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Physiological Adaptation of Blue Tits *(Parus caeruleus)* to Migration

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1. Introduction

Part of the populations of the Great Tit *(Parus major)*, Blue Tit *(Parus caeruleus)* and Coal Tit *(Parus ater)* breeding in Switzerland and South Germany emigrate in September and October to wintering quarters ranging from Provence to Northern Italy (SCHERRER 1972, FRELIN 1974, 1975). The most spectacular aspect of these movements is their great variability. Almost inexistant some years, they may attain a considerable amplitude some others. These movements are usually not considered as true migrations but as invasions or irruptions whose causes and consequences are poorly understood (SCHERRER 1972, WINKLER 1974, SVÄRDSON 1965, ULFSTRAND 1963, BERNDT & HENSS 1963, 1967). The matter of the present paper is to describe the physiological state characterizing invading blue tits as they reached the Alps by the means of a combination of field and laboratory studies.

2. Material and Methods

This study was carried out at the Ornithological station of La Golèze in the French Alps (Samoëns, Haute Savoie). The station, 4 km south of the Swiss station of Bretolet is located on a pass (elevation 1500 m abvove sea level). The valley of the Dranse de Morzine separates the passes of Bretolet and La Golèze. With respect to the Blue Tits migration system, La Golèze and Bretolet have an almost central position. As shown by ringing recoveries, most of the blue tits caught in the mist nets came from Switzerland and south Germany, went around the western ridge of the Alps, reached Provence and then Côte d'Azur and northern Italy (FRELIN 1974). The geographical position and the elevation of the station allowed us to catch between September 1st and October 20th, groups of migrating tits without major interference by sedentary birds (FRELIN 1971). Moreover, as a consequence of their migratory behaviour, most of the blue tits resting between two journeys or stopped by unfavourable atmospheric conditions stood down in the valley and were not caught in the mist nets of the station. Therefore all parameters considered in this study cannot be compared to either those of sedentary or resting blue tits. They all relate to migrating tits.

Trapped birds were weighted as soon as possible after catching and their age status was determined. Fat indices were defined as described for coal tits (FRELIN 1978). Mean fat indices were computed using the following correspondance: 1 = 1; 1+ = 2; 2– = 3; 2 = 4 and 2+ = 5. Since there is no evidence for the validity of this correspondance, no attempt will be made to use statistical tests for assessing differences in mean fat indices.

For fatty acid analyses, three blue tits were killed, defeathered and finely ground in a mortar with Fontainebleau sand. Lipids were extracted according to DELSAL (1944). The gas chromatographic analysis of the extracted fatty acids was conducted as described by CLEMENT & BEZARD (1961).

Heat production by resting blue tits was measured by indirect calorimetry. Blue tits, just being caught in the mist nets, were immediatly brought to the laboratory, kept for one hour without food in a black aviary and then placed into a plexiglass tubing (5 cm diameter) to allow as few movements as possible. This tubing was connected to a closed circuit of 1200 ml and air allowed to flow through the circuit at a rate of 2 liters per hour. Water was adsorbed in drying tubes containing calcium sulfate. At the end of the 30 minutes experiment, the pressure variation due to the difference in oxygen consumption and carbon dioxide release was measured using a manometer. The carbon dioxide liberated by the bird into the enclosed volume of the circuit was then trapped using a baryte solution at a concentration of 10 g/l. This solution was then titrated using a normal solution of hydrochloric acid. The rate of oxygen consumption was calculated according to the following formula

$$V^{o}_{2} = V^{co}_{2} + V \; \Delta P/P$$

where V is the volume of the closed circuit, P the atmospheric pressure, Δ P is the pressure variation at the end of the experiment and V^{co}_{2} is the rate of carbon dioxide release. Mean air temperature within the circuit was 15 ± 3 °C. All experiments were performed between 10 a. m. and 4 p. m., i. e. during the same

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phase of circadian activity for day active birds (ASCHOFF & POHL 1970). The mean heat production (M expressed in kcal) was calculated according to the following formula (ROMIJN & LOKHORST 1961)

$$M = 3.871\ V^{o}_{2} + 1.194\ V^{co}_{2}$$

where the rates of oxygen consumption and carbon dioxide release are expressed in liters. These experiments allowed moreover to compute respiratory quotients (RQ) which were not corrected for nitrogen excretion.

