THE CONDOR

AUTUMNAL PREMIGRATORY AND MIGRATORY PERIODS IN THE CHAFFINCH (*FRINGILLA COELEBS COELEBS*) AND SOME OTHER TEMPERATE-ZONE PASSERINE BIRDS

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This paper is a short review of the research on metabolism and behavior of some migratory birds carried out at the Biological Station of the Zoological Institute of the Academy of Science of the USSR located at the Kurishe Nehrung in the Baltic Sea. Most of the data on which this review is based have been published in various Russian journals.

MATERIALS AND METHODS

The Kurishe Nehrung is a long, narrow strip of sand hills covered by trees and shrubs. It separates the Kurishe Gulf from the Baltic Sea (fig. 1). In the spring and particularly in the autumn the Kurishe Nehrung is the route of very intensive daytime migration of birds. Many birds that nest in the northern part of the USSR and in Finland and spend the winter in southern and western Europe, Asia Minor, and Africa migrate through the Kurishe Nehrung. Formerly the Vogelwarte Rossitten was located there. Six great stationary traps (fig. 2) are set by our station and by Lithuanian ornithologists on the Kurishe Nehrung and on the opposite shore of the gulf (fig. 1). About 50,000 birds are trapped each year.

Immediately after trapping, the birds are banded, weighed, identified with regard to sex and age, the wing length is measured, the size of the cloacal protuberance in males and the stage of brood-patch development in females is recorded, and the molt and fatness are visually estimated by classes. Some birds are retained for experiments. These are confined either in outdoor aviaries (6 m long, 3 m high, 2.5 m wide) or in small cages (75 cm long, 70 cm high, 50 cm wide) in a room where they are exposed to fluctuations in outdoor temperatures and to natural photoperiods.

Total activity, feeding rhythm, and *Zugunruhe* were registered for groups of five birds in cages 100 cm long, 70 cm high, and 50 cm wide, or for single birds in cages 42 cm long, 21 cm high, and 21 cm wide. The method of registration was similar to that of Farner and Mewaldt (1953).

The orientation of birds was registered in Kramer cages (90 cm in diameter, 30 cm high, and with eight recording perches) placed under the open sky. In all instances the electric impulses from contacts at the perches were recorded by electromagnetic counters.

The autopsy of birds was made as follows. After weighing the bird it was decapitated, and the blood was collected into a beaker containing heparin (1 ml of blood to 2 ml of weak heparin solution). The concentration of sugar in the blood was determined by the method of Hagedorn and Jensen. The feathers were removed from the body, and the fresh weights of the feathers and body were obtained separately. The liver was then dissected out, and it and the body without the food from the esophagus and stomach and without the feathers were oven dried to constant weight at 96° C. They were then ground to a powder, and the liver and body fat were extracted separately with ethanol:diethyl ether (2:1) in the Soxhlet apparatus. Some American investigators make fat extractions using petroleum ether, which extracts all of the fats from the body. Ethanol
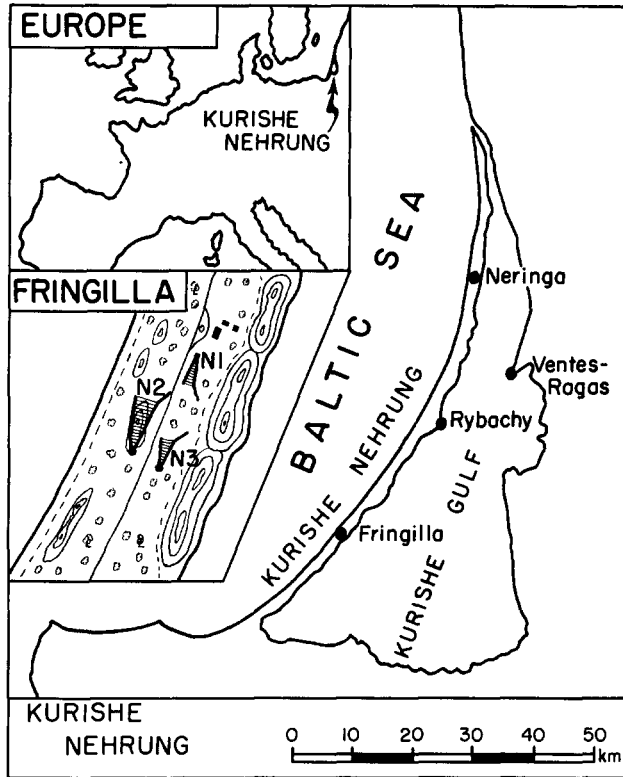
Figure 1. The Kurishe Nehrung. Location of trapping sites (black circles at the right) and of traps at "Fringilla" (V-shaped symbols at the left). Entrance of net no. 1 (N1) faces the south; entrances of nets no. 2 (N2) and 3 (N3) face the north.

and diethyl ether, however, extract only the fats directly useful in providing energy. For the differences between the class values with each method see table 1.

The mean value of each fat class was defined in milligrams of dry fat (table 1). In this report the fat equivalents rather than the fat classes will be used for analysis.

The postnuptial molt was recorded in relation to stage (pins, brushes, complete feathers) and intensity (light, heavy). The molt of primaries was scored in 11 stages (table 2). The sexual activity of males, determined by the height and width of the cloacal protuberance, correlated well in our birds with the weight of the testes (see also Wolfson, 1954). In females the development of the brood patch was correlated with the stages of the breeding cycle (see Bailey, 1952; Lyuleeva, 1965).

The intensity of daytime migration and its direction were measured either by visual observation or by the relative numbers of birds caught in the two traps at "Fringilla," one of which was directed to the south, the other to the north.

The Chaffinch, *Fringilla c. coelebs*, is the principal object of our investigations. It is one of the most abundant forest birds of Europe. Our data concern mainly populations of the Kurishe Nehrung and of eastern Finland and nearby regions of Karelia (fig. 3). The Chaffinches feed principally on insects during the summer and on plant seeds when migrating and wintering. Autumn migration is regularly to southwestern Europe. The species is primarily a daytime migrant in large flocks,
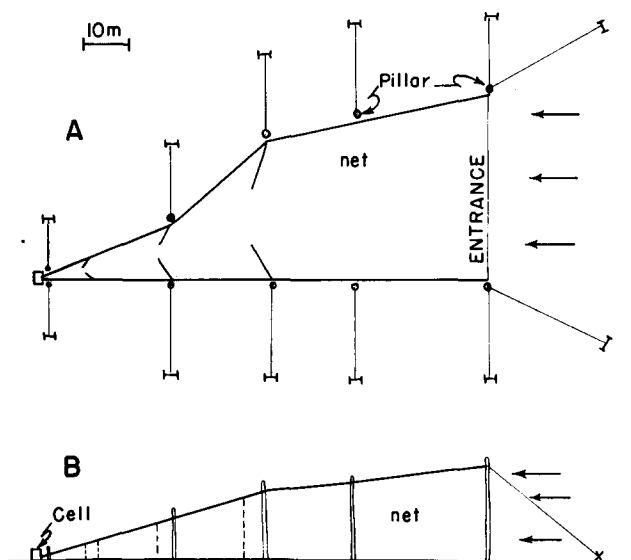
Figure 2. Plan of bird traps. A. From the top; B. From the side.

moving most actively in the morning and less actively in the evening. We have not observed either nocturnal migration or *Zugunruhe* in this species, but Chaffinches, obviously, migrate at night over the sea (Hansen, 1954). The time of migration of some different populations is shown in figure 3.

The Yellow Warbler, *Phylloscopus trochilus*, is an insectivorous species. It extends in Europe to the Arctic Circle, spends the winter in tropical Africa, and migrates during both day and night. We have data on the Kurishe and Karelian populations and on the birds migrating through the Kurishe Nehrung.

TABLE 1

BODY WEIGHTS AND FAT EQUIVALENTS OF FAT CLASSES ESTIMATED VISUALLY IN CHAFFINCHES

Fat class	Sex	Body weight during migration, g[a]	Increase in each fat class as % of "none"[b]	Extractable fat, mg	
				Alcohol:Ether[c]	Petroleum ether[d]
None	♂	21.00 ± 0.027	0	500 ± 10	800 ± 35
	♀	19.10 ± 0.026	0		
Slight	♂	21.82 ± 0.029	4	900 ± 15	1500 ± 100
	♀	19.86 ± 0.028	4		
Moderate	♂	22.89 ± 0.025	9	1600 ± 28	2500 ± 120
	♀	20.84 ± 0.025	8		
Heavy	♂	24.36 ± 0.029	16	2500 ± 42	4000 ± 200
	♀	21.96 ± 0.027	15		
Very heavy	♂	25.83 ± 0.030	23	6000 ± 57	—
	♀	23.49 ± 0.028	23		

[a] Mean ± SE, $n = 19,000$.
[b] $n = 19,000$.
[c] Mean ± SE, $n = 237$; sexes combined.
[d] Mean ± SE, $n = 21$; sexes combined.

TABLE 2

ARBITRARY STAGES OF MOLT OF PRIMARIES AND SECONDARIES OF CHAFFINCHES AT THE KURISHE
NEHRUNG, BASED ON PERIODIC OBSERVATION CF 62 BANDED WILD BIRDS AND 15 CAGED BIRDS

Molt stage	Number[a] and growth-phase of feathers			
	Old feathers	Pins	Brushes	New feathers
1	2–9, 11–18	10	—	—
2	2–8, 12–18	9	10, 11	—
3	2–7, 12–18	8	9, 10	11
4	2–6, 12–18	7	8, 9	10, 11
5	2–5, 12–17	6	7, 8, 18	9–11
6	2–4, 12–16	5	6, 7, 11, 17	8–11, 18
7	2–3, 14–16	4, 13	5–7, 12, 17	8–11, 18
8	2, 14–16	3	4, 5, 12, 13, 17	6–11, 18
9	2, 5	14	3, 4, 13, 16	5–12, 17, 18
10	—	—	3, 14–16	4–13, 17, 18
11	—	—	2, 15, 16	3–14, 17, 18

[a] Numbered from distal (rudimentary) feather to proximal.

The Great Tit, *Parus major*, of the Baltic region migrates to western Europe as far as England. The young from the first broods do not migrate as far as the young from the second broods. The adult females do not migrate as far as the young, and adult males are often sedentary. The breeding season is very long. Migration occurs in the daytime, with the birds in small flocks. We have data on the populations that breed on the Kurishe Nehrung and on the eastern coast of the Baltic Sea.

RESULTS AND DISCUSSION

PREPARATION FOR AUTUMN MIGRATION

The Chaffinch population of the Kurishe Nehrung (figs. 4, 5, 6). After the completion of breeding at the end of June, the adults begin the postnuptial molt, which is a complete one. The young begin a partial molt in the middle of July. In this period the adults are alone, and the young are in groups of three to five birds. The birds are very cautious, and feed almost entirely on insects. Roving birds, in particular the young but also some adults, move principally to the northeast; from 1 to 10 August when the most intensive molt occurs in the majority of birds, the movement stops. In this period the birds are very shy and difficult to trap.

When the molt nears completion, from the middle to the end of August, the birds move principally to the southwest. When the molt is completed, the birds gather in flocks of 10 to 20 individuals and begin to feed on the seeds of plants. The change in type of food consumed coincides with the beginning of hyperphagia. At the same time those birds that are slow in completing the molt remain in small groups and continue to feed on insects.

