1930, 1932) and MERKEL's discussions of decreasing basal metabolism as a possible basis for fattening in migratory birds are also interesting from the energetic point of view. There has been no experimental evidence to support this view. It has been based on the assumption that the slight rise in food consumption observed in migratory birds in cages would not suffice for energy storage. The experiments related here have given no sign of a change of basal metabolic rates in fattening ortolans except a slight rise during the time of rapid gain in weight. This finding is

in perfect accordance with the results reported by KEYS & BROŽEK (1953) from investigations on man, and by MAYER (1953b) from experiments with mice.

The basal metabolic level in itself is low. A diminution of it cannot appreciably facilitate the accumulation of fat. MERKEL (1937) presents data showing an increase in food consumption of 15—20 per cent in a whitethroat during the period of migration. Small birds consume much food in relation to their bulk owing to the rapid metabolism. Provided that the bird does not increase its activity, the increment in food intake leading to fattening need not be great. Assuming a net energy of only 40 per cent in the case described by MERKEL, the fattening of the bird may well depend on the observed slight increase in food intake only. During the time of »Zugdisposition» MERKEL observed a slow accumulation of fat which changed into a very rapid rise in weight immediately before the »Zugstimmung». PALMGREN (1944) reports marked inactivity in robins during days prior to nights with »Zugunruhe». In my opinion such a change in activity combined with a slight rise in the food consumption might well account for the fattening of migratory birds.

There has been much discussion concerning not only the quantitative, but also the qualitative aspects of the fattening. In this connection, however, almost no attention has been given to the biochemical mechanisms involved. ODUM & PERKINSON (1951) present data indicating an increasing phospholipid content in the liver during a short period when migration is setting in. This is the only observation known to me suggesting changes in this respect.

More data are available concerning possible changes in the secretion of certain hormones which could be linked with the mechanism of fattening. GROEBBELS discussed purely hypothetically the possibility of diminished basal metabolism owing to reduced secretion of dissimilatory hormones, mainly thyroxine and gonadal active principles. In contrast to this view, MERKEL (1937, 1938) was able to produce migratory restlessness by injection of thyroxine. MERKEL also gives some evidence but no proof for the rôle of thyroxine in the migration of birds in the wild state. SCHILDMACHER & STEUBING (1952) injected bramblings with gonadotropic and gonadal hormone, causing deposition of fat in the birds. The authors conclude that fattening in spring is due to the direct influence of gonadal hormone, or to its influence on the secretion from the pituitary of the principles regulating metabolism. WOLFSON (1945) induced fattening using Antruitin G. This result could be interpreted as depending on the action of the factors regulating the metabolism which are included in this extract from the pituitary. Antruitin G contains, however, some quantities of a gonadotropic principle, and thus WOLFSON's result can be interpreted as supporting the views of SCHILDMACHER

& STEUBING. In any case not a single fact in favour of the hypothesis of GROEBBELS is known.

It is perhaps not impossible that fat deposition in the spring may be connected with an increase in gonadal activity. But how then is the fattening in the autumn to be explained? STIEVE (according to SCHILDMACHER & STEUBING 1952) supposes an initial stimulus from the small and transient secretion of gonadal hormones occurring in the autumn. The correctness of this view is doubted by SCHILDMACHER & STEUBING on the basis of results from experiments performed by the former author. They hypothetically assume a different basis for the increase in weight in spring and in autumn.

Every attempt to explain the stimulus to migration or fat deposition as linked with the sexual cycle must lead to the construction of various auxiliary hypotheses to account for spring or autumn migration. It seems evident, however, that migration and deposition of fat are connected with each other in many true migrants. Energetically an increase in weight depends on excessive energy absorption. This in turn is due to changes in the mechanism regulating food intake.

The observation of SCHILDMACHER & RAUTENBERG (1952) that small injections of thyroxine caused increase in weight in chaffinches is very interesting. The result is interpreted as due to augmentation of appetite but not of basal metabolism. As mentioned above, MERKEL produced migratory restlessness by injection of thyroxine. He also (1937) discusses a physiological feeling of hunger as a possible basis for autumn migration. Perhaps the stimulus to both spring and autumn migration could be found through investigations in this direction. In my opinion the hormonal processes investigated in the works mentioned above need not be the only foundation for the accumulation of fat. Perhaps there is no causal relationship but merely correlation.

MAYER (1953a) points out that fattening in man is caused mainly by a disturbance in the mechanism regulating the appetite. This mechanism seems to be extremely complicated. Nothing of its nature in birds is known. But it controls food intake, and an increase in food intake above the level motivated by the energy requirements must be the basis for an increase in weight. Hence it seems logical to assume a change in this mechanism occurring twice a year in migratory birds accumulating fat. Perhaps no great change in the rapidity of fat deposition and mobilisation is needed, because small birds in the normal state are already provided with effective mechanisms for these processes, (see above the discussion of daily weight changes, p. 67).

In some cases, the mechanism seems rather unaffected by changes of external conditions, such as temperature. This fact is discussed by WOLFSON (1945). My ortolans were divided into three groups kept at different tem-

peratures during autumn 1953. Their weights, however, exhibited the same variations.

If changes in the regulation of appetite and food intake are linked with the deposition of migratory fat, some nervous mechanism must be involved. PALMGREN (1944) demonstrated changes in activity in connection with the disposition to migrate. This finding implies alteration of the nervous reactivity.

The migratory period is evidently a period of considerable stress. Perhaps it is connected with changes in the state of the general adaptation syndrome (compare SELYE 1950). The observation of diminished activity prior to »Zugunruhe» (PALMGREN l.c.) in my opinion supports such a view. SELYE (l.c.) points out that a particular stress put on the organism may promote a response at the expense of other activities. The ACTH cortisone system which is important in the general adaptation syndrome, may play a special rôle in this connection. Changes in this system caused by stress involve improved gluconeogenesis which must facilitate the rapid transformation of fat necessary during migratory flight.

The connection between migration and the moult has also been discussed. KOCH & DE BONT (1945) point out that the moult is generally finished immediately before the migration. They suggest a relation of the changes in energy utilization to »la poussée métabolique» demonstrated in connection with the moult. Such a relation is, however, unlikely from the physiological point of view. Besides, many migratory birds moult in the wintering area. MERKEL (1937), on the basis of differences in thyroidal activity during moulting and migration, regards the two processes as mutually exclusive. PUTZIG (1938) does not share this view, giving examples of migration in birds with an incomplete moult. Migratory flight in birds with incomplete wing quills does not, however, seem likely. PUTZIG (l.c.) mentions that rise in weight has been observed in connection with the moult. ODUM & PERKINSON (1951) made such an observation on *Zonotrichia albicollis*, but the lipid content was then at a minimum. A rise in weight in birds moulting in late summer does not necessarily imply the onset of fattening. In not a single ortolan did new feathers begin to develop until the fat had been used up. Thus in the ortolan moulting and the accumulating of fat seem to exclude each other.

13. SUMMARY OF THE RESULTS

1. Altogether, 200 determinations of the respiratory quotient were performed. From these, the following facts emerge:

a. Fasting yellow buntings and ortolans have an R.Q. of about 0.69, indicating the combustion of fat.

b. A postabsorptive condition is reached when the birds are deprived of food for some three hours.

c. The R.Q. of the two species during fasting is not affected by the diet.

d. The R.Q. of fasting ortolans is not altered during the period of fattening.