3. Results and Discussion

3.1. Estimates of fat stores: Migrating blue tits showed upon examination moderate subcutaneous fat deposits. The mean weight of fat stored may be estimated by the procedure used by HELMS & DRURY (1960) and MUELLER & BERGER (1966). If according to ODUM *et al.* (1964), fat is accumulated prior to migration in preexisting tissues without change in lean weight, the difference between the mean weight of each fat class index and that of the lowest fat class index should estimate the fat weight stored by the birds. Tab. 1 compares the mean weights of the six main fat classes. Fat weight estimations that can be deduced from this table are lower than 1 gr, i.e. less than 10% of fresh weight. For instance the majority of 1st year blue tits (fat index 2 —) have an estimated fat weight of 0.26 gr. This value is low when compared to estimates reported for other migratory species (MUELLER & BERGER 1966, HELMS & DRURY 1960). It is however very similar to fat weight estimates obtained for invading coal tits using the same method (FRELIN 1978). No direct quantification of the amount of fat stored was attempted. In the coal tit, a comparison of the estimated fat weight with the total weight of fat that can be extracted from carcasses using organic solvents revealed twofold differences. Higher amounts of fat are being consistently extracted from carcasses. The difference was unlikely due to non mobilisable fat engaged into cellular structures. It was concluded that the concept of homeostasis of non fat components did not apply to invading coal tits (FRELIN 1978).

Since fat weight estimates in the blue tits were similar to those obtained for coal tits, it is hypothesized that migratory fattening in the blue tit, as in the coal tit, is accompanied by a reduction in the lean weight. Fat weight estimates are therefore likely underestimates of the real fat weight.

3.2. Fatty acid composition of total fats: Since 20 carbons fatty acids are not commonly encountered in passerine birds (CALDWELL 1973; WEST & MENG 1968b), fatty acid analyses were stopped after the elution of 18- carbons unsaturated fatty acids. The distribution pattern of fatty acids in migrating tits is displayed in fig. 1. Oleate was the major fatty acid followed by palmitate (16:0) as is the case for most passerine species (WALKER 1964, CALDWELL 1973). Saturated fatty acids averaged 45% of total body fatty acids, palmitate being always more abundant than stearate (18:0). Polyunsaturated 18 carbon acids are quite low. An interesting feature is, however, the unexpected occurence of myristate (14:0) which, to our knowledge, has only been reported in such amounts in some north american warblers. Most authors agree however that the occurence of some fatty acids may strongly be influenced by the diet (WALKER 1964, CALDWELL 1973, WEST & MENG 1968a, b, BOWER & HELMS 1969). PALOKANGAS & VIKKO (1972) presented a study of the seasonal variations in fatty acid composition of the subcutaneous fat depots in the great tit breeding and wintering in central

Table 1: Comparative weights of migrating blue tits of different fat index.

Fat Index	Adult		1st year	
	M ± s. d. m.	N	M ± s. d. m.	N
1	10.40 ± 0.13	26	10.29 ± 0.08	73
1 +	10.40 ± 0.06	102	10.30 ± 0.04	237
2 —	10.44 ± 0.04	249	10.55 ± 0.03	493
2	10.90 ± 0.06	128	10.82 ± 0.05	183
2 +	11.40 ± 0.14	34	11.04 ± 0.09	64
3 —	—		11.67 ± 0.19	9