Premigratory hyperphagia begins yearly in our Chaffinches near 1 September. This stage is associated under natural conditions with (1) the appearance of flocks containing a few tens of birds, (2) the birds leaving the forests and feeding on the ground in open spaces, (3) a change to a seed diet, (4) feeding throughout the day but especially before sunset, and (5) a 20 to 30 per cent increase in the weight of the intestine and its contents.
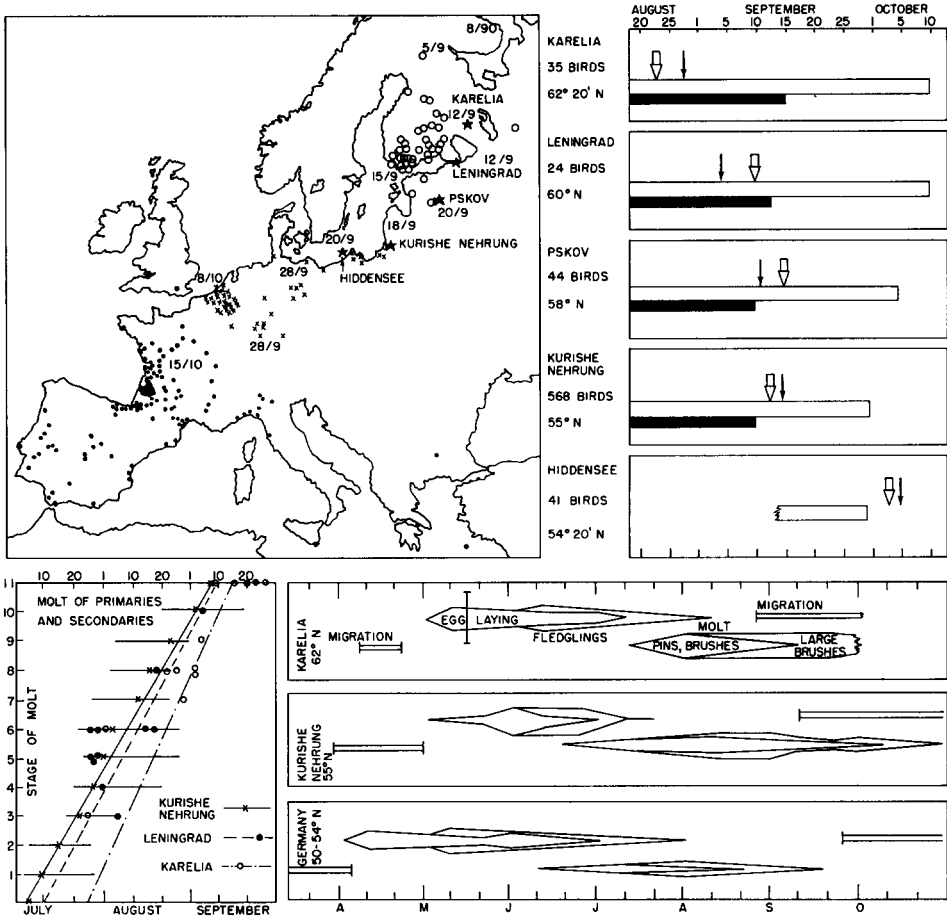
Figure 3. Geographical differences in seasonal cycles of wild Chaffinch populations. At the upper left: Chaffinches banded in the Kurishe Nehrung recaptured in the places of wintering (black circles), on the migration route (crosses), and on the nesting territories (open circles). Recaptures at the Kurishe Nehrung are not shown. The numerals are the dates on which intensive autumnal migration began at the various places. At the upper right: Time of molt (open bar = small body feathers; black bar = primaries and secondaries) and the beginning of fat deposition (open arrow) and migration (black arrow) in adults and immatures at five geographical points in 1962. At the lower right: Time of the vernal and autumnal migrations, breeding, and molt at three places, summarized for 1960–1964. Data include about 101 nests and 60 molting birds in Karelia, 510 nests and 10,000 molting birds in the Kurishe Nehrung. Data for birds in Germany are from Niethammer (1937). At the lower left: Time of primary molt in adults at three geographical points in 1962. Crosses for the Kurishe birds are the averages (with range) from 478 specimens; symbols for other points are the data for individual birds.

When hyperphagia develops, the ratio between fat and carbohydrate metabolism changes and the weight of the liver diminishes because of reduction of the glycogen reserves. Lipogenesis becomes an important function of the liver. This fat is deposited in adipose tissue, and as a result obesity develops. We assume that the intensity of protein metabolism is diminished in this period. This results in the reduction of water content in the organism and is accompanied by the change from food
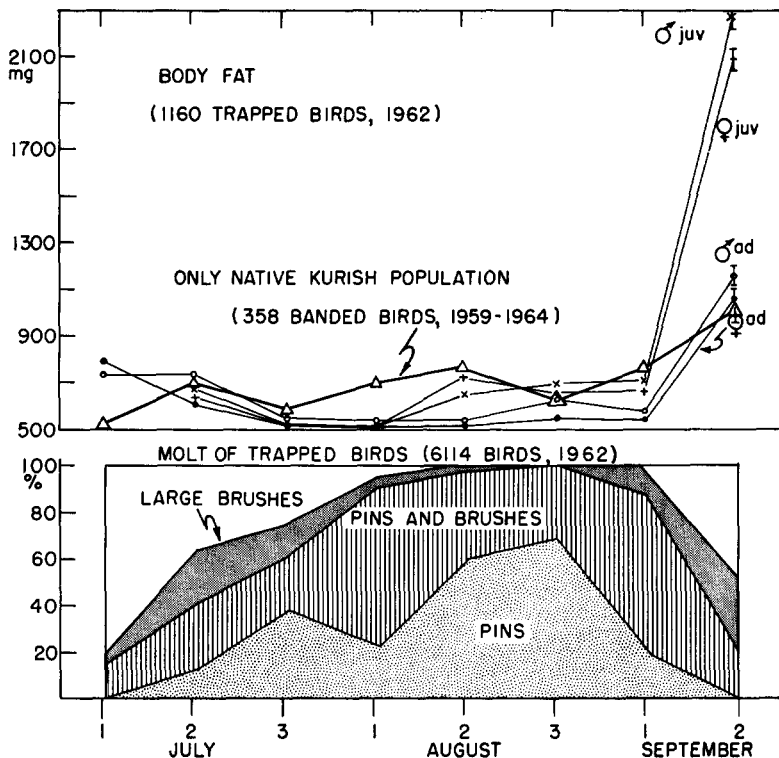
Figure 4. The postnuptial period in wild Chaffinches in the Kurishe Nehrung. Upper panel: Average fat estimated by the visual method. Lower panel: Percentage of birds in each of three molt stages (includes all birds trapped in 1962).

rich in proteins (insects) to food poor in proteins (seeds). Seeds are more readily available to migratory birds at this time of the year.

The local population departs from the Kurishe Nehrung by 15 September, before completing the premigratory period. The first flocks of Chaffinches that have finished the molt and are very fat come to the Nehrung by 5 September, and on about 14 or 15 September the mass migration of these birds begins. From 20 September, Chaffinches from Karelia and Finland migrate through the Kurishe Nehrung.

THE LATITUDINAL GEOGRAPHIC DIFFERENCES

The dates of breeding, molt, and autumnal migration in some populations of Chaffinches have been compared elsewhere (Blyumental, Dolnik et al. 1963, 1966; Blyumental and Dolnik, 1966). These are summarized in figure 3. The populations breeding in Karelia and in the Kurishe Nehrung begin and finish the spring migration during April. The flight of the northern birds, however, covers twice the distance of the southern birds. Breeding at the northern locality begins and ends scarcely later than at the southern locality. The autumn migration begins a half-month earlier, however, in Karelia than in the Kurishe Nehrung. The time available for the postnuptial molt is significantly shorter, therefore, for the northern population and may be considered an adaptation to permit an earlier migration.
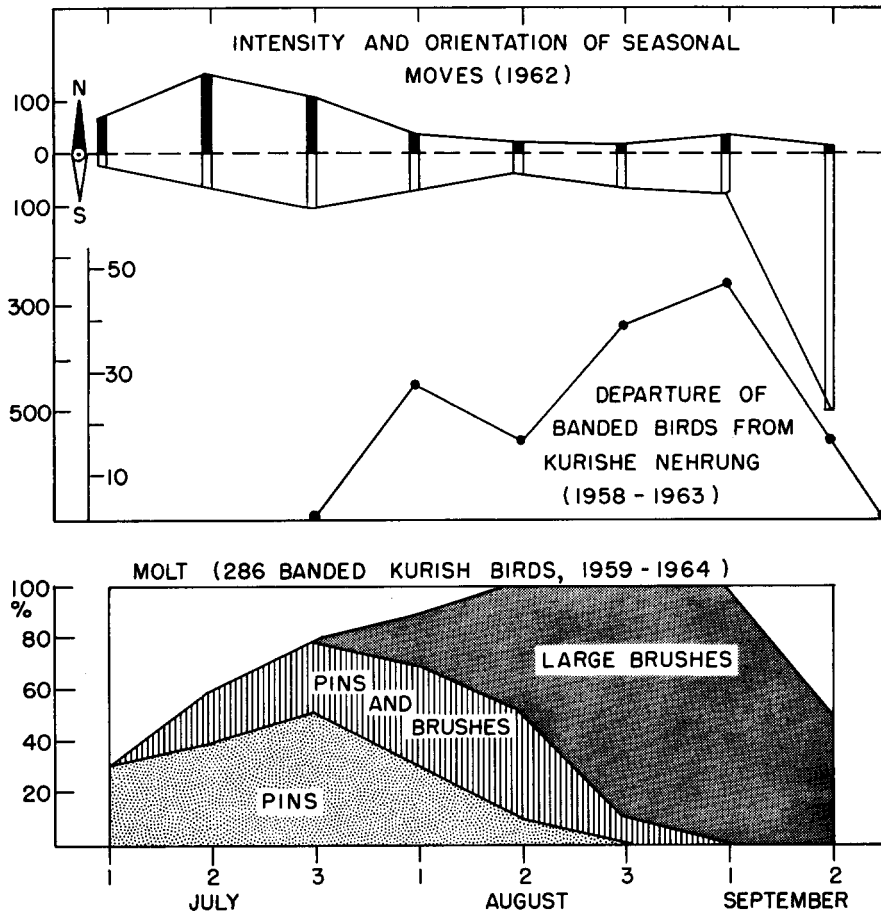
Figure 5. Postnuptial period in wild Chaffinches at the Kurishe Nehrung. Upper panel: Numbers of birds trapped in northward movement (trap N1, fig. 1) and in southward movement (trap N3), and number of last recoveries of local breeding birds, banded during the nesting season (inner scale at the left). Lower panel: Percentage of local, banded birds in each of three molt stages. Local birds leave their territories before fat deposition or at its beginning and are replaced by other birds during the premigratory period.

In Karelia the molt begins later than in the Kurishe Nehrung. But in the Nehrung the young Chaffinches begin to molt 20 to 30 days after completion of the growth of juvenal plumage. The formation of pin feathers is completed at about the same time in the north and in the south. The more rapid progression of the molt in the north, however, is the result of (1) the feathers of the various pterylae beginning to molt more nearly simultaneously, (2) more nearly simultaneous molt of feathers within each tract, and (3) more nearly simultaneous molt among individual birds in the northern populations. In Karelia three-fourths of the birds may be in the first stage of molt simultaneously, while in the Kurishe Nehrung only one-fourth are in this stage.

Some speculations can be offered to explain the adaptive significance of latitudinal differences in molt in different populations. In the north the summer is shorter
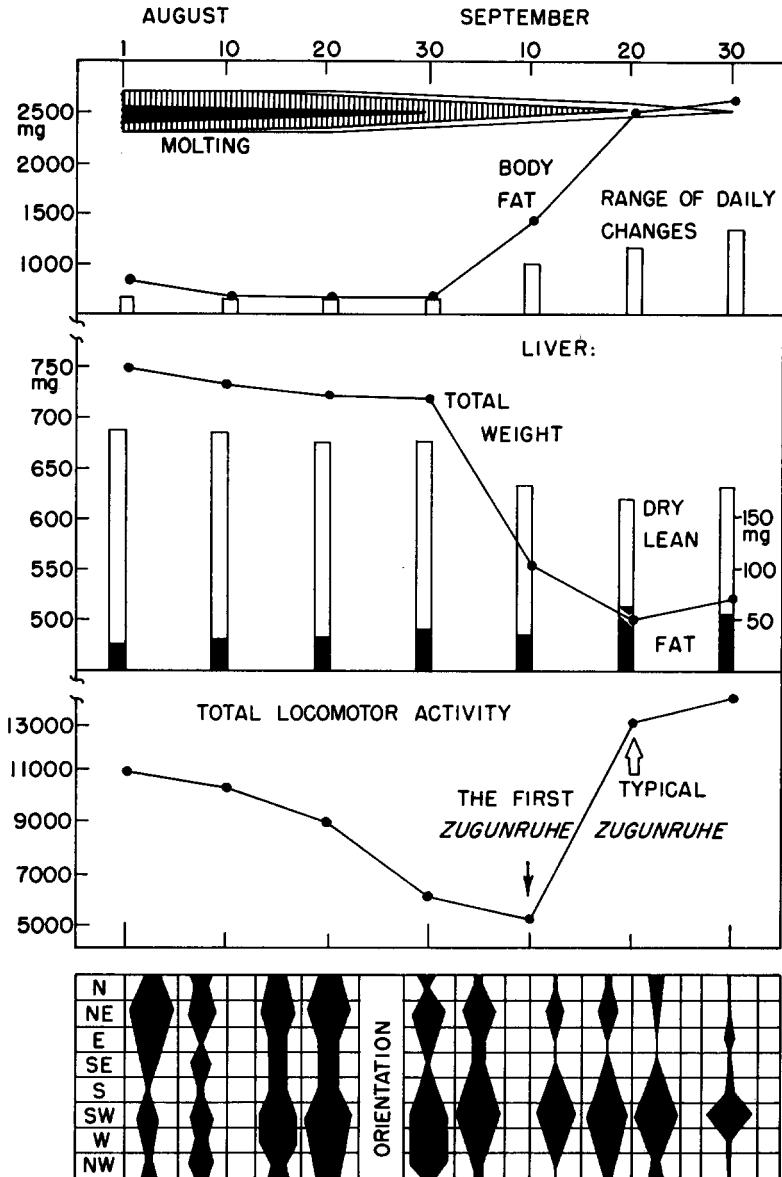
Figure 6. Postnuptial period in caged young Chaffinches in outdoor conditions at the Kurishe Nehrung. Numbers of birds: molt and average fat, by the visual method, 182; liver weight and composition, 109; locomotor activity, 687 bird-days (1962); orientation in round cages, 120 bird-days (1963–1965).