2. The standard metabolism within the range of temperature tolerance was determined. As a basis of reference the CO_2 output expressed as mg./gm. lean weight/hr. has been used. The following results were obtained:

a. The zone of thermal neutrality is between $+25$ and $+33^\circ\text{C}$. in the yellow bunting, and between $+32$ and $+38^\circ\text{C}$. in the ortolan.

b. The critical temperature of the yellow bunting is $+33$ — 34°C ., and that of the ortolan 38 — 39°C .

c. The lower lethal limit for room-adapted ortolans is about -15°C ., a temperature which can be endured for some 5—6 hours only. The corresponding value could not be obtained for the yellow bunting, but an extrapolation of the metabolic curve indicates that it is about -36 to -40°C . The metabolic quotient of the ortolans was 3.2.

3. Ortolans need some 1.5 hrs. to adjust the metabolic level when they are moved from room temperature to cold. The corresponding adjustment to warmth is performed in some 20—30 minutes in both species.

4. Using yellow buntings, the changes in metabolism caused by stay at natural temperatures during all seasons were studied, and likewise the changes in metabolism occurring in room-adapted birds during different times of the year.

a. The basal metabolism was constant throughout the year (except during the moult) regardless of the adaptation to different temperature conditions.

b. The metabolism in cold (determined at -11°C .) was lower in specimens acclimatized to winter than to room temperature.

c. The metabolism in the cold of room-adapted birds was at a minimum immediately after the moult and exhibited a steady rise until the maximum was reached before the moult in August.

5. The effect of prolonged stay at a constant high temperature was studied in both species. The birds were divided into three groups, kept in the following conditions:

Group I in a constant temperature chamber with an initial temperature of $+22.5^\circ\text{C}$. The temperature was raised by 2.5°C . at approximately 4-week intervals. At the end of the stay at each temperature, the basal metabolism of the birds was determined.

Group II: as group I, but placed for 8 hours each day in a cool room (temp. $+10$ — $+14^\circ\text{C}$.).

Group III: control group kept at room temperature.

The determinations of the basal metabolism gave the following results:

a. In the yellow buntings, the metabolism dropped 13.6 per cent below the normal value after three weeks at $+27.5^{\circ}\text{C}$. In the ortolans, a diminution amounting to 18.3 per cent was observed after three weeks at $+32.5^{\circ}\text{C}$. The limiting temperature is thus between $+25$ and $+27.5^{\circ}\text{C}$. in the yellow bunting, and between $+30$ and $+32.5^{\circ}\text{C}$. in the ortolan.

b. The basal metabolism of the birds in group II was not altered, with the exception of two yellow buntings exhibiting a drop in metabolism after exposure to $+32.5^{\circ}\text{C}$. A cool spell during the 24-hr. period facilitates the endurance of high temperatures.

c. The basal metabolic rate of the birds in group III remained unchanged from the beginning to the end of the experiment.

The experiments performed in cold (yellow buntings at -11° , ortolans at -1°C .) revealed a significantly higher metabolism of the birds in group I after their basal metabolic rate had fallen. No change was observed in groups II and III, which did not differ from each other.

6. The basal metabolism of the yellow bunting and the ortolan corresponds to an output of 4.36 mg. $\text{CO}_2/\text{gm. lean weight/hr.}$ ($= 3.14 \text{ ml. O}_2/\text{gm./hr.}$, or 1058 kcal./sq. m. body surface/24 hrs.). S.r. ($=$ the standard range of the population $= 3.24 \times \sigma$) is ± 20 per cent.

7. The thickness of the plumage was photographically determined. The yellow bunting has an insulation much better than that of the ortolan, and this must be one of the most important reasons for the difference in tolerance of the two species.

8. Experiments with individuals having defective plumage showed that the cold resistance decreased and the tolerance of heat was improved.

9. During the moult, the metabolism was generally above the normal level, and the dispersion increased. There was considerable variation in the basal metabolism of the same individual during this period.

10. The metabolism in air almost saturated with water vapour was determined from $+20^{\circ}\text{C}$. to the upper critical limit with the yellow bunting, and from $+25^{\circ}\text{C}$. with the ortolan. The minimum metabolism was slightly lower than in dry air. The critical temperature of the yellow bunting was not affected, but in the ortolan it fell to about $+33^{\circ}\text{C}$. The critical factor limiting heat tolerance in moist air seems to be the difference in vapour pressure between the respiratory and evaporating system, and the environmental air.

11. Vaporization increases markedly in both species at a temperature of about $+30^{\circ}\text{C}$. Some 40 per cent of the heat produced is bound in the evaporation of water at high temperatures.

12. Observations on the weight changes of the birds revealed no significant changes in the yellow bunting. The ortolans accumulated great quantities of

fat during the autumn. In the spring, there was a less marked increase in weight, and this only in a part of the individuals.

13. Determinations of the basal metabolism of fattening and fat ortolans indicated a slight rise of the total metabolism during the period of rapid gain in weight. The metabolism calculated per unit lean weight was otherwise quite normal, indicating the metabolic inertness of the fat. Experiments at low temperature gave identical results.

Altogether, 444 respiratory experiments comprising 2387 of 20 minute or $\frac{1}{2}$ hr. periods were performed. When the determinations of the R.Q. are included, the effective time thus amounts to some 900 hours.

II. ECOLOGICAL CONSIDERATIONS

1. PHENOLOGICAL DATA

As a background for the discussion to follow, an account will be given of the breeding and wintering ranges, and of the migration of the yellow bunting and the ortolan. So far as I know, there has been no review of the subject dealing with the yellow bunting. SPAEPEN's (1952) paper concerning the ortolan appeared when my material was already collected. Besides, I have had access to some literature not mentioned in SPAEPEN's treatise. The information presented here has been obtained from the periodicals listed on p. 102 before the list of other references. The species index was used. The locus of each separate notice is not given, because it is not the object of this work to give bibliographies on the literature concerning the species studied.

Additional information has been gained from works by SARUDNY (1888), SUSHKIN (1897, 1913, 1914), SARANDINAK (1909), HARTERT (1910), NESTEROV (1910, 1911), GYLDENSTOLPE (1911), ISPOLATOV (1911a and b), v. DOMBROWSKI (1912), STUDER & FATIO (1915), WITHERBY (1920), GROTE (1930.), MENE-GAUX (1939), RAITASUO (1946) and VAN BENEDEN (1951). The boundary for the breeding range of the ortolan in Finland is drawn according to LEHTONEN (1950). I am indebted to Dr. E. MERIKALLIO for permission to use his rich archives, and to Drs. BERGMAN and v. HAARTMAN, who placed the records from Signilskär at my disposal. For verification of the information from India, I wish to express my gratitude to Mr. SALIM A. ALI.

The different races belonging to the species *Emberiza citrinella* L. are in the following sections considered physiologically comparable. According to

VOIPIO (1951), the ortolan is monotypic. The taxonomic status of the species needs to be clarified. JOHANSEN (1944) expresses the opinion that at least four subspecies could be recognized. There is, however, no objective basis for exclusion of some part of the species.