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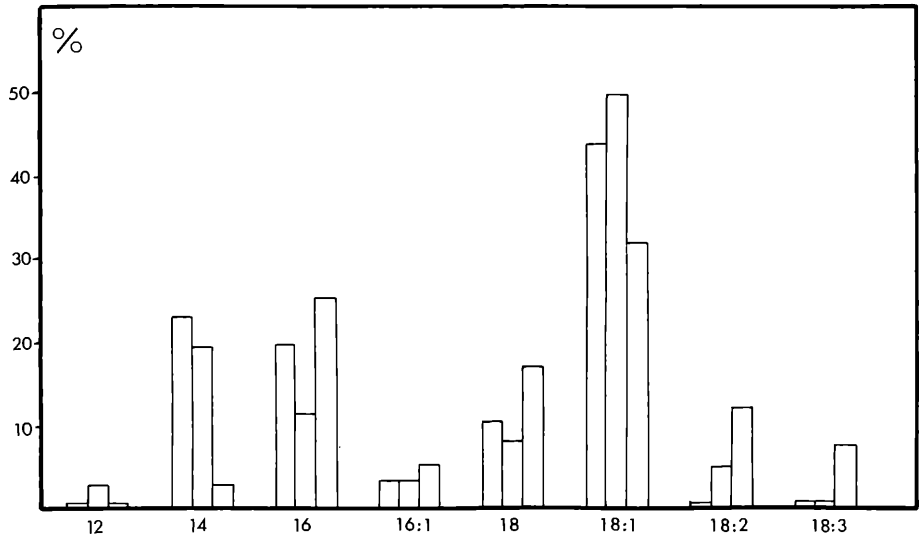

Figure 1: Fatty acid analyses of total fats from three different blue tits. The numbers in abcissa indicate for each fatty acid the number of carbon atoms per molecule and the number of double bonds per molecule. All first columns refers to a first year female (10.4 gr., fat index 2) caught on 10.10.1969. The second columns refer to another first year female (9.1 gr., fat index 2—) caught on 14.10.1969. The third columns refer to an adult female (9.4 gr., fat index 2—) caught on 16.10.1969.

Finland. The pattern that we obtained for migrating blue tits more closely fits their summer pattern than their winter pattern.

In conclusion, fatty acid composition of total fats in migrating blue tits is not significantly different from that of more typical migrant species.

3.3. Seasonal variations in mean weight and fat index: A common feature of migratory species, although a non necessarily prerequisite for migrating activity is the premigratory deposition of fat. Seasonal variations in mean body weight and fat index were considered to search for possible evidences of a premigratory fat deposition. Tab. 2 shows that the mean weight of first year blue tits was relatively stable or decreased slightly from the beginning of September to the end of October, indicating no obvious premigratory deposition of fat. Fat indices showed a different pattern of variation. The mean fat index increased progressively with time (tab. 3), which could suggest a premigratory fattening step. However, since these variations were not parallelled with body weight data and since the differences in

Table 2: Seasonal variations in mean body weight. First year birds caught in 1966, 1967, 1968 and 1972 have been considered. Numbers of measures for each time period may be considered as estimates of the importance of the migratory flights.

	Dates	M ± s. d. m.	N
September	1— 5	10.75 ± 0.12	55
	6—10	10.73 ± 0.10	62
	11—15	10.76 ± 0.10	94
	16—20	10.66 ± 0.08	148
	21—25	10.35 ± 0.03	621
	26—30	10.57 ± 0.04	565
October	1— 5	10.53 ± 0.04	645
	6—10	10.31 ± 0.13	66
	11—20	10.50 ± 0.14	22

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Table 3: Seasonal variations in mean fat index.

Dates	Fat indices 1	1+	2—	2	2+3—	total number	Mean
August	5	8	2	1	—	16	1.94
September —1	50	24	33	11	8	126	2.23
September —2	6	47	137	47	9	246	3.02
October —1	11	64	198	78	37	388	3.17
October —2	6	22	39	13	4	84	2.85

