

Seasonal variation in the dynamics of ptiloerection and shivering correlated changes in the metabolic rate and body temperature of the pigeon

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Summary. A study was made of effects of cold exposure (5 °C) on the dynamic nature of ptiloerection and shivering in outdoor pigeons in winter and summer and in cold-acclimated (31–34 days at 5 °C) pigeons in summer. Shivering (integrated pectoral muscle EMG), and cloacal and foot temperatures were measured and the magnitude of ptiloerection was evaluated as a feather index at 1-min-intervals. A feedback control mechanism was assumed to apply to both ptiloerection and shivering. Their variations with time were described by functions $F(t)$ and $S(t)$ in Eq. (1) and (2), respectively. The parameters in the functions were determined by minimizing the χ^2 -value of the fit to the experimental data. To estimate static thermal adaptation of thermoregulatory effector mechanisms to cold, the metabolic rates (\dot{M}) of the pigeons were tested at 5 and 26 °C, and the plumage wet weight of birds was also determined.

The results show no significant evidence on seasonal or artificial thermal adaptation in thermoregulatory effector mechanisms of pigeons to dynamic or static conditions.

Introduction

The strategy of seasonal acclimatization is species specific. Small birds, like common redpoll (Pohl and West 1973) and cardueline finches (Gelineo 1969; Dawson and Carey 1976) adapt to winter conditions mainly by stimulating their heat production, while big arctic gallinaceous birds manage

to maintain homeothermy effectively by insulative means (West 1972).

Generally the birds become more heavily feathered before the winter season (e.g. Veghte 1964; Barnett 1970; Palokangas et al. 1975; Dawson and Carey 1976). Until now studies of seasonal variation in insulation have concentrated on measuring the number (Wetmore 1936) and weight of feathers (op cit). However, it has been shown that feather movements also serve as a rapid and effective means of temperature regulation in pigeons (Burchard et al. 1933; Hohtola et al. 1980), in yellow buntings (Wallgren 1954) and in barbary doves (McFarland and Baher 1968; McFarland and Budgell 1970), affecting both the quantity and mobility of the air layer kept within the plumage and the surface density of the feather covering. Thus it was decided to study whether there are seasonal differences in the dynamics of ptiloerection.

In previous studies (e.g. Hart 1962; West 1965), showing no seasonal adaptation in shivering of birds, three separate electrodes and the peak-to-peak technique in the measurements of breast muscle electromyogram (EMG) have been used. In this study we analyze not only seasonal variation in shivering levels but also seasonal changes in the dynamics of EMG in the pigeon, using fixed arrangements of the electrodes, and using rectified and integrated EMG which recently has been shown to be most reliable predictor of total heat production in the pigeon (Hohtola 1982). Metabolic rates, body and foot temperatures and plumage weight of pigeons were determined to describe static thermal adaptation of thermoregulatory effector mechanisms to cold.

Materials and methods

Animals

Adult pigeons (*Columba livia*, mass 0.31–0.39 kg) of both sexes, captured in South-Finland, were used. The birds were divided

Abbreviations: BMR basal metabolic rate; C thermal conductance; CA cold-acclimated; EMG electromyogram; FI feather index; \dot{M} metabolic rate; S_i summer/indoor; S_o summer/outdoor; T_a ambient temperature; T_b body temperature; T_f foot temperature; \dot{V}_{O_2} oxygen consumption; W_i winter/indoor; W_o winter/outdoor

into three groups. Group 1 was housed in covered wire netting cages (approx. 0.73 m³) located in an undisturbed courtyard (outdoor pigeons). Group 2 was accommodated in similar cages (one pigeon in each) under laboratory conditions (indoor pigeons), ambient temperature, $T_a = 21 \pm 1$ °C, R.H. 40–50%, a 12L:12D light-dark cycle (photophase 0600–1800). Group 3 was acclimated to $T_a = 5$ °C during 31–34 days in July–August (cold-acclimated pigeons, CA). The housing conditions were maintained otherwise similar as for Gp. 2. During the adaptation and experimental period, food (feedoat, vitaminous chicken food and once a month grains of sand) and water (snow in winter for outdoor pigeons) were freely available. The pigeons appeared to stay in good condition and maintained their body weight throughout the year on this diet.