A. BREEDING RANGE

a. Yellow bunting. Map 1 (on the back) shows the approximate boundaries of the breeding range of the two species. The yellow bunting is common in Western Europe, and in Scandinavia as far north as the forest boundary. In Russia it breeds to the 64th—65th parallel, and in Siberia its northern limit at Ob and Yenissei coincides with the 64th parallel. Its breeding seems to be more restricted to cultivated land in the north than in the south.

Eastwards, the bird has been observed breeding as far as the environments of Kansk east of Yenissei.

Along the southern boundary of its range in the Mediterranean area, the yellow bunting breeds in the mountains only. In Rumania, the bird occurs both on the plains and in the mountains. In Southern Russia it breeds on the western coast of the Black Sea and the northern part of the Crimea, but is absent during the summer, for example, from the environments of Rostov. Along the Don and the Volga, its range extends to 49—48°N. From regions farther south, there is one record of a pair of yellow buntings breeding 700 m. above sea level in Calabria. According to SEEBOHM (1883) and SUSHKIN (1914), the race *E. c. erythrogenus* occurs in Caucasia and Transcaucasia, mainly on the northern slopes of the mountains down to some 1000 m. above sea level. The present state of this population is not known to me, and it has not been included in the map, because the statement seems somewhat doubtful.

In Western Siberia, the southern boundary approximately follows the 50th northern parallel, extending, for example, to Semipalatinsk on the Kirghizian steppe. In the mountains east of Turkestan, the bird breeds as far south as the Altai, Tarbagatai, and Ala tau.

b. Ortolan. The main part of the ortolan's breeding range coincides with that of the yellow bunting. In Western Europe, it does not breed in the British Isles, in Northwestern France, Southwestern Belgium and a narrow area along the continental coast of the North Sea. Likewise, it is absent from Denmark and from Vestlandet in Norway. In the latter country, it occurs in the north at Tromsø. The distribution in the mountainous regions of Scandinavia is not clear. The northern boundary in Lapland approximately follows the line Arjeplog, Jokkmokk, Kiruna, Palojoensuu and Ivalo. In-

formation concerning its northward distribution in Russia has not been available. According to JOHANSEN (1944) it does not occur far north of the trans-Siberian railway, i.e. to about the 55th northern parallel. It presumably breeds as far north as farming is practised, because it is confined to the culture steppe in the northern part of its range.

In the south, it breeds in Northwest Africa in a restricted area in Morocco. In Central and Southern Spain, it occurs in the mountains only, whereas it is a common bird in Northern Spain, the South of France, and Italy. In the latter country, it does not, however, breed south of Latium. It is absent from the isles in the western part of the Mediterranean Sea. On the Balkan Peninsula it occurs on the plains e.g. in Bulgaria, but in Greece, the Aegean Isles, and Crete, it is a mountain dweller solely. In Russia, it occurs as far south as the neighbourhood of Rostov and Astrakhan. In Caucasia it breeds in the mountains and at Batum, but reliable information as to its occurrence on the plains between the Black and the Caspian Seas has not been obtainable. In Turkey, Syria, Iran, Afghanistan, and east of Turkestan, it breeds high in the mountains only. It has been recorded at Kobdo in Mongolia, and in the environments of Minussinsk and Krasnoyarsk. On the steppes of Western Asia, it occurs to Aral in the south, but is absent from the lowland areas in Turkmenistan and Uzbekistan.

The ortolan's absence from westernmost Europe could be interpreted as the bird's expanding its breeding range in this direction. There is, however, evidence indicating that the bird is no new immigrant in this area. ENGSTRÖM (1951), for instance, writes that a hundred years ago, it was much more common as a breeder in Southern and Western Sweden than it is today. Similar information is given by HEYDER (1916) from Sachsen. A decline in Western Europe during the last hundred years thus seems likely. The northwestern boundary of the ortolan's range may be conditioned by maritime influence as supposed by ENGSTRÖM (l.c.) and DURANGO (1948). KALELA (1949) and KEVE & V. UDVARDY (1951) report analogous effects of the recent climatic changes on some other species of birds. The ortolan is apparently rather xerophilous, and it seems to be commoner and more evenly distributed in Southeastern than in Western Europe.

The ortolan is characterized by a greatly fluctuating frequency in restricted localities. This feature is observed by many authors, earlier and recent, but remains unexplained. Could the cause be the trapping in the Mediterranean region, where the bird has been a popular delicacy since ancient times (compare above, p. 66)? SPAEPEN (1952) supposes that the increase in numbers of the ortolan in Western Europe during recent times may be due to the prohibition of snaring issued in France and Belgium in 1932.

B. DISTRIBUTION DURING THE WINTER

a. Yellow bunting. The whole range of the yellow bunting shifts southward at the approach of the cold season, and simultaneously it turns from northeast to southwest (see map 2 on the back). The southern boundary approximately coincides with that of the breeding range of the ortolan, and the bird sometimes extends the wandering to Algeria and Palestine. The main part of the wintering area overlaps the breeding range.

The northern and northeasternmost parts of the summer area are emptied in the autumn. The information available from the Soviet is unfortunately meagre. Apparently, the boundary runs from the Altai in a northwestern direction to the White Sea. From Finland and Sweden only does the material suffice for drawing boundaries of yearly and occasional occurrence during the winter (lines 1 and 2 on the map).

b. Ortolan. The information as to the occurrence of this species during the winter is incomplete. The bulk of the records indicate wintering in Yemen, the interior of Eritrea and French Somaliland, the Ethiopian uplands as far as the 6th—7th northern parallel, and Eastern Sudan (e.g. in Darfur). ARRIGONI DEGLI ODDI (according to SPAEPEN 1952), states that the ortolan winters in Southern Italy and in Sicily. GEYR VON SCHWEPPENBURG (1917) reports its occurrence in Northwest Africa. Neither statement is supported by other information in the literature available, and verification is thus needed. As SPAEPEN (l.c.) points out, it seems very likely that some ortolans winter in West Africa south of the Sahara. In early April 1926, ortolans were observed flying northwards along the shore of Rio de Oro (STRESEMANN 1926). H. & T. HEIM DE BALZAC (1951) have also observed ortolans on spring migration in West Africa, viz., April 8 and 10, 1947, at Atar, and April 20 and 21, 1942, at Tindouf. BREHM (1884) states that the species winters in West Africa, but he does not mention the source of this information.

On map 2, the wintering range in Arabia and East Africa is approximately indicated. A question mark represents the hypothetical winter quarters in West Africa.

In Southern Europe, the ortolan is an extremely rare winter visitor. Individuals have been recorded in Silesia (February 10, 1876, BASIUS & AL. 1878), at Selmech Banya in Hungary (February 2, 1898, SCHENK 1899) and three times in Switzerland. Moreover, there is one observation from Iraq in January (MEINERTZHAGEN 1914). The species thus prevailing winters outside the breeding range.

The species does not winter in India. From this country, only three observ-

ations are known, all from Kashmir. Two specimens have been obtained at Gilgit (May 9 and 26) and one in the neighbourhood of Srinagar in March (ALI *in litt.*).