and the number of bird species, probably, is smaller, and the competition among species is less severe and simpler. The best feeding conditions and the longer feeding days occur during the molt period (Pitelka, 1958); but in the Temperate Zone the best conditions occur during the breeding period (Lack, 1954). This, perhaps, per-
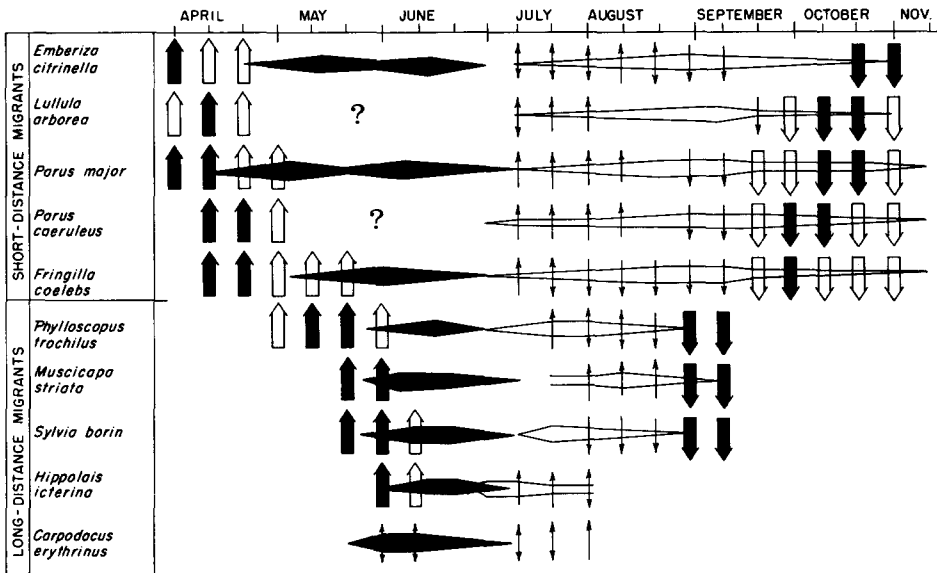
Figure 7. Time of breeding (black polygons), molt (open polygons), vernal and autumnal migration (wide arrows: black = intensive migration, open = weak migration), and prevailing direction of summer movement (thin arrows) at the Kurishe Nehrung, 1959–1964. Data derived from examination of 140,000 birds caught in traps directed to the north and to the south.

mits more nearly simultaneous and intensive molt in the northern regions, although the favorable period is short and the completion of molt is impossible there.

In the north the migratory state sets in during the time of molt, while in the Kurishe Nehrung and in western Europe the birds preparing to migrate have completed their molt or are in the last stages of it. Relations similar to these exist in northern and southern populations of Great Tits and Yellow Warblers (Blyumental and Dolnik, 1966; Blyumental, Dolnik *et al.*, 1966).

Differences among species. In the Kurishe Nehrung about 140,000 birds of eight species were caught from 1960 to 1964, inclusive, in the two traps facing to the north

TABLE 3

DIFFERENCES IN THE DATES OF EVENTS OF THE POSTBREEDING PERIOD IN IMMATURE BIRDS AT THE KURISHE NEHRUNG, BASED ON ABOUT 7000 TRAPPED WILD SPECIMENS

Species	First flying of fledglings[a]	Start of molt	End of molt stage 6	Completion of molt
Phylloscopus trochilus	—	35[b]	30[b]	30[b]
		Jl(1)–A(1)[c]	Jl(3)–A(2)[c]	A(1)–A(3)[c]
Fringilla coelebs	50	45	30	25
	Jn(1)–Jl(2)	Jn(1)–A(1)	A(1)–A(3)	S(1)–S(3)
Parus major	70	55	40	25
	Jn(1)–A(1)	Jl(2)–A(3)	A(3)–S(3)	O(1)–O(3)

[a] Data based on ca. 300 immatures banded in the nest.
[b] Individual difference in days.
[c] Code designates (in parentheses) the first, second, or third 10-day period in June (Jn), July (Jl), August (A), September (S), or October (O).
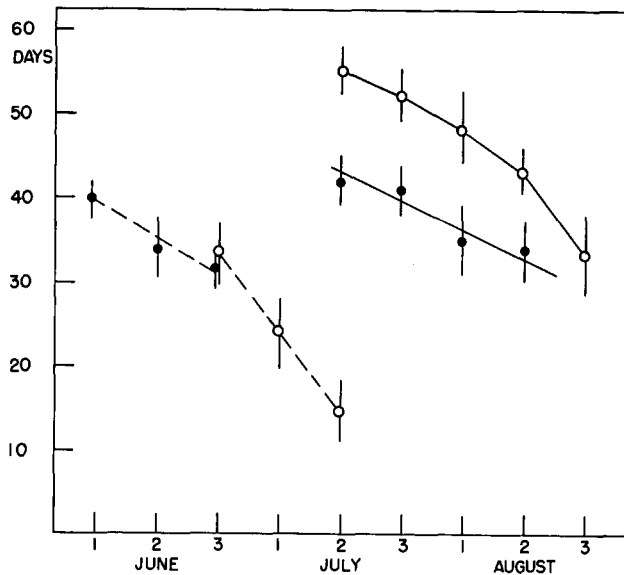
Figure 8. Decrease of molt duration (ordinate) in relation to date in young Chaffinches (black circles, 123 birds) and Great Tits (open circles, 48 birds) banded and recovered in the Kurishe Nehrung in 1960–1963. The abcissa shows the dates on which the birds were first examined. The broken line indicates the period from abandonment of the nest to the beginning of molt; the unbroken line indicates the period from the beginning to the end of molt.

and to the south. All of the birds were banded. In about 80,000 of these the reproductive condition, stage of molt, fat reserves, and body weight were recorded. About 1600 were recaptured and examined again. A comparison of seasonal cycles in these species is shown in figure 7.

During the period of the molt the newly arrived long-distance migrants (*Phylloscopus trochilus, Sylvia borin, Muscicapa striata*) are caught to an equal degree in the north-facing and south-facing traps. The beginning of true migration is characterized by an abrupt increase in the intensity of bird movement and by the assumption of an exclusively southern direction. The beginning of the migratory movement in these species is also marked by the completion of the molt and the storage of great reserves of body fat.

In the short-range migrants (*Fringilla coelebs, Emberiza citrinella, Lullula arborea, Parus major, Parus caeruleus*) that arrive early and depart late and which end their breeding significantly earlier than do long-distance migrants, the northern direction of movement prevails in early July. At the time of greatest intensity of molt, directional movement in these species becomes essentially random. Then, during waning of molt the southern direction predominates. The beginning of southward migration in these species is also characterized by an abrupt increase in the intensity of movement and by the occurrence of fat birds.

The short-range migrants molt over a longer period but with lesser intensity than the long-range migrants. They do not begin deposition of fat and autumnal migration until the molt is ended. The predominance of northern direction in early-summer movements of these species, possibly, reflects some inequality in bird distribution in this period. For example, it may be an adaptation to using some increasing natural re-
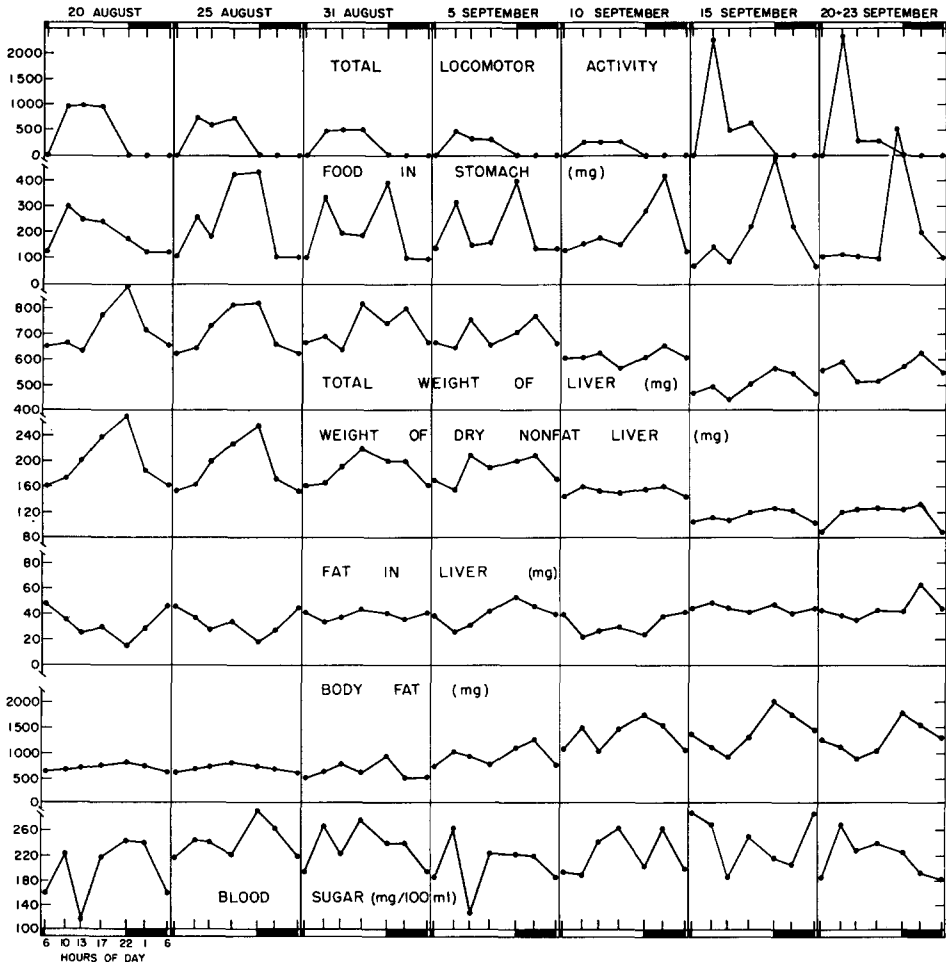
Figure 9. Diurnal variations in activity and metabolic indexes in caged young Chaffinches in outdoor conditions in the Kurishe Nehrung during the autumnal premigratory period. Each point is the mean value for three birds except in the case of locomotor activity and visible body fat, where each point is the mean value for 20 birds. Dates are representative of the termination of molt (20 to 30 August), the period of premigratory fat deposition (5 to 15 September), and the beginning of the migratory period (20 and 23 September) in 1962. Black and open bars on the abcissa represent the periods of darkness and light, respectively.

source in the north in early summer when local birds are already distributed on nesting territories, but the number of local birds has not yet begun to increase because of the later start of breeding in the north compared with the south.

The synchronization of the individual cycles in the population during the premigratory period. In the breeding period there is an inevitable desynchronization of individual annual cycles (Newton, 1966) because of inequality of food, weather, nesting conditions, nest destruction and renesting, age differences in nesting success, and so on. This desynchronization mostly disappears during the autumnal premigratory period (Blyumental and Dolnik, 1966; Blyumental, Vilks, and Gaginskaya, 1966).