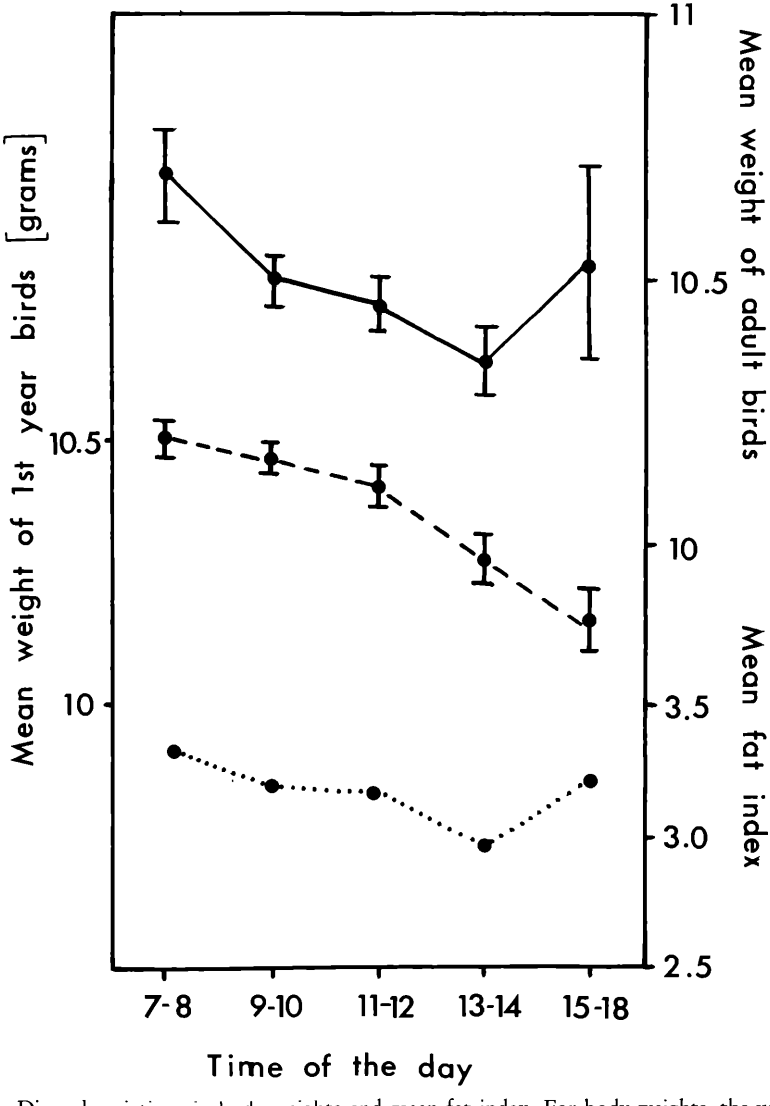

Figure 2: Diurnal variations in body weights and mean fat index. For body weights, the vertical bars represent the range of ± s. d. m. For the clarity of the figure, the scales of body weights for first year and adult blue tits have been displaced. For each hour, the mean body weight of adult blue tits did not significantly differ from that of first year blue tits.

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mean fat index cannot be assessed statistically, no definite conclusion could be drawn. The apparent absence of premigratory fattening may be due to sampling bias for only migrating tits were caught in the mist nets of the station. At least these data may be interpreted as evidences of a rather constant migratory state throughout the migratory period.

3.4. Diurnal variations in mean weight and fat index: Day time weight variations in both adult and first year birds are shown in fig. 2. Both age categories showed a similar pattern, i.e. a regular decrease in weight of about 3.5%. Mean fat indices also decreased regularly with day time, the extent of this variation is, however, small and its significance is difficult to assess. The weight of passerine birds usually increased with day time, the extent of increase varies following the species considered from 3.5% to 15% (NICE 1946). Since all the migratory movements of the blue tits took place in the morning, showing a peak between 10 and 12, the decreasing body weight should be related to the migratory movement. Two hypotheses may be proposed. It may be considered that all migrating tits start their journey early in the morning and stop it between 12 and 13. The decreasing mean body weight and fat indices could therefore represent the mobilization of fat stores. It may be expected, however, that blue tits recover their initial weight during the afternoon or even higher body weights than in the morning to compensate for energetic expenditures for the night. The data presented in fig. 2 indicate that this is not the case. A second hypothesis may be that blue tits caught at different hours of the day belong to subpopulations of migrating tits in different physiological states. Early in the morning birds may be in a better physiological disposition as evidenced by the higher body weight and fat index. These birds usually migrate faster, spending less time in the trees below the pass than their followers. This may also indicate higher migratory disposition. These birds may progressively stimulate blue tits in a lesser disposition (lower

Table 4: Annual variations in the mean weight of adult and first year blue tits migrating through La Golèze. Numbers of captures may be considered as estimates of the importance of the migratory movements.