C. MIGRATION

a. Yellow bunting. A clear picture of the migratory movements of this species is not easily obtained. It is usually described as a vagrant. Local wanderings, caused by fluctuations in the food supply, tend to confuse the issue.

The information collected makes the following general description possible.

Practically all over Europe, autumn migration has been observed from September to December. In Northern and Central Europe, the migratory movements culminate in October, in Southern Europe in November.

In Southern Europe the northward flight begins in January. In Central and Northern Europe, it does not grow conspicuous until March. It seems that the migrating part of the population returns to Southern Finland and Central Scandinavia in late March and early April, whereas Northern Finland and Sweden are reached during the former half of April, and the northernmost parts of Scandinavia during late April — early May.

During exceptionally cold winters, a considerable proportion of the birds normally wintering in Southern Finland and Central Sweden are apparently forced to migrate, but soon return. Thus, a great northward flight during late February 1922 was observed in Denmark. During the time February 11—March 3, 1940, yellow buntings were reported as migrating northward at Hälsingborg. In both cases, the preceding winter had been very severe.

b. Ortolan. The first ortolans arrive at their winter quarters in late September, and the last individuals disappear in early April. The spring migration begins in late March, when the bird has been recorded in Egypt and along the shores of North Africa, and has sometimes advanced as far as Dalmatia, Hungary and Southern Russia. The major part of the migratory flights is performed during April. Before April 15, the birds have usually been observed in the Mediterranean countries, the South of France, the Danubian region, Southern Russia, and Turkmenistan. The majority of the birds in Central Europe as far as the Baltic, Russia, and Western Siberia seem to be on the breeding grounds in late April. During the first days of May, the ortolans arrive in the southern and central parts of Scandinavia and Southern Finland, and in the middle of May, migration as a rule is completed, and the breeding season has commenced. The material at hand does not permit the drawing of isepipteses, but it seems likely that the ortolans on spring migration generally do not cross the $+4^{\circ}\text{C.}$ isotherm.

The autumn migration generally begins in August, and the main movements occur in early September. Even in the southernmost parts of its breeding range, it is seldom observed after the expiration of September.

The ortolan evidently migrates during both day and night. A great part of the observations published have been made during the day-time, but there are many records of dead individuals found at lighthouses.

D. SUMMARY

The ortolan is a typical migrant with migratory flights confined to distinct periods. No part of its breeding range coincides with the wintering quarters.

The yellow bunting is mainly a wintering species. Migratory movements occur throughout the cold season, and are evidently frequently typical «weather movements» caused by local fluctuations in the food supply (e.g. in connection with snowstorms) and the temperature. Within the major part of the breeding range, wintering occurs, and only a small portion of the total population extends its wanderings beyond its southern boundary.

There are resemblances between the two species as to food (see e.g. O. & M. HEINROTH 1924), breeding biology and behaviour (compare HOWARD 1920, STEINFATT 1940, DIESSELHORST 1949, 1950, DURANGO 1948). In the following sections, some of the factors possibly connected with the complete difference in the reaction of the two species to changing seasons are to be discussed.

2. PHOTOPERIOD AND AVERAGE TEMPERATURE WITHIN THE RANGES OF THE TWO SPECIES

A comparison of the photoperiods and temperatures in the breeding and wintering ranges of the yellow bunting and the ortolan clarifies the different stresses put on their energy balance. The different combinations of these factors appear from the climographs in figs. 12—16 which have been constructed by means of the method used by KENDEIGH (1934).

The photoperiods (on the abscissae) are computed as the time from the rise of the upper edge of the sun to 6° below the horizon till the setting of the sun as far below the horizon. They thus include the periods of civil twilight in morning and evening. According to my own field observations (WALLGREN, unpublished) and data given by FRANZ (1944) this corresponds well to the daily periods of activity of the yellow bunting as well as to that of the ortolan (unpublished data). The data for the latitudes from the equator to the 60th parallel are from the Berliner Astronomisches Jahrbuch 1952. In this publica-

Fig. 12 (left). Climograph showing the combinations of average temperature and photoperiod within the wintering area of the ortolan in South Arabia and East Africa from October 1 to March 31. Further explanations in text.

Fig. 13 (right). Climograph showing the combinations of average temperature and photoperiod within the breeding range of the ortolan from May 1 to August 31.

tion, only the nautical twilight (the upper edge of the sun 12° below the horizon) is given. The approximate length of the civil twilight was obtained by interpolation. The length of the photoperiods at the 60th, 65th, and 70th parallel have been computed by Dr. KALAJA, who placed his material at my disposal. I was thus able to compare the values for the photoperiods at the 60th parallel as calculated from the Berliner Astronomisches Jahrbuch with those obtained by KALAJA. Errors greater than 10—15 minutes do not occur in the values given for more southern

Fig. 14. Climograph showing the combinations of average temperature and photoperiod within the wintering range of the yellow bunting from October 1 to March 31. For meaning of the lines AB and CD, see p. 92.

Fig. 15. Climograph showing the combinations of average temperature and photoperiod within the breeding range of the yellow bunting from April 1 to September 30.

Fig. 16. Combined climographs. Full thin line = ortolans during the summer. Broken thin line = ortolans during the winter. Full heavy line = yellow buntings during the summer. Broken heavy line = yellow buntings during the winter.

latitudes than 60°. The effect of cloudiness and terrain on the photoperiod could not be considered.

On the ordinates, the average temperatures within the ranges of the two species are given. The data pertaining to every month of the year are taken from works by HANN (1910, 1911), KÖPPEN & GEIGER (1932, 1939) and HAURWITZ & AUSTIN (1944). The least reliable data are those concerning temperatures in Africa, and the Asiatic regions outside the Soviet.

The climographs are constructed on the basis of points representing the combination of photoperiod and temperature at some place at a time when the species in question occurs in this place. A great many such points from every country where the birds occur were determined. The outermost were connected, and the polygons obtained thus cover the range within which the photoperiod and mean temperature may vary on the distributional area of the two species.

In the climographs for the ortolan, the months when migration culminates, viz., April and September, have been excluded. One of them encloses the time from October 1 to March 31, when the bulk of the species is within the wintering range. The other applies to the breeding area during May, June, July and August. The temperature conditions to which the species is exposed during different seasons are remarkably steady. The photoperiod varies from ca. 12 hours (in Yemen in December) to 24 hours.

The majority of the yellow buntings winter in energetically much less favourable conditions. The combinations most extreme are a 6 hr. 20 min. photoperiod combined with the temperature -9.8°C ., and 9 hr. 30 min. photoperiod at -19.9°C . During the warm season (April and September are included in the climograph) the yellow bunting lives in an environment within which the combination of these two factors is about the same as for the ortolan. During both winter and summer part of the latter, however, are exposed to warmer temperatures than the former.