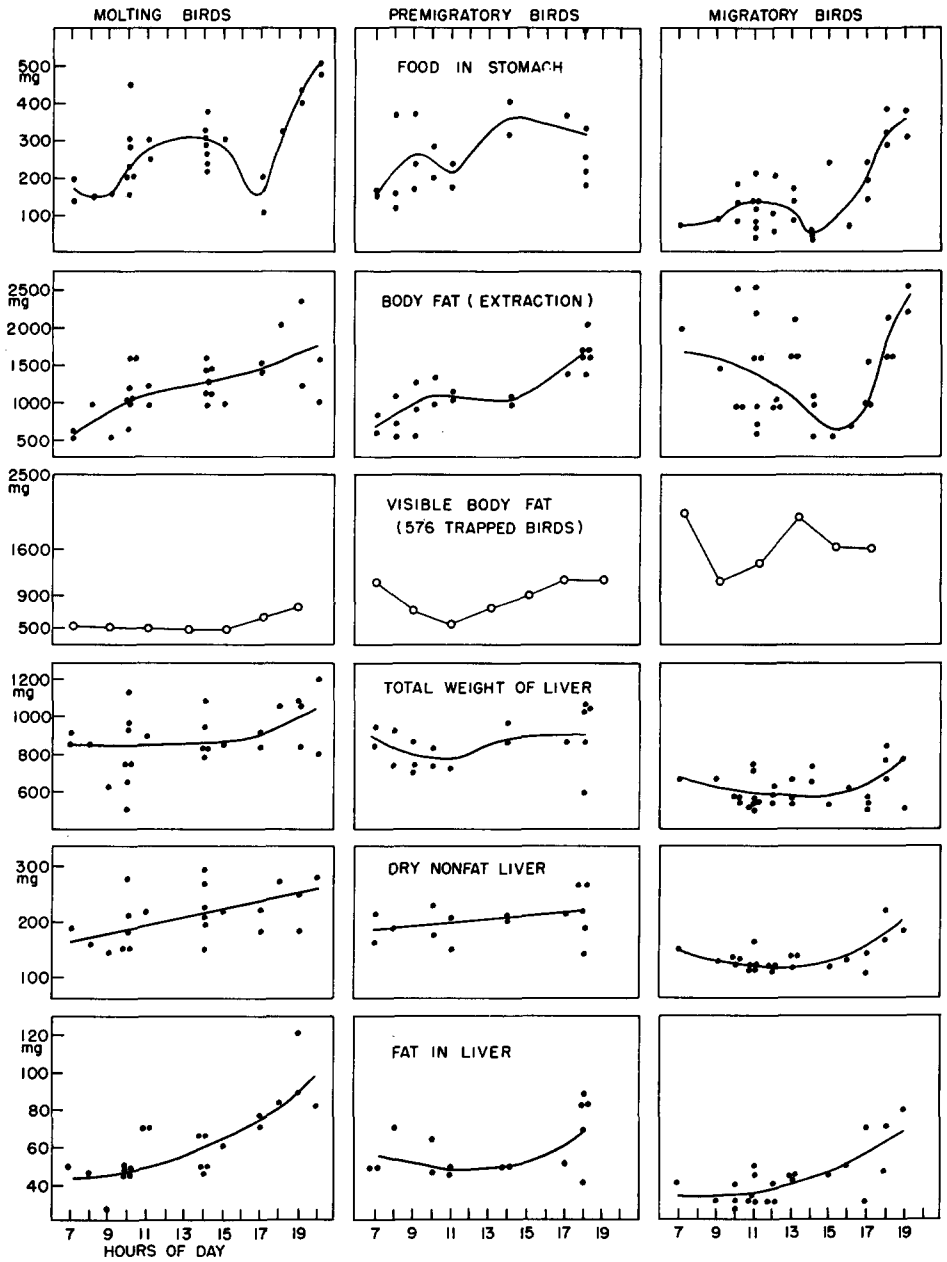Figure 10. Diurnal variation in metabolic indexes in wild Chaffinches (mainly immatures) shot in autumn at the Kurishe Nehrung. Each point represents one bird; the lines are fitted by eye. Molting birds were collected from 25 August to 4 September; premigratory birds (molt completed), from 25 August to 4 September; and migrating birds, from 4 September to 3 October.

Resynchronization of the cycles becomes apparent in the timing of the postjuvenal molt, which begins in the last broods of the season at a lower age than it does in birds of the earlier broods. Moreover, the duration of molt becomes progressively less with the advance of the season. These variations tend to make the late-summer molt simultaneous in most of the individuals of a population (fig. 8).

The great amount of individual variation in the timing of seasonal cycles which occurs at the beginning of autumn migration reflects the genetic structure of populations. This variation is of biological importance in the first place in distributing the nesting through the whole period of favorable conditions which is, generally, more continuous than the duration of the breeding cycle in any individual bird. In the second place, reproduction in only part of the population will be affected if weather or other conditions become unfavorable. Moreover, for some individuals with a different genetic composition, the new conditions may actually be optimal. This varied composition gives greater stability to the population and greater plasticity in an evolutionary sense. In particular, it provides an opportunity for the population to spread into a greater variety of continental and mountainous regions without readjusting the physiology of each bird (for details, see Farner, 1964a; Blyumental and Zimin, 1966).

THE AUTUMNAL PREMIGRATORY PERIOD

Let us consider the circadian rhythms of metabolism and behavior directly in relation to the autumnal premigratory period (Blyumental, 1962; Dolnik, Blyumental et al., 1963, 1966; Dolnik, 1965a, 1966a, b).

The Chaffinches of the Kurishe Nehrung. During the day a sample of three birds was taken at each of six times: just before sunrise (about 0600); at 0900—the time of the most intensive migration of the chaffinches; at 1300—the time of day when there is a pause in activity; at 1700—the time of the most active evening feeding; at about 2200—just after sunset; and at 0100.

The change from predominately carbohydrate metabolism to fat metabolism is well shown in figure 9. We regard the variation of nonfat dry weight of the liver as an approximate index of variation in glycogen content. During August there are large daily fluctuations in the weight of the dry nonfat liver but very little in body fat. During September daily fluctuations in liver glycogen decrease while fluctuations in body fat progressively increase. Before reduction of liver weight there was a decrease of amplitude in circadian rhythms of glycogen reserves in liver. It appears that during the early part of the season, in the molt period, carbohydrates furnish the chief source of energy. In the migratory period fat serves this role. The same picture in wild Chaffinches is shown in figure 10.

During the premigratory period there are changes in additional physiological circadian rhythms. In the molt period diurnal rhythms of total activity, feeding, weight of fresh liver, dry nonfat liver, body fat, and level of sugar in blood are correlated positively. In the migratory period diurnal rhythms of the total activity and level of sugar in blood are correlated negatively with rhythms of feeding activity, weight of liver, and body fat. These alterations appear to be a result of the onset of antagonism between lipogenesis and glycogenesis. Probably the hyperphagia of the migratory period is strengthened in Chaffinches as a result of these changes in intermediary metabolism. An instability of blood-sugar level occurs, perhaps as a result of the reduction of carbohydrate reserves and their participation in metabolism. Merkel (1958, 1960) pointed out the lability of metabolism in the migratory period, but could not explain it.
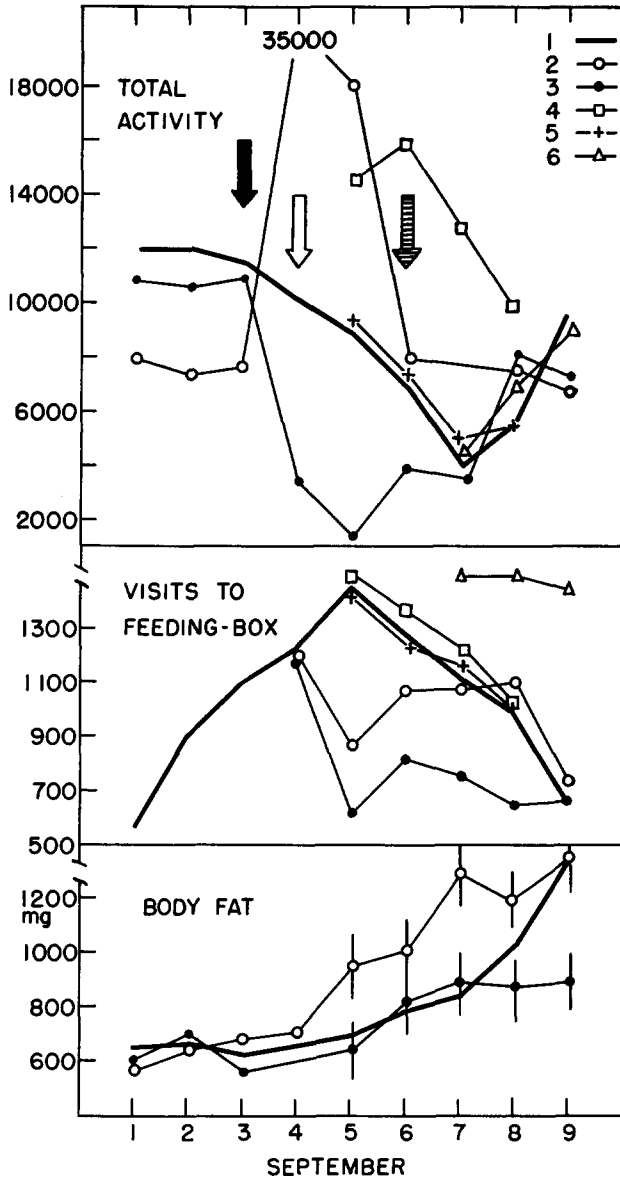
Figure 11. Experimental influences on 35 caged young Chaffinches during the premigratory period in 1963. Treatments (symbols at upper right): 1. Control birds; 2. 1 ml (25 mg) hydrocortisone by intramuscular injection, 3 September; 3. 1 I.U. protamine-zinc insulin by intramuscular injection, 3 September; 4. 0.08 mg methyl phenidyl hydrochloride (Ritalin) fed to each bird, 4 September; 5. 0.08 mg reserpine fed to each bird, 4 September; 6. 0.8 ml of plant oil is injected into subcutaneous adipose tissue of each bird, 6 September. Arrows show the dates of administration.

TABLE 4

SOME METABOLIC INDEXES IN VARIOUS SPECIES IN RELATION TO SEASON

Species	Place of investigation	Season	Body fat[c] mg		Liver fat[c] mg		Wt. of dry nonfat liver[c] mg		Blood sugar[c] mg/100 ml	
			Mean	Δ	Mean	Δ	Mean	Δ	Mean	Δ
Fringilla coelebs	Kurishe Nehrung[a]	Autumn migration	1500	585	53	15	122	28	218	86
		Winter	2070	1380	64	77	184	73	213	54
		Spring migration	1700	700	40	37	134	30	184	95
		Molt	500	200	34	14	191	72	230	58
	Karelia[b]	Molt and start of autumn migration	900	900	50	40	200	79	—	—
	Kurishe Nehrung[b]	Molt	780	200	50	30	210	75	—	—
		Autumn migration	1400	800	40	85	140	40	—	—
Spinus spinus	Kurishe Nehrung[a]	Molt	1700	200	32	20	100	50	128	65
		Autumn migration	2000	500	25	10	90	35	260	90
		Summer migration ("Zwischenzug")	2100	500	26	17	92	47	100	80
Passer d. domesticus (sedentary race)	Kurishe Nehrung[b]	Autumn	900	250	75	50	350	300	—	—
		Winter	900	250	80	65	410	300	—	—
Passer d. bactrianus (migratory race)	Tadjikistan[b] (Middle Asia)	End of molt	1030	1500	30	—	120	—	—	—
		Autumn migration	3800	4000	85	—	100	—	—	—
Passer m. montanus	Kurishe Nehrung[a]	Autumn	1700	700	112	100	308	220	—	—
		Winter	1000	250	110	100	319	225	—	—
Sturnus vulgaris	Kurishe Nehrung[a]	Molt	4000	1300	100	73	960	367	230	25
		Autumn migration	2300	1700	136	110	700	267	205	105
Erithacus rubecula	Kurishe Nehrung[a]	Molt	900	200	80	70	160	110	200	150
		Autumn migration	900	700	80	40	145	10	290	100
Sylvia borin	Kurishe Nehrung[a]	Molt	1600	200	55	25	175	40	70	130
		Autumn migration	2100	450	100	100	175	60	240	100
Phylloscopus trochilus	Karelia[b]	Molt	410	200	18	20	120	40	—	—
		Autumn migration	450	500	25	25	125	50	—	—
	Kurishe Nehrung[b]	Molt	250	130	10	10	75	10	—	—
		Autumn migration	550	500	20	25	85	50	—	—

[a] Caged birds in outdoor conditions; 18 birds in each season.
[b] 20 to 30 wild specimens in each season.
[c] Mean daily level and amplitude (Δ) of daily changes.