Year	Adult M ± s. d. m.	N	First year M ± s. d. m.	N
1966	10.39 ± 0.05	153	10.36 ± 0.02	975
1967	10.37 ± 0.08	57	10.34 ± 0.07	92
1968	10.50 ± 0.04	213	10.42 ± 0.05	156
1969	10.47 ± 0.09	39	10.35 ± 0.08	59
1970	10.60 ± 0.17	10	10.44 ± 0.20	9
1971	10.52 ± 0.09	48	10.82 ± 0.12	49
1972	10.71 ± 0.09	210	10.67 ± 0.02	1065
1973	10.63 ± 0.07	89	10.43 ± 0.08	63
1974	10.81 ± 0.14	26	10.63 ± 0.11	23

Table 5: Annual variations in the mean fat index of adult and first year blue tits.

Year	1st year		Adult	
	M ± s. d. m.	N	M ± s. d. m.	N
1966	3.17 ± 1.15	201	3.09 ± 1.11	45
1967	3.03 ± 0.92	80	3.04 ± 0.86	46
1968	2.54 ± 0.74	147	2.91 ± 0.88	207
1969	2.55 ± 0.84	75	2.57 ± 0.74	53
1970	2.33 ± 1.05	9	3.00 ± 1.00	16
1971	2.56 ± 1.22	50	2.14 ± 1.40	50
1972	2.98 ± 1.16	1067	3.18 ± 1.28	220
1973	3.26 ± 0.83	65	3.30 ± 1.17	89
1974	2.57 ± 0.97	23	2.47 ± 1.03	32

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body weight and fat index) to follow them. As a consequence, the mean body weight of the migrating population should decrease more rapidly than expected from energetic expenditures. This hypothesis is strenghened by the analysis of local controls of ringed birds. The majority of blue tits that have been ringed early in the morning is controlled, i.e. tryed to cross again the pass, during the same day, while most birds caught in the middle or late in the morning, spend one or two days in the valley before starting again their migratory journey. A similar behaviour has been described for migrating coal tits (SCHERRER 1972).

3.5. Annual variations in mean body weight and fat index: Although very variable in importance, the migratory movements of the blue tits display the same regular phenology every autumn (FRELIN 1971) This situation contrasts with the variable behaviour of a typically invading species: the coal tit (SCHERRER 1972, WINKLER 1974, FRELIN 1975) or of a „pseudo invading species": the goldcrest *(Regulus regulus)* (FRELIN & CORNILLON 1974).

Considering that the mean weight and fat index are indices of the physiological state of migrating tits, it may be concluded from tab. 4 and 5 that migrating blue tits are in the same migratory disposition whatever the numerical importance of their autumnal movements may be. This confirms previous observations on the stability of the migrating behaviour of the blue tits and contrasts strickingly with the situation described by SCHERRER (1872) for invading coal tits.

3.6. Respiratory quotients: Using indirect calorimetry, the mean metabolic rate of resting blue tits measured at the time of maximum diurnal activity was estimated to 580 kcal/24 hours/kg (N = 25), which is reasonably close to estimates obtained for birds of similar weight (KENDEIGH 1939, STEEN 1958). These measurements allowed to estimate the respiratory quotients. In three cases, RQ lower than the theoretical minimum value of 0.70 were found. All 22 other estimates fall within the range 0.70—0.98, but most of them were found between 0.70 and 0.80 (tab. 6). These low values of RQ indicate that fatty acids are used as main fuel. Tab. 6 shows in addition that the highest RQ, indicating lower fat metabolism were associated with lower fat indices.

3.7. Theoretical flight range: The theoretical flight range may be estimated in two different ways. The combustion of 0.26 gr. of fat (estimated fat weight of 1st year tits with a fat index of 2—) yields about 10 Joules and would allow a tit to rest without food for about 9 hours. Different authors have tried to estimate the energy requirements for flight in small passerine birds, which can conveniently be expressed as a multiple of the standard metabolism. Different values have been proposed, most of them ranging from 8 to 12 (ODUM 1960, RAVELING & LEFEBVRE 1967, NISBET 1963, YAPP 1962, HART & BERGER 1972). As a consequence, 0.26 gr. of fat would allow blue tits to fly for about one hour.