3. ECOLOGICAL SIGNIFICANCE OF THE PHYSIOLOGICAL DIFFERENCES DEMONSTRATED

A. COLD TOLERANCE, AUTUMN MIGRATION, AND WINTERING

The lower lethal temperature appearing from ordinary determinations of the standard metabolism represents a zone where thermoregulation breaks down independently of existing energy stores. Theoretical considerations and experimental evidence indicate that in nature the limiting temperatures are considerably higher. The ability of a bird to maintain its energy balance in

winter conditions cannot be exactly judged without knowledge concerning the following points: its capacity for energy absorption per unit time, and its total energy requirements during natural activity at various temperatures. The latter problem especially is complicated. Firstly, quantitative determinations are needed of the fluctuations in energy consumption at different temperatures and photoperiods, conditioned by variations in daily rhythm and activity. Secondly, the temperatures at the roosting places of the birds should be known. According to KENDEIGH (1934) the critical effect of low temperatures is exerted by the «average night temperature in conjunction with the number of hours of darkness».

Under special conditions, there may be another critical effect of low temperatures than that postulated by KENDEIGH (1934), viz., the day-time temperature. Many birds roost in shelters. But during the day-time, rather strenuous activity is needed in securing food, escaping from enemies, and so on. To what extent activity consumes the energy stores in the cold cannot be exactly judged. RUBNER (according to HART 1950b) assumed a compensation of thermogenic energy consumption by the heat production connected with muscular work. This concept is supported by results obtained by MANGE (1920) and LEFÈVRE & AUGUET (1931, 1933, 1934). But in contrast, the works by GIAJA (1932) and HART (l.c.) indicate that the combustion connected with muscular work is always added to the resting metabolism regardless of environmental temperature. If the latter view is correct, it would mean that the energy reserves are consumed at a much faster rate during work than during rest in cold. The increased mobility of the air layer close to the body further tends to decrease the ability to withstand cold during muscular exercise. In any case, thermoregulation soon breaks down and body temperature begins to drop during strenuous work in severe cold: an identical temperature may be endured for a considerable time by the organism at rest.

An adaptive roosting behaviour may enable a bird to survive during very cold nights, but the days must be sufficiently mild to permit feeding. The house sparrow may serve as an example. In determinations of its standard metabolism, it died of cold at -40°C . (KENDEIGH 1944). But in 1945 KENDEIGH showed that the ability of the bird to withstand cold was much poorer. From starvation experiments it appeared that at -19°C . the birds could survive only 14.5 hrs. without food. The longest night the house sparrow is exposed to within its range in North America happens to be 14.5 hrs.

The house sparrows both in America and Europe survive during considerably colder, and in Europe also during longer nights. Nightly means down to -35 to -40°C . have been reported within areas where the species has survived, although decimated. As KENDEIGH points out, this must be

due to its roosting in shelter. From some districts in Northern Finland, the house sparrows have disappeared during winters with day-time temperatures occasionally dropping below -40°C . (see above p. 33). The birds probably got frozen to death when they were forced out to seek food. Thus I am inclined to regard the minimum day-time temperature as being at times a critical factor.

A comparison of my results for the yellow bunting and the ortolan with the data on the energy relationships of the house sparrow obtained by KENDEIGH (1944, 1945, 1949) may make some conclusions possible.

Roosting yellow buntings during the winter exhibit an adaptive behaviour comparable with that of the house sparrows. They spend the night near the ground in dense shrubberies of small spruces, at times almost covered by snow (observations in S.W. Finland, WALLGREN, unpublished). Presumably the bird is thus able to survive during cold nights. This adaptation does not, however, seem as efficient as that of the house sparrow, but the yellow bunting is more hardy. Room-adapted individuals withstand cold about as well as KENDEIGH's winter-adapted birds. As shown above (p. 38), winter-adapted yellow buntings tolerate cold much better.

The importance of the combination length of night — mean temperature of night appears from the northeastern boundary of the wintering range of the yellow bunting. In Finland, it is a regularly occurring winter bird as far north as Brahestad in places with enough food. The northernmost locality in which wintering has been recorded is Turtola on the River Torneå. From Western Soviet, the bird is reported as remaining the whole winter in Uhtua and Archangel, 64.5°N . In Western Asia it does not winter farther north than in southern Altai and on the plains to the west of Turbagatai. The northeastern boundary thus apparently runs in a northwestern direction to the White Sea and hence crosses both the parallels and the isotherms obliquely (compare map 2). Severe cold reduces the ability of the bird to survive long nights, but it exhibits an adaptive behaviour securing the proper balance between photoperiod and temperature.

In MERIKALLIO's archives there are records of yellow buntings observed as far north in Lapland as Kittilä and Inari during middle and late January, although they have not wintered. January in these regions is considerably colder than December. But the darkest period of the year around Christmas and New Year, with short spells of gloomy twilight only, is apparently less favourable.

The cold-sensitive ortolan spends the night in the open field (own observations). True, the vegetation can give some shelter during a great part of the year; but when snow covers the ground, an animal with such roosting habits is inevitably exposed to wind and cold. The records from the meteorological

stations give no adequate picture of the thermal environment of the wintering yellow buntings. But supposing that the ortolan were neither to migrate nor to change its behaviour, they might suffice for an estimation of its chances to survive a winter in the breeding area.

Above (p. 21) the view of SEIBERT (1949) was cited: that the rate of hourly food intake would determine the northward spread of a species during the winter. This pertains to species with identical capacity as to thermoregulation: but differences in this respect are bound to cause differences in northern boundaries even in species with identical digestive ability.

Assuming identical maximum capacity of energy absorption per unit time for both species, and equal physiological strain caused by temperatures producing the same standard metabolism, the climograph for wintering yellow buntings (fig. 14, p. 87) may be used as a basis of comparison. One of the sides, AB, connects the point of 6 hrs. 20 mins. photoperiod and -9.8°C . with the point of 9 hrs. 20 mins. photoperiod and -19.5°C . This is about the limit of tolerance of the yellow buntings in the natural state. Starting from the temperature $+5^{\circ}\text{C}$. at which the standard metabolism of the ortolan is identical with that of the yellow bunting at -9.8°C ., a line CD parallel with AB may be drawn, representing the hypothetical tolerance of the ortolan. This being correct, the ortolan would need 8 hrs. at 0°C ., and 9 hrs. 40 mins. at -5°C . to maintain its energy balance.

This theoretical value is presumably too optimistic, as the roosting behaviour of the yellow bunting places it in a position more favourable than that of the ortolan. The values are not, however, very far from those derived from the experiments in which the effect of low temperature and short photoperiod on the fattening of the ortolans was studied. The results of these determinations presumably pertain to normal ortolans too, because the metabolism per unit lean weight was identical in fat and normal individuals. In the experiments, a 10 hr. photoperiod at $+2$ — $+3^{\circ}\text{C}$. was required for weight maintenance. The situation can be improved by acclimatization to low temperature, but on the other hand, natural conditions are energetically less favourable. On the basis of the present evidence, it seems likely that ca. 0°C . and a 10 hr. photoperiod represent limiting conditions. If this is true, wintering is not quite safe even within that part of the ortolan's breeding range having the the mildest winter, viz., the north coast of the Mediterranean. And in adjacent areas, such as Central Spain, the mountains of the Balkan Peninsula and the upland of Asia Minor and Iran, minimum temperatures down to -20 to -30°C . are not uncommon, thus rendering migration necessary for the ortolan.