Experimental procedure

Experiments were performed with 6 pigeons from each group in late March and repeated in late August. At the time of measurement the photophase for outdoor pigeons in winter was about 12L:12D and in summer about 14L:10D, and the mean T_a 's were -14.2 and $+9.5$ °C, respectively.

The magnitude of ptiloerection was evaluated as a feather index at 1-min-intervals according to the method devised by McFarland and Baher (1968) for the barbery dove, and described for the pigeon by Hohtola et al. (1980).

Shivering was measured as rectified and integrated pectoral muscle EMG by two-channel signal-processing device constructed in our laboratory. The EMG-registration method and fixed arrangements of the electrodes allowed comparisons to be made between subsequent experiments. The method has been described accurately by Hohtola et al. (1980) and Hohtola (1982).

Body temperature (T_b , from the cloaca) and foot temperature (T_f , naked tarsometatarsus) were picked up with small diode probes and plotted on a Foster Clearspan P250L recorder.

The pattern of heat production as oxygen consumption (\dot{V}_{O_2}) was measured with a Beckman E 2 paramagnetic oxygen analyzer. The flow rate of dried and CO₂-free air was adjusted by a Rotameter 1,100 flow meter to 2 l/min. The expired CO₂ was adsorbed on granular soda lime and water on silica gel.

Function fitting and statistical analysis

In this present study of dynamic nature of ptiloerection and shivering, the feedback control theory of feather movements introduced by McFarland and Budgell (1970) was applied. According to this theory the time dependence of ptiloerection $F(t)$ is described by the function

$$F(t) = F_0 + \Delta F(1 - e^{-t/T_f}) \quad (1)$$

where F_0 is the basal level of FI, and ΔF is the difference between final and basal levels of FI. The time constant T_f summarizes the thermoregulatory control mechanism. A similar feedback control mechanism was assumed to apply to shivering $S(t)$, yielding the following time dependence

$$S(t) = S_f(1 - e^{-t/T_s}) \quad (2)$$

The constant S_f is the final level of shivering reached in the experiment and T_s is again the time constant. The parameters appearing in the functions $F(t)$ and $S(t)$ were determined by minimizing the χ^2 -value of the fit to the experimental data. Estimates of the errors in the parameters were obtained from the covariance matrices. These matrices can be evaluated when the functions $F(t)$ and $S(t)$ are linearized with respect to the unknown parameters in the neighbourhood of the above minimum.

For statistical comparisons of the measured quantities an analysis of variance and *t*-test were performed. The multiple range comparison was achieved according to the Tukey test.

Experimental protocols

Experiment 1. In the first experiment, the electrodes for the measurement of shivering and diode probes for T_b and T_f were fixed with adhesive tape without disturbing the normal arrangement of feathers; the pigeon was then transferred to a cold room ($T_a = 4$ °C, light intensity 100 lux) and placed in a small cage. An infrared lamp (250 W) was positioned above the pigeon to raise T_a to 28 °C. Shivering, T_b and T_f were monitored continuously and FI was estimated through a TV-monitor (Philips LDH25 camera and Finnvideo VM 12 FI monitor) at 1-min-intervals. Measurements were not started until the equilibration of variables after at least 45 min.

To examine the effect of cold exposure on the variables of pigeons, the IR-lamp was switched off, whereafter T_a decreased within 10 min to 5 °C (registered in a calibration run with a diode located inside a perforated black test body, see Fig. 1). Light intensity stayed at 100 lux. the measurement of variables continued for 30 min, i.e. until the changes of variables reached a balance.

Experiment 2. In order to find out if there was a difference in heat production between groups, the birds were placed in a dark metabolic chamber for 30 min. The decrease of T_a to 5 °C was like in Exp. 1. The EMG, T_b , T_f and \dot{V}_{O_2} values were recorded.

Experiment 3. One day fasted pigeons were placed in a dark metabolic chamber at 26 °C (i.e. within the thermoneutral zone) in order to measure their stabilized (after 45 min) oxygen consumption (\dot{V}_{O_2}), i.e. to estimate their basal metabolic rate (BMR). The metabolic rate (\dot{M}) was calculated as W/kg both in Exp. 2 and 3. The energy equivalent of 1 ml of O₂ was assumed to be 4.7 cal.