The geographical differences. We compared the metabolism and behavior of Chaffinches and Yellow Warblers in the premigratory period at the Kurishe Nehrung and in Karelia (Blyumental, 1965, 1966). In the latter place this period coincides with the molt. In this time body weight and the fat reserves in northern birds are higher than in southern ones at the same stage of molting. But this fat is not analogous, functionally, to migratory obesity and apparently serves as a compensation for the large nocturnal expenditures of energy for thermoregulation resulting from the great daily changes in air temperature and the great intensity of molting. In this connection, in northern birds fat is deposited not only on the apteria, as in Kurishe birds, but also on the pterylae. The latter does not become reduced during the night.

In the north the typical migratory deposition, obviously, was not observed. The birds depart from their breeding territories without large fat reserves and, apparently,

migrate with low intensity. This agrees with the data of Odum (1960a). The types of circadian rhythms of metabolism and behavior in northern birds are intermediate in relation to those of molting and migrating birds in the south.

Experimental investigation of the autumnal premigratory period in Chaffinches. We tried to influence hyperphagia, fat deposition, and development of migratory behavior in the young Chaffinches at the Kurishe Nehrung (fig. 11). The injection of small doses of insulin depressed locomotor activity, and small doses of hydrocortisone increased it abruptly. The activity rhythm became similar to that of migratory birds. These substances did not significantly influence fat deposition and feeding. Reserpin and Ritalin exerted, respectively, strong depressing and exciting influences on the activity of the animals, but not as strongly as the hormones. During the premigratory period the bird's activity was not changed by the experimental injection of fat into the fat depot.

It seems that these data support the theory of independent origin and regulation of fat deposition and migratory behavior (King and Farner, 1963; Lofts, Marshall, and Wolfson, 1963; Dolnik, 1963, 1965b, 1966b). The inability of the process of fat deposition to respond directly to hormones and metabolically active substances, apparently, supports the supposition that the sequence of steps is more likely the following: hypothalamus → feeding center → hyperphagia → changes in intermediary metabolism and fat deposition, rather than that of another scheme: hypothalamus → changes in intermediary metabolism → hyperphagia and fat deposition.

Special metabolism of the migratory period. It is generally known that migration is almost always accompanied by fat deposition (see reviews by Farner, 1955, 1960; Blyumental, 1961; Dolnik and Blyumental, 1964). We compared the metabolism in some species of birds during the migratory period with that of other seasons and that of sedentary species (Blyumental, 1965, 1966c; Dolnik, 1965, 1966a; Dolnik, Dobrynina, and Blyumental, 1965; table 4; compare with Farner *et al.*, 1961; Zimmerman, 1965).

In migratory species during both spring and autumn migration carbohydrate metabolism is depressed or relatively less expressed, and fat metabolism predominates. This picture prevails both in species migrating with large fat reserves (*F. coelebs, Ph. trochilus, S. borin, Spinus spinus, Passer d. bactrianus*) and in species which lack great fat reserves during the migration (*Erithacus rubecula, Sturnus vulgaris*). The latter situation occurs also both in the Chaffinches and Yellow Warblers at the north where the molt coincides with the migration and in the *S. spinus* during the summer migration. The intensification of fat metabolism becomes apparent either in increasing daily amplitude of the body-fat or liver-fat cycle or in increase of the level of liver-fat reserves. Metabolism in migratory birds in the nonmigratory periods and autumnal metabolism in sedentary species do not show such a picture. In these instances carbohydrate and fat metabolism are equally active (winter obesity in *F. coelebs, Passer d. domesticus, Passer montanus*; autumnal state in *P. d. domesticus, P. montanus*) or carbohydrate metabolism predominates (in molting of all the species). In the northern birds in which molt coincides with migration, the intensification of fat metabolism is not so great. In these birds we do not find such intensive migration and such fat birds as in the temperate latitudes. Moreover, the completion of molt is slow in northern birds (fig. 3). This demonstrates the metabolic foundation of the antagonism between molt and migration and the adaptive significance of the temporary separation of these processes; their coincidence retards both processes.

So it seems that the principal metabolic peculiarity of the migratory period is the

relaxation of carbohydrate and the intensification of fat metabolism. Probably, this is not the only bioenergetic adaptation to migration, but is one of the important physiological bases of it.

THE MIGRATORY PERIOD

We summarize here the results of our work on the role of body fat depots and changes in intermediary metabolism in the regulation of *Zugunruhe* and migration (Blyumental, 1961, 1963, 1966a; Blyumental and Dolnik, 1962, 1963; Dolnik, 1963, 1965a, 1966a, b; Dolnik and Blyumental, 1964).

The changes of fat reserves in birds at the time of migration at the Kurishe Nehrung. Data on the obesity in some species of wild birds are shown in table 5. The larger reserves are in long-distance migrants, especially in those crossing wide ecological barriers (Mediterranean Sea and Sahara Desert). The weight equivalents of visual fat classes also show greater obesity in long-distance migrants as well. In general, in our birds the autumnal obesity is greater than the vernal (see for com-

TABLE 5

BODY FAT IN SOME SPECIES CAPTURED DURING AUTUMN MIGRATION AT THE KURISHE NEHRUNG, 1960–1964[a]

Species	N	Mean wt. of lean birds[b] g	Difference (%) in weight between lean and fat birds				Per cent of specimens in each fat class			
			Slight	Moderate	Heavy	Very heavy	None	Slight	Moderate	Very heavy
Sylvia borin	1262	17.5	3	8	16.5	26	21	24	24	31
Phylloscopus trochilus	1866	8.1	4	9	18	22	23	35	26	16
Muscicapa striata	1000	14.3	4	11	18	22	20	34	35	12
Fringilla coelebs ♂	8020	21.0	4	9	16	23⎱	16	20	28	36
♀	10,880	19.1	4	8	15	23⎰				
Carpodacus erythrinus ♂⎱ ♀⎰	189	20.9⎱ 20.0⎰	3	9	15	—	77	18	4	1
Hippolais icterina	1135	12.9	4	7	15	—	52	33	9	—
Anthus pratensis	2370	16.0	2.5	7.5	14	—	41	34	19	6
Pyrrhula pyrrhula ♂⎱ ♀⎰	522	29.0⎱ 28.1⎰	4	7	14	—	10	36	42	12
Aegithalos caudatus	204	8.65	3.5	6	13	—	35	54	10	1
Chloris chloris ♂⎱ ♀⎰	828	26.4⎱ 26.2⎰	6.6	8	12	—	8	30	40	22
Lullula arborea	801	26.7	2	7	10.5	—	20	29	31	20
Parus major ♂⎱ ♀⎰	4371	17.3⎱ 16.3⎰	3	6	10	—	31	41	24	4
Parus coeruleus	868	10.7	2	4	6	—	38	41	18	3
Acanthis flammea ♂⎱ ♀⎰	394	13.0⎱ 12.2⎰	2	3	6	—	37	37	18	8
Emberiza citrinella ♂⎱ ♀⎰	427	28.4⎱ 27.5⎰	1	3	5	—	54	24	18	4

[a] Species are listed in order from long-distance migrants to nonmigrants, at the bottom.
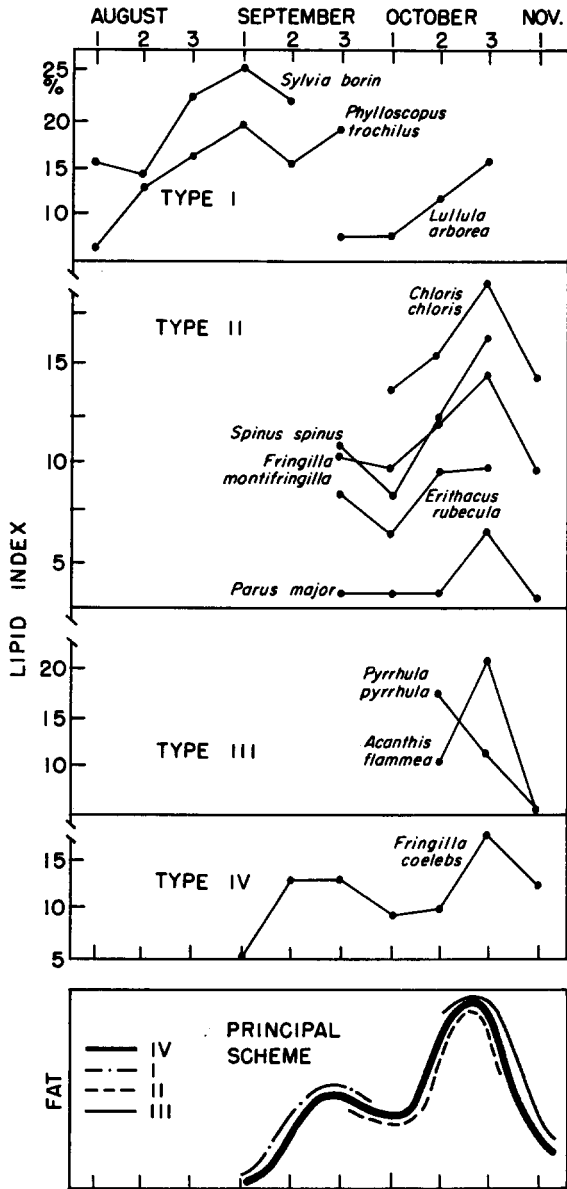[b] Fat-class "none."

Figure 12. Types of change in the average level of body fat in relation to the place of capture on the migratory route, based on wild birds taken at the Kurishe Nehrung during autumn migration. Type I, near the start of the migration route; type II, near the middle of the route; type III, near the end of the route. In Chaffinches (type IV), the Kurishe Nehrung is at the start of the migration route for local breeding populations, near its middle for birds breeding in northern Europe, and at its end for birds arriving late in migration to winter near the Nehrung. Type IV, therefore, is a composite pattern, combining the characteristics of the other types.

TABLE 6

ENERGY EXPENDITURE OF MIGRATORY FLIGHT IN THREE SPECIES, BASED ON DIFFERENCES IN BODY
WEIGHT AND CALORIC DENSITY OF WEIGHT LOSS BETWEEN BIRDS TRAPPED AT "NERINGA" AND
"FRINGILLA" (SEE FIG. 1) DURING INTENSIVE AUTUMN MIGRATION IN 1962 AND 1963

Species	No. of days	No. of birds	Mean body wt., g	Mean flight speed, m/sec[a]	Mean weight loss (± SE), g	Mean energy loss, kcal/hr[b]	Rate of energy loss divided by rate of: Standard metabolism	Resting metabolism	Existence energy	Distance between breeding and wintering areas, km[c]	Energy required for migration, kcal	Mean energy reserve in migration period, kcal
Fringilla coelebs	17	5352	22.00	14.5	0.72 ± 0.15	4.58	15.8	7.9	5.2	2500	230	15.2
F. montifringilla	4	414	23.25	16.0	0.69 ± 0.060	4.35	14.5	7.3	4.9	3000	226	12.4
Spinus spinus	3	517	12.46	15.0	0.40 ± 0.041	2.52	13.0	6.6	4.4	2000	93	14.8

[a] Based on visual estimates.
[b] According to data from laboratory experiments, statistical estimates based on data in table 1, and a comparison of
body weight and fat loss between birds trapped at "Neringa" and "Fringilla," the caloric density of weight loss is
6.28 ± 0.57 kcal/g.
[c] Based on banding data from the Kurishe Nehrung (*F. coelebs*, 301 recoveries; *F. montifringilla*, 63 recoveries; and
Spinus spinus, 160 recoveries).

parison, King *et al.*, 1963, 1965). It seems this is connected with the location of the
investigation site in relation to that of breeding and wintering regions (fig. 12).

The energy of migratory flight. Estimations of the energy required in migratory
flight published in the last few years (Pearson, 1950, 1954; Odum, Connell, and
Stoddard, 1961; Lasiewski, 1962, 1963; Lord, 1962; Nisbet, Drury, and Baird, 1963;
Dolnik, Gavrilov, and Eserskas, 1963; Dolnik and Blyumental, 1964; LeFebvre,
1964) confirms the supposition of Brody (1945) that the energy expenditure of mod-
erate muscular work is 2–4 times existence energy or 4–8 times resting metabolism.
In the autumn of 1963 we determined flight-energy requirements in three species. The
average fat classes and weights of large groups of birds trapped during the migratory
flight at "Neringa" and at "Fringilla" (see fig. 1) were compared. These localities
are separated by about 50 km, and the differences observed enable us to estimate the
energy expended in flying this distance (table 6).