Theoretically, the ortolan might well winter along the south and east coasts of the Mediterranean. During historical time, there have been winters

much more severe than the ones prevailing now (ANGERVO & LEIVISKÄ 1944): but the establishment of wintering populations during very short spells of time in connection with climatic changes is known. Such has been the case, for instance, with part of the Scandinavian and Finnish chaffinches and blackbirds (*Turdus merula*). Within the Mediterranean area, however, the ortolan is a rare winter visitor only.

Considering temperature and photoperiod only, it thus appears that the ortolan migrates »unnecessarily» far southwards. KENDEIGH (1934) supposes the existence of a zone of a »feeling of physiological discomfort», serving as a warning at the approach of unfavourable conditions. This »feeling of discomfort» would be the essential driving force in the adaptation of the organism to the environment. This hypothesis, combined with the necessity to cross the great deserts of North Africa, may serve as an explanation of the present position of the winter quarters of the ortolan.

Other climatic factors, too, may contribute to explain why the ortolans leave the Mediterranean area for the winter. There is a common feature in the wintering areas of the species: summer rains prevail, whereas the winters are rather dry. On the coasts of the Mediterranean Sea offering suitable habitats for ortolans, precipitation is mainly confined to the winter months. As mentioned earlier, the ortolan is considered a xerophilous species. Rain together with temperature and photoperiod is perhaps the most important physical factor determining its winter range. On the other hand, the most profound influence may be that of choice of habitat. The vegetation is, however, influenced directly by climate, and thus habitat selection ultimately depends on climatic factors. Much more exact information is needed concerning the wintering of the ortolan before the matter can be definitely settled.

The autumn migration of the ortolan is performed during a time before any danger is apparent. The change most easily observed is the shortening of the light period, but even in the northernmost parts of the breeding range the energy balance can presumably be easily maintained, especially as the ortolan is a seedfeeder. The present time of autumn migration seems conditioned rather by heredity than by changes in the environment. The postponing of the autumn migration to too late a period might impair the deposition of fat, which seems to be a necessary prerequisite for migratory flight.

A comparison of the experimental results (table 23, p. 72) with temperatures (from KERÄNEN 1952), and photoperiods in Finland during the autumn shows that by middle and late October, the conditions even in the southernmost part of the country would inhibit fattening in captive birds. In nature, fat deposition does not, however, occur in such a favourable environment as in the experiments: more energy is needed for other ends, such as activity, and the food is not as easily obtained. Further, rapid accumulation

of fat is presumably important. In our latitudes, it may be considerably slowed down even by late September, especially during unfavourable autumns. I am inclined to suppose a direct selective advantage of early migration in the northern and eastern parts of the breeding range of the ortolan. The later the departure, the greater the risk is of inhibition caused by cold spells. Farther south other factors, however, may be more important, because migration begins at about the same time as in the north. But the factor discussed here may have been in operation during earlier stages of the evolution of the ortolan's migration.

B. HEAT SENSITIVITY AS CORRELATED WITH SPRING MIGRATION AND THE SOUTHERN BOUNDARIES OF THE BREEDING RANGES

By migrating in autumn, the ortolans escape death from cold and restricted availability of food. The northward flight in spring must offer some advantages, and these may partly be explained on the basis of known effects of high temperature.

The ortolans begin to leave the wintering regions in mid-March. It is a period of rising temperature, and simultaneously, the annual rainy season begins. The combination of these factors seems essential. As shown above (p. 63), the ability of the ortolan to withstand heat is seriously impaired in moist air. And even if these factors do not provide a direct stimulus to migration, there are nevertheless other, less obvious effects of rising temperature and humidity, which could well render breeding in the winter quarters impossible.

There is no clear understanding of the factors underlying critical effects of high temperature. MERRIAM (1894) writes: »The southward distribution of . . . species is determined by the mean temperature of the hottest part of the year». This conclusion has been criticized by many authors (see for instance BOWEN 1933). BALDWIN & KENDEIGH (1932) and KENDEIGH (1934) consider the daily maximum temperature as the factor critical for birds. True, relatively moderate temperatures may constitute upper lethal limits for birds because of their poor protection against overheating. Not enough about the effects of high temperatures is known, however, to warrant abandonment of MERRIAM's theory. On the contrary, I am inclined to interpret the results of my experiments concerning the effect of warmth as indicating that this concept may in some cases be very valuable.

HESSE (according to WACHS 1926) supposes that one of the advantages of spring migration for species wintering in tropical regions might be the procuring of longer photoperiods for the breeding season. Birds in a tropical climate tend to have smaller clutches than species breeding in temperate

zones. HESSE thinks that the photoperiod would not suffice for rearing the young, especially as a resting period during the hottest hours of the day may be necessary. Such a quiet period is perhaps not required by species perfectly adapted to tropical conditions. But with the present ability of the ortolan to withstand heat, it seems likely that this factor might be of some importance.

In connection with breeding, intense activity is needed. The body temperature of birds is variable, and the variations are mainly due to muscular activity (HILDÉN & STENBÄCK 1915, BALDWIN & KENDEIGH 1932). In this study, a temperature zone was demonstrated in which the basal metabolism of the ortolan was lowered (compare above p. 47). This limiting temperature was somewhere between $+30$, and $+32.5^{\circ}\text{C}$. In the natural state average temperatures lower than this may have a similar effect provided that cool periods do not occur, because the activity must be much greater than that of the caged birds used in the experiments. Further, there may be other associated phenomena directly linked with too high a temperature. Impaired spermatogenesis could be one of the consequences of ortolans remaining to breed within the wintering area. In this connection the observation deserves attention that the testes of migrating birds are frequently not fully developed until the migratory flight or when they have arrived at the breeding grounds.

Already in 1871 ALLEN (according to KENDEIGH 1934) suggested rising temperatures in southern latitudes as a possible cause for the spring migration. The idea has occasionally been put forward later, but it has never been submitted to experimental test. KENDEIGH (l.c.) suggests that changing light periods and increasing daily maximum temperatures may regulate and time the northward spring migration. The rôle of photoperiods for species wintering near the equator has been doubted (compare ALLARD 1928 and the reviews by FARNER 1950 and SCHÜZ 1952). TWOMEY (1936), on the basis of climographs, concludes that high temperatures may be essential in the regulation of migratory flights. THOMSON (1953) likewise expresses this opinion.

According to MAYR & MEISE (1930), the exact reason for northward migration was not known in any one case. Since then no more information as to this problem has been gained. It seems, however, that high temperatures make breeding of the ortolan impossible within its wintering range.

Warm climate as a factor controlling the distribution of birds is discussed by EKMAN (1909, according to v. UDVARDY 1951), MERIKALLIO (1917) and KEVE & v. UDVARDY (1951). KENDEIGH (1945) and SALT (1952) note that two species with poor heat tolerance within the southern part of their breeding range move in the cooler mountain areas to breed. v. UDVARDY (1951) demonstrated a good correlation between heat tolerance and the occupation of more or less temperate habitats.

Along the southern boundary of the breeding range, both the yellow bunting and the ortolan are typical mountain dwellers, (compare map 1, where these areas are indicated with dots and circles). The yellow bunting occurs in these regions from slightly less than 1000 m. height up to the forest boundary, whereas the ortolan has been recorded still higher, up to 3000 m. above sea level in Iran. The absence of the ortolan from the hot plains east of the Caspian Sea and from central Iran is also very conspicuous.