Experiment 4. The feathers of summer pigeons (S_0 , S_i and CA) were plucked, and the plumage excluding the large feathers of wings and tail was immediately weighed (= wet weight). The feathers of winter pigeons (W_0 and W_i) were plucked from birds housed in similar conditions as pigeons used in experiments. The plumage weight is expressed as milligrams per square centimeter of body surface. The body surface (A) was calculated according to equation

$$A \text{ (cm}^2\text{)} = 10 M^{0.67} \quad (3)$$

giving the surface in square centimeters when body weight (M) is expressed in grams (see Calder and King, 1974).

Results

A pigeon placed in a cage under the warming IR-lamp was at first quite active, pecking and walking around before settling to rest. After switching off the IR-lamp the bird became passive and even drowsy within 5 min. The ptiloerection of different body regions and the EMG activity gradually increased, excluding some active phases when sleeking occurred and the EMG activity decreased. During the experimental period of 30 min, T_b and T_f decreased.

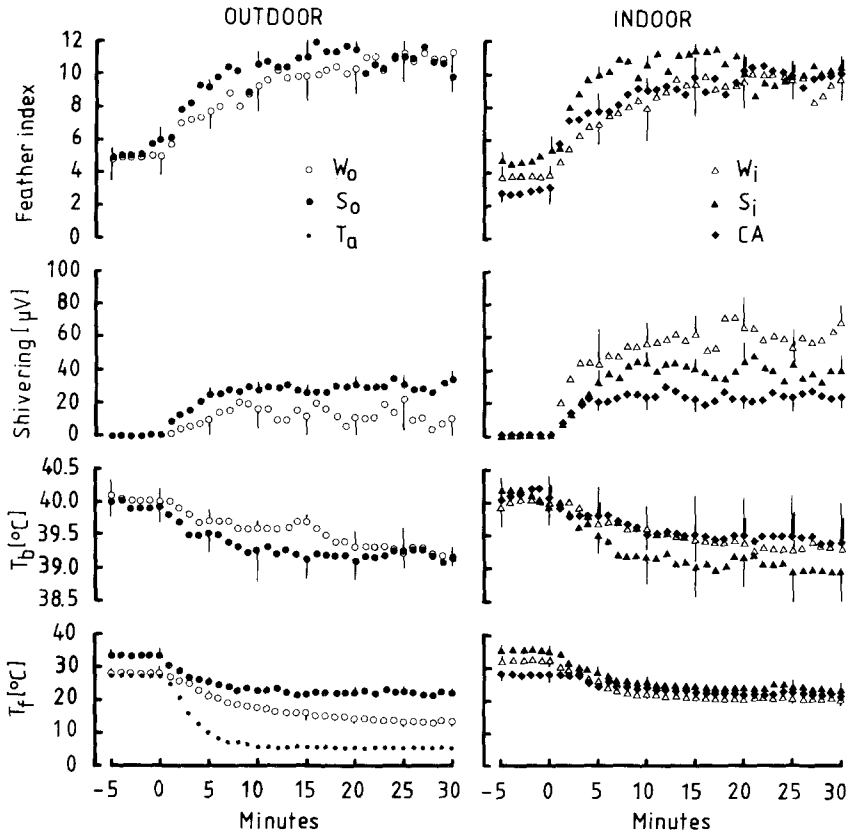


Fig. 1. Effects of cold exposure (induced by switching off a warming IR-lamp) on feather index, shivering, body temperature (T_b , from the cloaca) and foot temperature (T_f , from the naked tarsometatarsus) of winter/outdoor (W_0), summer/outdoor (S_0), winter/indoor (W_i), summer/indoor (S_i) and cold-acclimated (CA, 31–34 days at 5 $^{\circ}\text{C}$ 12L:12D, relative humidity $48 \pm 2\%$) pigeons. Each symbol represents a mean of six pigeons and vertical bars indicate standard errors. The dotted line indicates the decrease of ambient temperature (T_a , recorded with a probe located inside a perforated black test body) after the heating period