From their extensive studies on the energetics of flight BERGER & HART (1974) have derived the following formula:

$$t = 36.f.W^{0.28}$$

where t represents the potential flight duration in hours, f is the initial fractional fat content and W is the initial body weight in grams. Using the data of tab. 1, the potential flight duration for blue tits of different fat indices are: 2—: 1.7 hours, 2: 3.4 hours, 2+: 4.8 hours and 3—: 8.5 hours. Considering that blue tits with fat indices of 1 and 1 + have no mobilizable fat

Table 6: Distribution of respiratory quotients in migrating blue tits. The relationship to fat indices is suggested. Only 19 tits of 25 have been scored for their fat indices.

Respiratory Quotients	Fat indices 1—1+	2— — 2	N
0.66—0.80	3	8	16
0.81—0.90	1	3	4
0.91—1.00	4	0	5

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reserves, the mean potential flight duration was estimated to 1.7 hours, which is likely an underestimate since the real fat reserves have been underestimated.

To convert these estimates into flight range, the flight speed has to be defined. It was estimated to be slightly higher than a running man in open areas but much lower when trees are present. Migration blue tits or coal tits did not fly straightforward but perch very often in the trees (see BIBER 1972 for a description of this behaviour). Flight speed should therefore be comprised between 10 and 30 km/hour. As a consequence the average flight range of migrating tits should be comprised between 20 and 50 km per day. These figures are underestimates since fat reserves have likely been underestmated.

Three ringing recoveries between Sempach and Bretolet indicate average daily trips of 30, 37.5 and 50 km/day (FRELIN 1971) Between Hahnenmoos pass and La Golèze, the average journeys were estimated to 16.7, 22.3 and 22.3 km per day (FRELIN 1971). Five other blue tits were ringed at Bretolet or la Golèze and controlled a few days later in their wintering quarters. The average flight speeds computed on distances ranging from 150 km to 300 km were 20, 20.4, 24, 25.8 and 50 km per day. From these 11 recoveries an average flight speed of 29 ± 3.6 km per day is obtained. This is likely an underestimate since blue tits did not fly straight to their recovery place. Furthermore blue tits may not migrate every day.

The similarity between the theoretical flight range and the average flight speed estimated from ringing recoveries indicates that the amount of fat accumulated by migrating blue tits should be just sufficient to match the energetic expenditures for migratory flights. One interesting possibility could be that fat reserves actually limit migratory flights and that blue tits have to find additional energetic fuel during migration. Numerous observations (FRELIN 1971, BIBER 1972, SCHERRER 1972) have shown that migrating tits perch very often in the trees; they usually fly rapidly to the lower branches, stop there silently for a few seconds and began to climb up while searching for food. As the top of the tree is attained, feeding stops and tits seem to wait for other migrating tits in the neighbouring trees. The frequency of calls increases and quickly a whole group of tits leaves the trees and flyes to the next group of trees. Regular observations of the stomacal content of blue tits revealed the presence of food at any time of the day. Such a continuous feeding during migratory flight might explain why body weight and the average fat index showed only small diurnal variations. Further studies are however required to determine how important and critical this additional source of energetic fuel for the migratory flights might be.

4. Conclusion

Migrating birds accumulate important reserves of fat prior to their migration (FARNER 1955, ODUM *et al.* 1961, HELMS & DRURY 1960, KING 1972). Fats serves as the main fuel for the migratory flights. Premigratory fattening results from complex physiological changes which are under the control of photoperiod (DOLNIK 1970). These processes have evolved in an adaptative way so that the largest amounts of fat are encountered in bird species undergoing long distance flights over seas and deserts (ODUM 1960) or in species that achieve their migration very quickly (HELMS & SMYTHE 1969). Short range migrants have usually moderate fat reserves (HELMS 1959, JOHNSTON 1962).