NIETHAMMER (1943) explains the breeding of the ortolan above the forest limit (1500 m. above sea level) on Peloponnesus as owing to competition of the nearly related *Emberiza caesia*. The latter is a typical Mediterranean species. Of course, such competition may be at times essential in the vertical distribution of some species: but it does not seem to account for the fact that the ortolan breeds solely in the mountains along the whole southern boundary of its range. Besides, no possible competitor of the yellow bunting has been reported. The conditions in southern France are typical: the yellow bunting is confined to the hills, whereas the ortolan breeds on the coastal plain.

The only part of Africa to which the breeding range of the ortolan is extended is the northwesternmost corner of the continent, which is cut off by the July isotherm of 24°C. This can hardly be a matter of chance. The isotherms on map 1 are reduced to sea level: the breeding of the ortolan seems, however, to be mainly restricted to the areas limited by the 26° isotherm in Europe, and the 28° isotherm in the continental parts of Asia. This is reflected in the climograph, fig. 16, too. The southern boundary of the breeding range of the yellow bunting approximately follows the 22° isotherm in Europe, and the 24° isotherm in Asia.

The critical temperature of the ortolan is some 6°C. higher than that of the yellow bunting. There is about the same difference between the temperatures at which an effect on basal metabolic rates was observed. Microclimatologic circumstances may enable the yellow bunting to breed in temperatures relatively somewhat higher than those limiting the breeding of the ortolan. The former is a typical inhabitant of forest edges and shrubberies, whereas the latter lives on open ground.

In Asia, both species breed in somewhat warmer regions than in Europe. This may be partially explained by the greater ability of homoiotherms to withstand warmth in variable temperatures. The typically continental climate of Asia presumably implies greater contrast between day and night temperature than in Western and Southern Europe. The air is drier, and both these factors tend to facilitate the endurance of heat.

Further evidence in support of the view that high temperatures may be of critical importance in the distribution of the two species is given by SARUDNY

(1888). Near Orenburg, he observed ortolans seeking shelter in the shadow of the vegetation during hot days, and remaining quiet until the cooler period in the late afternoon. During less warm weather, the males were singing all day. He also reports that the nests were usually placed on northward slopes. PALMGREN (1932), HANCOCK (1911, according to KENDEIGH 1934), SAUNDERS (1929, according to KENDEIGH l.c.) and LONG (according to BALDWIN & KENDEIGH 1938) have all observed a decrease in the activity of birds during hot weather.

Many of the facts related above seem to indicate that relatively moderate temperatures may inhibit normal activity and thus constitute ecological barriers almost as important as upper lethal temperatures. As pointed out above, it is likely that in nature such a temperature might be lower than that influencing basal metabolism during the experimental conditions. On the other hand it is of course hardly identical with that indicated by the isotherms running along the southern boundaries of the breeding ranges. The boundaries are produced by long-term effects, in which local disturbances in the climate come into play, some years being warmer and others cooler than the means indicated by the isotherm. I do not wish to deny the importance of the daily maximal temperature as a limiting temperature: but it is worth while to take into serious consideration the possibility of other factors being in operation.

C. SUMMARY

A comparison of the temperature characteristics of the yellow bunting and the ortolan with climographs showing the combinations of mean temperature and photoperiod, and with other available information concerning the conditions within their breeding and wintering areas, has led to the following conclusions:

1. The breeding ranges of the two species are determined, *inter alia*, by the following circumstances:

- a. In the north, the yellow bunting follows human settlements as far as the forest boundary. In the west, its breeding range is limited by the Atlantic, in the east by the Siberian taiga and the mountains and steppes of Central Asia. The southern boundary seems to be influenced in an important manner by the tolerance of the species to high temperatures. As to the mechanism of influence of warmth, it seems necessary to consider two types of critical effect: on the one hand the daily maximum temperature, on the other the action of long periods with steady high temperature. In this study there has been demonstrated an effect of prolonged exposure to warmth, indicating the existence of a physiologically and ecologically important temperature limit, not hitherto precisely defined.

b. The northward distribution of the ortolan seems to depend mainly on the extension of farming. In westernmost Europe there are some areas where the ortolan does not breed, presumably because of the humid, maritime climate. The eastern boundary approximately coincides with that of the yellow bunting. The southward extension also seems to be conditioned to a great extent by high temperatures. The greater heat tolerance of the ortolan is reflected in the fact that it breeds farther to the south than does the yellow bunting.

2. For most ortolans, autumn migration is absolutely necessary. The yellow buntings, in contrast, are able to winter within the breeding range except for the northern- and northeasternmost parts of it, provided that food suffices. This is made possible by their cold tolerance, and an adaptive feature in their roosting behaviour.

3. Ortolans live throughout the year in a remarkably constant thermal environment. The mean temperatures vary with an amplitude amounting to 27°C. at most, and the difference between the extremes is about the same in the breeding and the wintering area. In some American migrants TWOMEY (1936) has demonstrated similar conditions. By migration energetically very constant conditions are secured.

The differences between the highest and lowest mean temperatures to which yellow buntings may be exposed is 45°C. The fluctuations in photoperiods are also much greater than, within the range of the ortolan, and all yellow buntings spend the winter in a more severe environment than that of the ortolan.

The behaviour of each species secures a margin of safety of about identical magnitude between the climatic extremes and the experimentally demonstrated critical temperatures.

4. The boundaries of the wintering areas are obviously influenced by the following factors:

a. The importance of the combination length of night — mean temperature during night (KENDEIGH 1934) appears on the northeastern boundary of the area of the yellow bunting. The availability of food, and severity of cold during the day-time may at times constitute critical limits, too. In the west the Atlantic, in the east the mountains of Central Asia prevent further wandering of vagrant individuals. The reason for the limitation of the movements in the south and southeast is not as evident. Perhaps it is conditioned by a weak migratory urge ebbing out when the vagrant bird arrives at some suitable locality. The yellow bunting is a very hardy species, and obviously the selective value of prolonged southward wandering has not been great enough to make stabilization of such behaviour possible.

b. The wintering areas of the ortolan are poorly known. Precipitation in addition to temperature conditions may act in determining their boundaries. Whether the winter quarters are chosen under the guiding effect of climatic factors or by habitat selection is impossible to judge in the present state of our knowledge.

5. The environmental factors most effective in stimulating northward migration in the ortolan seem to be rising temperature and the beginning of the rainy season. In my opinion the species in its present physiological status would not be able to breed successfully within the wintering area.

6. It does not seem possible to demonstrate an environmental stimulus directly influencing the autumn migration of the ortolan. The present behaviour of the species is presumably the outcome of an evolutionary process in which temperature and photoperiod have been important factors. The migrating populations of yellow buntings are more directly influenced by weather and fluctuating food supply, but of course it may be a matter of differences in degree, and not in kind.