TABLE 7

CHANGES OF BODY WEIGHT AND DURATION OF STOP-OVER AT THE KURISHE NEHRUNG, BASED
ON REPEATED OBSERVATIONS OF BANDED BIRDS DURING AUTUMN, 1960-1964

Species	Fat class at first capture	No. of birds	Change of body weight at time of second capture, g	Duration of stop-over, days
Parus major	None	8	0.0	2.3
	Slight	9	0.0	2.2
	Moderate and heavy	4	−0.3	1.2
Parus ater	None	3	+0.6 ⎫	
	Slight	9	−0.1 ⎬	1.7
	Moderate and heavy	7	−0.1	1.1
Fringilla coelebs	None	13	−0.2 ⎫	
	Slight	7	−0.5 ⎬	1.2
	Moderate and heavy	10	−1.1	1.1

TABLE 8

SPEED OF MOVEMENT AND CHANGES OF BODY WEIGHT IN BIRDS CAPTURED AT TWO STATIONS
IN THE KURISHE NEHRUNG DURING AUTUMN MIGRATION

Species	Route (See fig. 1)	Fat class at first capture	Number of birds												Mean change in body wt. g	Mean elapsed days
				Days between 1st and 2nd capture							Changes of body weight				
			Total	0	1	2	3	4	5	6	Loss	None	Gain		
Parus major	Neringa-	None	8	0	1	2	1	1	1	2	1	1	6	+0.8	3.6
	Fringilla	Slight	6	0	2	1	2	0	0	1	2	0	3	+0.5	2.7
		Moderate and heavy	1	0	1	0	0	0	0	0	1	0	0	−0.5	1.0
Parus ater	Neringa-	None	21	0	4	8	5	0	3	1	1	3	15	+0.4	2.7
	Fringilla	Slight	40	2	21	7	6	2	2	0	12	4	19	+0.2	1.7
		Moderate and heavy	11	5	1	2	2	1	0	0	7	2	1	−0.2	1.4
Fringilla	Neringa-	Slight	3	0	2	1	0	0	0	0	3	0	0	−2.4	1.3
coelebs	Fringilla	Moderate and heavy	4	0	2	2	0	0	0	0	4	0	0	−3.4	1.0
	Rybachy-	None	2	0	0	2	0	0	0	0	1	0	1	−0.3	2.0
	Fringilla	Slight	3	0	2	1	0	0	0	0	3	0	0	−1.3	1.4
		Moderate and heavy	3	1	2	0	0	0	0	0	2	1	0	−1.5	0.6

Replenishing of fat reserves during the fall migration. The Kurishe Nehrung is not a very favorable place for the replenishing of fat reserves in wild birds during the migratory period. However, data are available on the rate of deposition and changes of fat in 177 banded birds, recaptured by the traps (tables 7 and 8). About 70 per cent of these recaptures were lean birds. The duration of the migratory pause is greater in lean than in fat birds, varying from two to four days. During the stop, lean birds are generally depositing fat and fat birds are losing fat (Stresemann, 1944a, b; Helms and Drury, 1960; King, 1961). Lean birds deposit up to 0.5–1.0 g per day (compare with data in Stack and Harned, 1944; Borror, 1948; Zimmerman, 1952; Wolfson, 1954b; Szulc-Olech, 1965; Mascher, 1966).

Relation between obesity and migration. In the Kurishe Nehrung there is a correlation between the level of fat reserves of birds and their migration (tables 9 and 10). The data on the speed of banded birds do not indicate the real speed of migration because of the interruptions due to trapping, but it seems that the comparisons shown may have some significance. The Great Tits move slowly, feed, and raise their weight during migration in the beginning of migratory period when their average obesity is not so great. But in the second part of this period when many birds have a moderate quantity of fat, the speed of their moving increases and their energy balance becomes negative.

Fat reserves and Zugunruhe. The data on the registration of activity in cages confirm the relation between the level of fat and migratory unrest (figs. 13, 14). The experiments show that the decrease in feeding under limited diet and the diminishing of bird weight and obesity suppress nocturnal unrest. This also occurs in caged birds feeding freely when their obesity is diminishing (fig. 15).

The injection of fat into lean birds during migration. As shown above, the presence of fat reserves during migration is correlated with migratory restlessness. The injection of fat extracted from plant and animal oils or from the body of birds into the subcutaneous depots of living birds is harmless, and the fat is utilized in the same

TABLE 9

CORRELATION BETWEEN INTENSITY OF VISIBLE MIGRATION AND DAILY MEAN BODY FAT
IN SOME SPECIES CAPTURED DURING MIGRATION

Species	Dates of migration	No. of birds	Correlation ($r \pm$ SE) between mean fat reserves and intensity of migration
Fringilla coelebs	21 Sept–9 Oct 59	317	0.82 ± 0.102
	9 Oct–29 Oct 59	325	0.78 ± 0.139
	13–18 Sept 60	1023	0.82 ± 0.134
	29 Sept–14 Oct 60	1217	0.66 ± 0.188
F. montifringilla	9–16 Oct 60	295	0.81 ± 0.153
Chloris chloris	9–29 Oct 59	75	0.95 ± 0.039
Acanthis flammea	9–29 Oct 59	500	0.82 ± 0.013
Parus coeruleus	9–29 Oct 59	40	1.00
Parus ater	9–29 Oct 59	63	0.79 ± 0.181
Aegithalos caudatus	9–29 Oct 59	90	0.93 ± 0.041

manner as the bird's own fat (Dolnik, 1963, 1966a, b). We suppose that the fat influences the migratory behavior by causing changes in intermediary metabolism.

Metabolism at various levels of obesity. The differences in daily rhythms of activity, feeding, weight of liver, liver fat and glycogen, and sugar in blood show the more active fat and weak carbohydrate metabolism in fat birds (fig. 14, table 10). These differences in metabolism may be the cause of different migratory activity of lean and fat birds. During the migratory period the injection of fat into lean birds increases their activity to resemble that in fat birds, but in other periods and in sedentary species this effect did not occur.

TABLE 10

MIGRATORY STATUS, FEEDING ACTIVITY, AND FATNESS IN RELATION TO SOME NUTRITIONAL INDEXES
IN CHAFFINCHES TRAPPED IN THE MIDDLE OF A MIGRATORY WAVE AT THE
KURISHE NEHRUNG, 21–23 SEPTEMBER 1962

Flock status	Fat class	No. of birds	Body fat mg[a]	Total liver wt.	Total liver mg[b]	Blood sugar mg/100 ml[b]	Food in stomach mg[b]	Wt. of intestine mg[b]
Feeding, nonmigrating	Moderate and heavy	17	2200	·527 ± 6		145 ± 5	137 ± 5	913 ± 12
	None and slight	34	900	600 ± 7		116 ± 3	205 ± 4	1000 ± 10
Flying, nonfeeding	Moderate and heavy	37	2600	530 ± 5		210 ± 6	107 ± 4	606 ± 11
	None and slight	17	900	556 ± 8		114 ± 4	135 ± 5	854 ± 15

[a] Estimated by the visual method.
[b] Mean ± SE.

Therefore we think that during the migratory period regulation of migratory and feeding behavior is related to the amount of fat present in birds. This regulation, probably, is mediated through the intermediary metabolism.

THE BIOENERGETICS AND TIMING OF BIRD MIGRATION UNDER NATURAL CONDITIONS

The hypothesis stated above allows us better to interpret the natural rhythm of migration in some birds (Blyumental, 1961, 1963, 1966a; Belopolsky *et al.*, 1963;
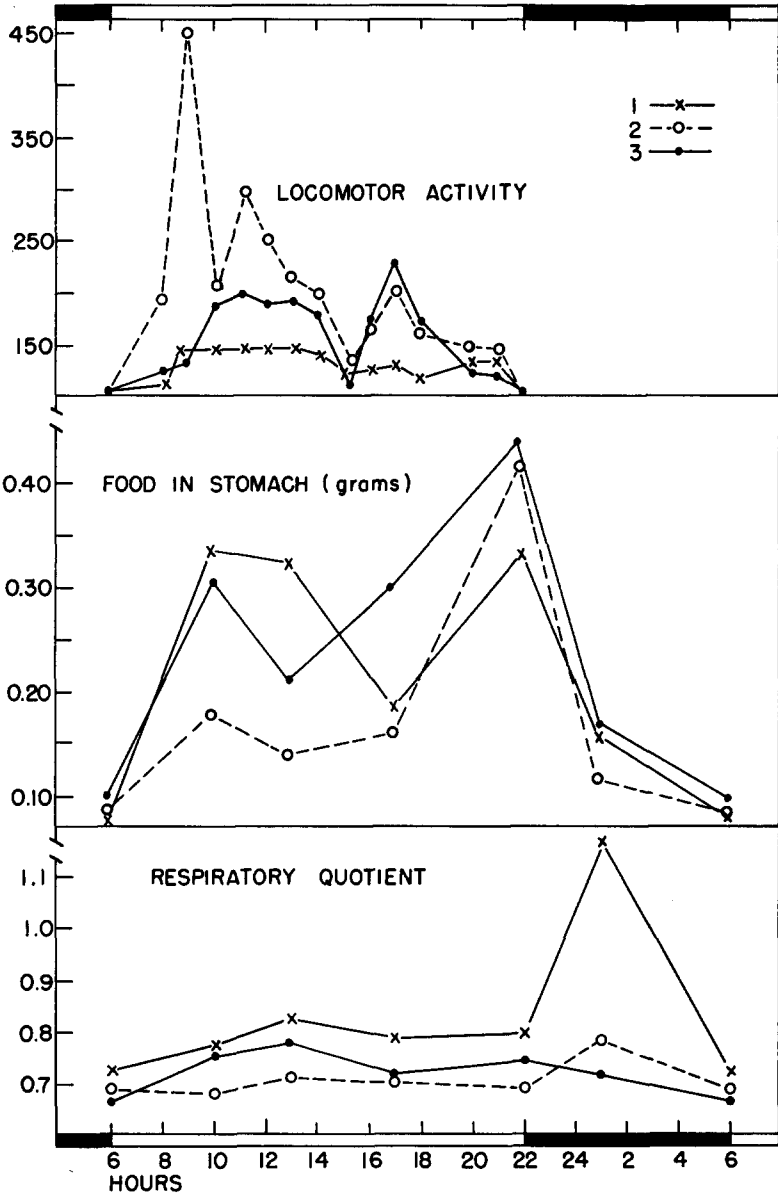
Figure 13. Diurnal variation in locomotor activity and metabolic indexes in caged young Chaffinches at the Kurishe Nehrung during autumn migration. Group 1 (symbols at upper right), birds with slight fat reserves; group 2, birds with moderate to heavy fat reserves; group 3, 0.8 ml of plant oil injected into subcutaneous adipose tissue of each bird with slight fat reserves. There are 18 birds in each group. Locomotor activity is the mean of 112 bird-days of recording in each group.
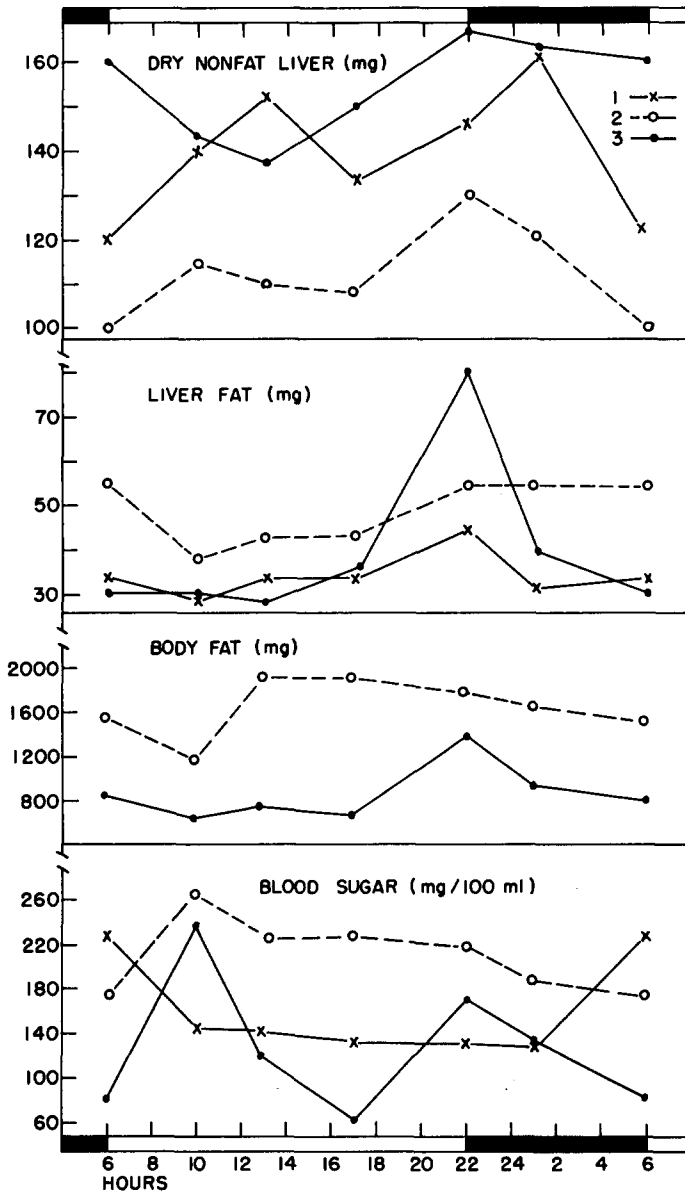
Figure 14. Diurnal variation in metabolic indexes in Chaffinches shown in figure 13.