Migrating blue tits are short range migrants whose migratory movements are still poorly known. The data presented in this paper shows that the physiological state characterizing migrating blue tits did not differ from that of typical migrant species. Blue tits have moderate depots of fat essentially in the form of oleic and palmitic acid and used them as energetic fuel. These reserves are just sufficient to allow for the daily migratory trips. Additional energetic fuel may be obtained by feeding during the numerous short stop over periods that interspersed the migratory flight.

This physiological state was found every autumn whatever was the importance of the migratory movements which confirms previous data on the regularity of their migratory behaviour (FRELIN 1971). Thus the blue tit ought not to be considered as an invading species but rather as a typcal migrant species. The number of blue tits engaged every autumn into migration is, however, highly variable. The reason for this variability has still to be found, but it is certainly not caused by variation in migratory disposition.

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5. Summary

Blue tits *(Parus caeruleus)* migrating through the Alps have moderate fat reserves mainly as oleate and palmitate. Their resting metabolism was estimated to 580 kcal/24 hours/kg. Respiratory quotients were low suggesting the utilization of fat reserves. The average theoretical flight range was estimated to 20—50 km. Ringing recoveries indicated that daily trips averaged 29 km. This suggests that fat reserves are just sufficient to support dailly migratory flights. Additional energetic fuel may be obtained by feeding during migratory flights.

It is suggested that the physiological and metabolic mechanisms underlying migration in the Blue Tit are similar to those operating in typical migrant species. This physiological state was found stable whatever was the numerical importance of the migration.

6. Zusammenfassung

Physiologische Anpassung der Blaumeise *(Parus caeruleus)* an den Zug.

Die über die Alpen wegziehenden Blaumeisen *(Parus caeruleus)* weisen geringe Fettreserven, besonders in Form von Öl- und Palmetinsäure, auf. Ihr Ruhestoffwechsel beträgt etwa 580 kcal/24 Std/kg. Gemessene RQ-Werte sprechen für Fettverbrennung. Ihre tägliche Flugfähigkeit wird auf 20—50 km geschätzt. Aus Ringfunden errechnen sich tägliche Durchschnittsstrecken von etwa 29 km. Das bedeutet, daß die Blaumeisen mit ihren Fettreserven ihre Tageswanderungen bestreiten könnten. Dazuhin mag während der Wanderungen zusätzliche Energie durch Nahrungsaufnahme für den Zug gewonnen werden.

Den vorliegenden Untersuchungen nach entsprechen die physiologischen und Stoffwechselmechanismen, die mit dem Zug der Blaumeise in Zusammenhang stehen, denen ausgeprägter Zugvögel. Der physiologische Zustand während des Zuges war einheitlich und unabhängig von der Intensität des Zuges.

7. References

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Jugendentwicklung südfinnischer und süddeutscher Gartengrasmücken *(Sylvia borin)* unter denselben Bedingungen

Von Eberhard Gwinner

Herrn Professor Dr. Lars von Haartman zum 60. Geburtstag gewidmet

Frühere Untersuchungen an handaufgezogenen Fitissen *(Phylloscopus trochilus)* und Gartengrasmücken *(Sylvia borin)* hatten gezeigt, daß Vögel aus nördlichen Populationen ihre Jugendentwicklung schneller durchlaufen als Artgenossen aus südlichen Populationen. Dies galt auch für Vögel, die unter gleichen Umweltbedingungen aufwuchsen (Gwinner *et al.* 1972, Berthold *et al.* 1974, Berthold 1977). Berthold (1977) zog südfinnische und südwestdeutsche Gartengrasmücken vom 3. bis 5. Lebenstag an sowohl unter der simulierten Photoperiode ihres jeweiligen populationseigenen Lebensraums als auch unter der simulierten Photoperiode der jeweils anderen Population auf. Unter beiden Bedingungen entwickelte sich das Gefieder bei den südfinnischen Vögeln schneller als bei den südwestdeutschen und die südfinnischen Vögel kamen früher in herbstliche Zugdisposition. Diese Befunde stimmen mit dem Verhalten freilebender Artgenossen zumindest qualitativ überein und legen nahe, daß die Populationsunterschiede genetisch fixiert sind.

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