4. CONCLUDING REMARKS

The results obtained by KENDEIGH (1934, 1939, 1944, 1945, 1949), TWOMEY (1936), SEIBERT (1949) and SCHILDMACHER (1952) together with the findings in this investigation show great differences in the temperature tolerance of Palearctic and Nearctic migratory and resident birds. The correlation with their migratory or resident status is obvious. In some cases at least, a causal relationship may exist between migratory behaviour and physiological peculiarities of this kind. Already we can imagine, as in the case of the ortolan, the chain of biological requirements forcing a species to perpetually recurring wandering: northward to breed, southward to survive the winter. An all too long stay in the north or in the south — and disaster ensues.

In 1945, BULLOUGH in a review accepts without hesitation the earlier view held by ROWAN, according to which migration is »a particular phase of sexual behaviour». This statement is based on the fact that it had been possible to produce sexual prematuration by means of artificial lighting. Personally I should regard the conclusion of BULLOUGH as erroneous, with the possible exception of some singular case. Migration has probably a more general biological significance. It secures reproduction, and to this extent it may be included in the yearly sexual cycle. But I do not regard migration as more directly linked with sexuality than is the flight for life of a small bird persecuted by a predator. Detailed criticism of the hypothesis of release of migration by gonadal hormones is given by FARNER (1950).

BULLOUGH's statement reflects the long held inclination to deny any direct influence of biological factors on migration. The main reason has been that such factors cannot provide a general explanation of migration. Material is, however, accumulating which indicates that a general theory is merely Utopian. Research in bird migration is in a period of transition. On the one hand, some experimental workers have concluded that not only migration, but also the beginning of the breeding season, regardless of latitude, can be explained in terms of the influence of the light period, (KIPP 1936; ROLLO 1951; WOLFSON 1949, according to WAGNER & STRESEMANN 1950). On the other hand, WAGNER & STRESEMANN (l.c.) emphasize the importance of many factors other than light periodicity. These are different for different species. They include especially factors which in one way or another may be critical for the raising of the young: the supply of suitable food or nest material, precipitation, excessive heat or dryness, the developmental state of the vegetation, and so on.

Further works pointing in the same direction as this most interesting paper by WAGNER & STRESEMANN, are those by LACK (1950a and b), MOREAU (1950), SKUTCH (1950) and VOOUS (1950), which have been provided with an introductory comment by THOMSON (1950). All these authors conclude that the tropical birds are brought into a disposition to breed by an inherent »timing» mechanism which has been developed by selection and thus brings the reproductive urge into operation during the most favourable time of the year: the breeding activity is then released by certain combinations of external factors which are different in different cases. Presumably the pituitary plays a central rôle in this connection. LACK (1950b), however, supposes photoperiodicity to be the decisive factor in Europe (and other temperate regions?). But initiation of breeding as well as migration may also be influenced by other factors within these regions. SVÄRDSON (1953) enumerates several cases indicating that migration in Fennoscandia may at times depend on the food supply. DIESSELHORST's (1949) and my own (WALLGREN, unpublished) observations indicate that the breeding activity of the yellow bunting begins on dates that differ considerably in different years, owing to temperature and snow conditions. The spring migration of the ortolan is presumably not directly regulated by photoperiodicity, and a study of the origin of migration in this species (which is to be discussed in a paper that will appear later) indicates that this may pertain to the autumn migration as well.

The widespread occurrence of sexual behaviour in autumn among resident and migrating birds (see e.g. the review by KALELA 1954) seems to be an important phenomenon in this connection. Probably there is no fundamental difference between this and the sexual latency of tropical birds.

The very fact that all species treated with light, tropical and temperate, re-

ardless of their origin, have exhibited changes of the sexual cycle, seems to argue against the concept of light as the decisive factor for all species in their natural surroundings. The existence of sexual latency, such as mentioned above, has not been fully taken into account in the interpretation of the results of such experiments. It is interesting to note that SCHILDMACHER & STEUBING (1953) have described a case of decreasing sexual activity following exposure to artificially prolonged light periods.

From a more general point of view, we may state that the experiments have revealed that the inherent physiological rhythm may be altered by external influences: but this does not mean that the factor operating in nature is identical with that artificially produced. Light cannot, in my opinion, be accepted as the predominant external factor in the yearly cycle of any bird, until it has been demonstrated by thorough analysis that there are no other factors of significance. It is, of course, the ultimate cause of migration as well as of other seasonally recurring phenomena within temperate regions: but the proximate factors may be of quite a different nature.

During recent years, facts have accumulated making a reconsideration of the terms »innenweltbedingte» and »aussenweltbedingte Zugvögel» (PUTZIG 1938) desirable. The degree of dependence on the environment varies from case to case, but a stereotyped cycle, completely divorced from its connection with the seasons, is not likely to be found in a single migratory species. Such a yearly cycle is known in one instance only, viz., the famous *Sterna fuscata* on Ascension, breeding 5 times within 4 years.

There is one path to success in research on bird migration: different species exhibiting different types of migratory pattern, must be subjected to exhaustive analysis as to all aspects of their life. In this task, the rôle of laboratory and field workers is of equal importance. A search for a general explanation implies wasting of time: it is more useful to start from the assumption that all species differ as to the origin and mechanism of migration.

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LIST OF PERIODICALS

that have been used in gathering information concerning distribution and migration.

- Alauda* 1929—1953.
- Ardea* 1924—1950.
- Aquila* 1894—1930, 1939—1943.
- Berichte des Vereins Schlesischer Ornithologen* 1922—1938.
- Dansk Ornitologisk Forenings Tidsskrift* 1906—1950.
- Der Ornithologische Beobachter* 1923—1939.
- Fauna och Flora* 1924—1950.
- Hørrings Fuglene ved de Danske Fyr* 1911—1932.
- Ibis* 1876—1882, 1903—1907, 1912—1914, 1927—1943, 1945—1953.
- Journal für Ornithologie* 1853—1950.
- Limosa* 1928—1950.
- Mitteilungen des Vereins Sächsischer Ornithologen* 1922—1938.
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Map 2, showing the wintering range of the yellow bunting (dotted line), and the ortolan (shaded areas). The double boundary in Fenno-Scandia represents the northern limit of (1) yearly and (2) occasional occurrence of the yellow bunting throughout the winter. The question mark indicates probable wintering quarters of the ortolan. January iso-

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14	Line 18—19	For »P-value greater», read »P-value smaller».
23	Table 4	For »Multiplication of the CO ₂ values by 7.02», read — — — by 3.51» and for — — — by 485 as kcal./sq.m./hr., read — — — by 242 as — — —.
23	Table 5	For »Multiplication of the CO ₂ values by 6.97», read — — — by 3.49» and for — — — by 480 as kcal./sq.m./hr., read — — — — — by 240 — — —.
61	Line 11	For »see p. 4», read »see p. 41».
76	Line 4	For »Ai diminution», read »A diminution».

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Map 1, showing the breeding range of the yellow bunting (dotted line), and the ortolan (broken line). Black circles indicate that the yellow bunting, open circles that the ortolan breeds only in the mountains. July isotherms (according to ANGERVO & LEIVISKÄ 1944) included.

Map 2, showing the wintering range of the yellow bunting (dotted line), and the ortolan (shaded areas). The double boundary in Fennoscandia represents the northern limit of (1) yearly and (2) occasional occurrence of the yellow bunting throughout the winter. The question mark indicates probable wintering quarters of the ortolan. January isotherms (according to ANGERVO & LEIVISKÄ 1944) included.