Dolnik, 1963; Dolnik and Blyumental, 1964; Dolnik, 1965a; Blyumental, Gavrilov, and Dolnik, 1966).

It is well known that migration in small birds commonly proceeds by waves. Days with intensive migration are followed abruptly by days without migratory activity; then another wave comes along. Usually one seeks the cause of these waves in the changes of weather conditions. It is supposed that the migratory drive re-
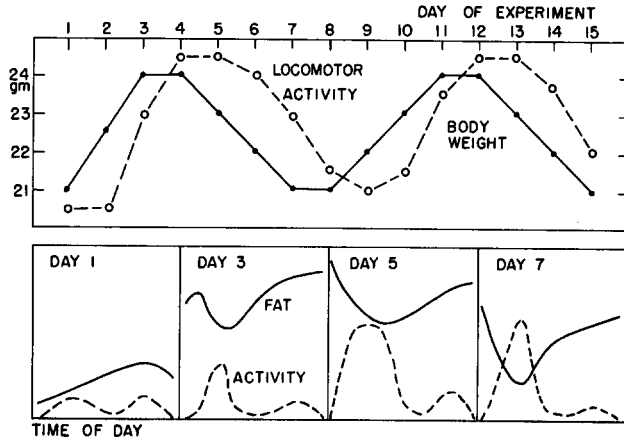
Figure 15. Day-to-day (upper panel) and representative diurnal (lower panels) variations in locomotor activity and body weight and fat in 32 caged young Chaffinches kept in standard conditions outdoors during autumn migration at the Kurishe Nehrung in 1960. Cycles of individual birds were not necessarily congruent, but were put in phase in the calculation of average values in the upper panel. Locomotor activity is given in arbitrary linear units.

mains constant in birds and that variations in the weather are responsible for changing the intensity of migratory movements.

At the Kurishe Nehrung these migratory waves of Chaffinches occur on almost the same dates yearly (Belopolsky et al., 1963). It is possible to predict the time of flight each autumn. This regularity of migratory waves also occurs at other places in the Baltic region (see Blyumental, Gavrilov, and Dolnik, 1966).

Paevsky (1963) showed that the different migratory waves do not consist of different geographic populations of Chaffinches. Likewise, they are not composed of separate sex and age groups (Dobrynina, 1963). The comparison of migratory waves of Chaffinches with movement of cyclonic conditions in Europe does not show a regular connection between weather and migration (Blyumental, Gavrilov, and Dolnik, 1966).

The only factor which is well correlated with the flight of Chaffinches at the Kurishe Nehrung is the fat level of the migrating birds. Figures 15 and 16 and tables 9 and 10 show that the formation of migratory waves and of bird behavior during the wave results from the difference in daily rhythms of activity, feeding and changing of fat reserves, and the changing proportion of fat and lean birds in the migrating flocks.

On the first day of the wave only the fat birds fly (fig. 17). The total number of migrating Chaffinches is relatively low, and migration begins at sunrise without previous feeding, and the birds fly continuously for four hours. Then there is a pause for feeding for one to three hours, and this is followed in the evening by another two hours of flight. The flocks are homogenous in relation to level of fat reserves in individual birds. The change of average fat during the day either correlates positively with the intensity of migration or its level slowly decreases toward the evening. The evening feeding is very weak, and generally after the daytime flight there are few, if any, birds at the Kurishe Nehrung.
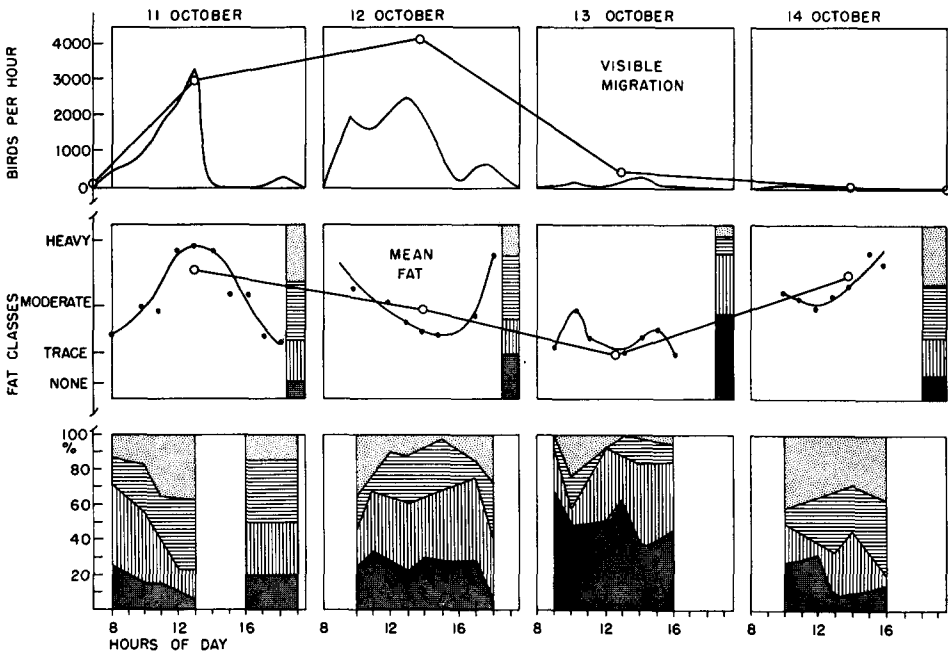
Figure 16. Some characteristics of a typical migratory wave (11 to 13 October 1960) and the first day of migratory pause (14 October) in wild Chaffinches trapped at the Kurishe Nehrung. Upper panels: Diurnal (curved lines) and day-to-day (open circles) variations of the intensity of visible migration. Middle panels: Diurnal (black circles) and day-to-day (open circles) variations of average fat levels in 1200 trapped Chaffinches. Histograms show relative proportions of visible fat classes (from top to bottom, heavy, moderate, slight, none) in birds trapped on the individual days. Lower panels: 24-hour variations in the percentage of birds in the four fat classes, based on examination of 1200 birds.

On the next day of the wave, which is usually the day of the most intensive migration, the flight also begins at sunrise. The first birds are very fat and fly constantly onwards. In the succeeding hours, both lean and small fat birds appear in the flocks, and the number of lean birds increases toward evening. These birds have fresh food in the stomachs. During the day they often stop for feeding and attract the fat birds also to stop, although the latter do not feed (table 10). The migration progresses on the average for seven hours with a pause in the middle of the day. The average level of fat in migrating birds becomes reduced significantly during the day. The flocks, except for the birds migrating during the first hour of flight, contain birds of various fat levels. In the second part of the day many birds feed on the ground. In the late evening the fat birds are generally the only ones flying.

In the last day of a migratory wave the migration does not begin at sunrise but only after a period of feeding. The number of flying birds is less, and they fly with frequent stops and at low elevations. Some flocks fly in a reverse direction. The most intensive flight occurs in the evening. The total duration of migration movement is, on the average, eight hours, sometimes extending up to 11 hours. On this day almost all flying birds are lean, or their average fat level is low. Some feeding occurs throughout the day.
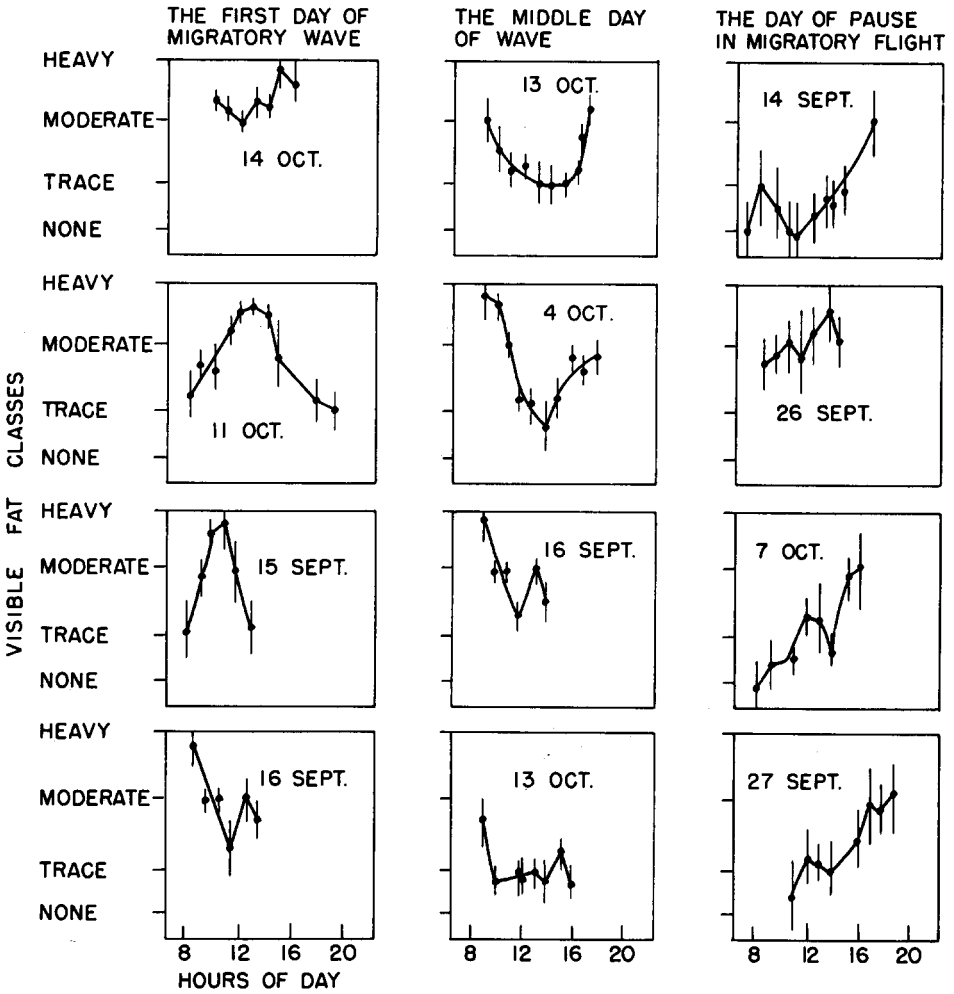
Figure 17. Examples of diurnal changes of fat (mean and range) in migratory Chaffinches in various days of a migratory wave, based on 3743 birds examined during some waves in 1960.

The migratory wave continues from one to seven days but usually lasts three days. After it is over, the following pause lasts from one to eight days but averages three days. During the pause there are only a few birds at the Kurishe Nehrung; they feed intensively throughout the day and increase their storage of fat.

Even in caged birds (fig. 15) obesity changes are cyclic, alternating some days with active feeding and some days with active *Zugunruhe*. It is possible that during the stopovers in migration the deposition of fat alone is not necessarily a sufficient stimulus for migration in Chaffinches. However, it is fat birds that predominate in the first day of the wave. The stream of flying flocks of fat birds exerts a strong stimulus which impels other fat birds to participate in the flight; and the larger the stream of flying birds the more drawing strength it exerts. The spending of fat by the flying birds and the differences in the daily rhythm in lean and fat birds and in the
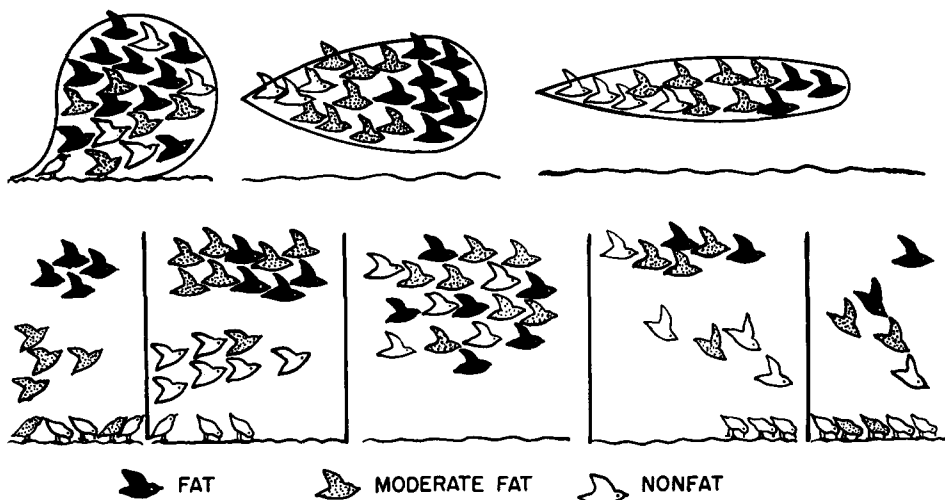
Figure 18. Possible causes of a migratory wave. At the top: nonfat birds fly less distance per day than fat ones. At the bottom: flying flocks of fat birds draw nonfat ones.

speed of their moving explain the picture which is observed in the succeeding days of the wave. After the reserve fat is exhausted in the majority of birds, the stopping of lean birds pulls down also the rest of the fat birds (fig. 18).

Thus in this reasoning we attach great importance to the drawing influence of flying birds on the birds physiologically uninclined to migrate at the given moment. In another study (Blyumental and Dolnik, 1963) we have shown that the attraction of one species by another, even between taxonomically distant species, often is an important factor influencing the dynamics of migration. The autopsy of lean and fat Chaffinches in various days of a wave shows that the attractive tendencies are developed intraspecifically even greater than interspecifically (Dolnik, 1966a).

It is possible that under natural conditions the migratory wave arises as the result of synchronization of rhythms among individual birds (fig. 16). Changes in the weather or the influence of one bird on another may be important factors in this synchronization.

The adaptive significance of wavelike migration, obviously, is in speeding the birds through foodless places and in having the stops occur where food is plentiful. The wavelike migration allows the species to use more efficiently the mosaic of food conditions along the migratory route as well as to take advantage of periods of favorable weather. Banding results confirm that birds migrate with frequent pauses. One migratory wave lasting one to three days may cover as much as 500 km, during which individual birds expend 2 to 3 g of fat (Blyumental, Gavrilov, and Dolnik, 1966).

We think that the variations of migration intensity in nature are not random, but are part of an orderly, adaptive phenomenon.

CONCLUSIONS AND A WORKING HYPOTHESIS

The aim of our research is to understand the physiological foundation of bird migration. The following hypothesis is the synthesis of our recent ideas concerning the
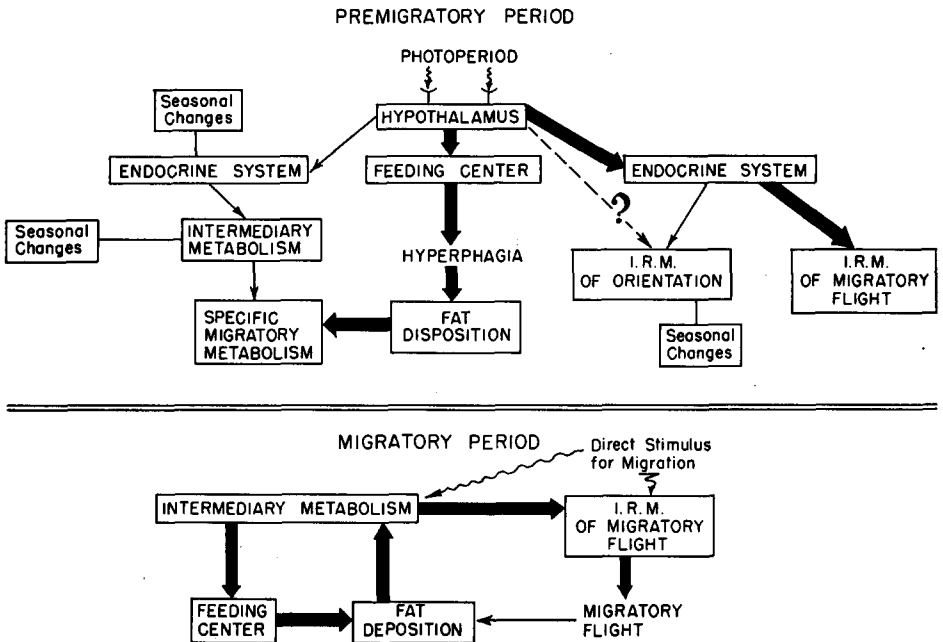
PREMIGRATORY PERIOD

Figure 19. A working hypothesis of functional interactions in the development of the migratory state. I.R.M. = "innate releasing mechanism."

cause and development of the migratory disposition in the organism (Dolnik, 1963, 1965b, 1966c).

Migratory disposition is characterized by the integration of several physiological and psychical processes that may be, at other times of the year, partially or completely independent of each other. During the premigratory period the basic annual cycles of the photoperiodic regulators, the endocrine system, energy metabolism, intermediary metabolism, the feeding centers, and the innate releasing mechanisms (I.R.M.) of migratory flight and orientation are unified to a stage from which actual migration may be released by only slight additional adjustments. This phase may be basically similar in migratory and sedentary species of birds (fig. 19).

We believe that the first step involves the reception by the hypothalamus of the proper external stimulus in the form of a definite photoperiodic pattern (and to a lesser degree stimulus by proper air temperature and humidity) and integrating it with the internal rhythm. The activated hypothalamus in accordance with an inborn program stimulates the feeding center to hyperphagia and simultaneously changes the hormonal balance. Changes in the endocrine system turn off behavior patterns related to the nesting territory. Then adaptive activity of the bird takes it away from this territory. Compass orientation, which from some data seems to have an independent regulation, guides the movement of the bird in a definite direction.

Hyperphagia results in the loading of the organism with abundant energy and changes the equilibria of intermediary metabolism to intensify fat metabolism. The changes in intermediary metabolism and in the endocrine system reduce the threshold for the innate behavior pattern of migration (fig. 20).
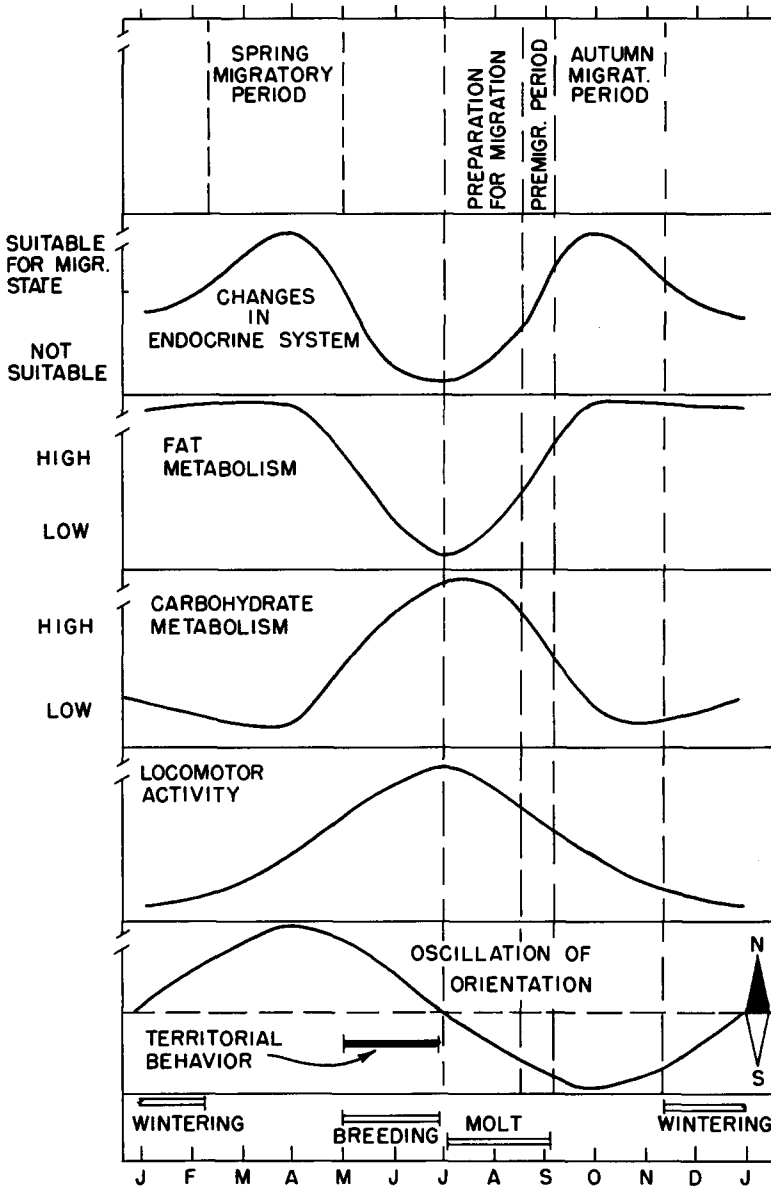
Figure 20. Hypothetical scheme of the development of autumn migratory state from summer physiological state. The latter is the same in migratory and nonmigratory species.

Sedentary species, races, and individuals do not develop the migratory condition from the initial stage because the hypothalamus lacks the proper integrating program, or in these birds the total hormonal situation is different, or the instinct for migratory flight is absent. This difference among birds may be the result of one or a few mutations. During ontogeny the transition from a sedentary to a migratory status may result from small changes in physiology.

Groebbels, 1932

FAT
DEPOSITION

E

ZUGUNRUHE

Kendeigh et al., 1960

FAT
DEPOSITION

E

ZUGUNRUHE

King and Farner, 1963

FAT
DEPOSITION

E

ZUGUNRUHE

Dolnik, 1963
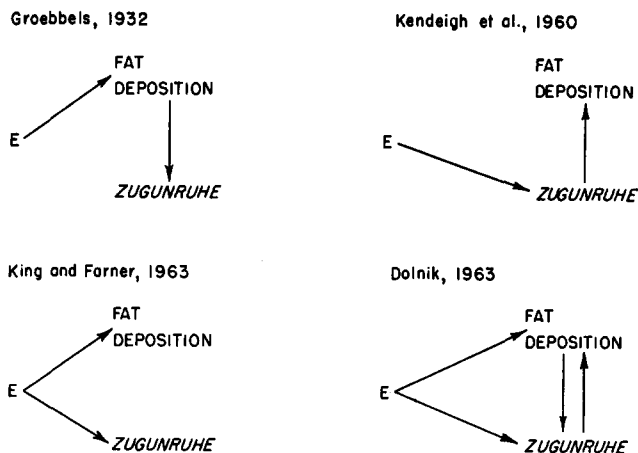
FAT
DEPOSITION

E

ZUGUNRUHE

Figure 21. Working hypotheses of the relationship of fat deposition and *Zugunruhe*, together with our hypothesis uniting them. "E" refers to environmental effects; the arrows depict routes of action.

At the end of the premigratory period the innate releasing mechanism of migratory flight comes into play as the threshold for its activation is lowered. In this case we have a typical example of the "Instinktvogel" of various German authors. If the internal stimulus is very weak, the migration begins only after the action of strong external stimuli (for example, changes of temperature, food, and perhaps psychical influences). These have definite metabolic or endocrinal effects. In this case we have a typical "Wettervogel."

The I.R.M. of migratory flight is influenced by three factors: internal metabolic conditions, external conditions affecting metabolism (food resources, weather), and social interactions. In other words, migration is regulated by the amount of fat reserves in the body, the availability of food in the environment, the weather, and the migratory behavior of flocks of the same species or other species.

We think that this hypothesis (fig. 21) includes many elements of those of Groebbels (1928), Schildmacher (1952), Wagner (1958), Merkel (1960), Kendeigh *et al.* (1960), and King and Farner (1963).

ACKNOWLEDGMENTS

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