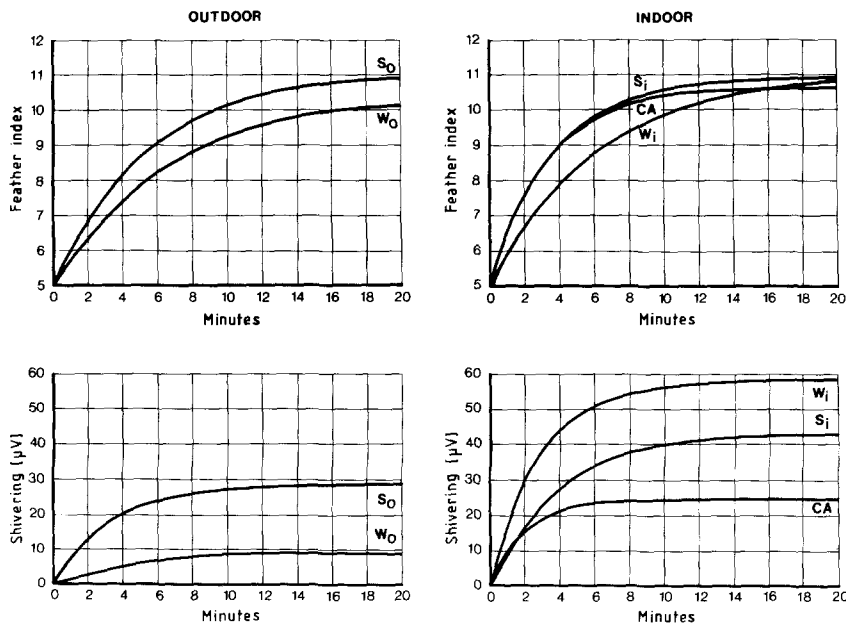


Fig. 2. Functions $F(t)$ of piloerection and functions $S(t)$ of shivering defined in Eq. (1) and (2) respectively. The parameters in the functions were determined by minimizing the χ^2 -value of the fit to the experimental data. The parameters with their error estimates are given in Fig. 3. and the corresponding χ^2 -values of the fit in Table 1. $N=6$ in each case. For further explanations see Fig. 1

Figure 1 shows the mean dynamic responses of thermoregulatory effector mechanisms to cold exposure in outdoor and indoor pigeons in winter and in summer. The functions $F(t)$ describing the piloerection of different groups of pigeons are pre-

sented in Fig. 2. The χ^2 -fitting was done using data from the first 20 min of responses. The parameters with their error estimates are given in Fig. 3 and the corresponding χ^2 -values of the fit in Table 1. The curves in Fig. 2 show distinctly cold exposure

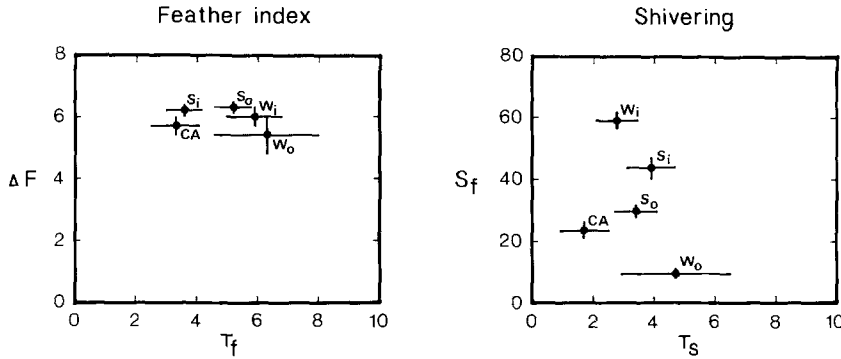


Fig. 3. The values and the estimated standard errors of the constants appearing in the functions $F(t)$ and $S(t)$ of Eq. (1) and (2). The constant ΔF is the difference between the final and basal levels of feather index, the constant S_f is the final level of shivering reached in the experiment and the representative time constants of the phenomena are T_f and T_s . $N=6$ in each case. For further explanations see Fig. 1

Table 1. The values of $\chi^2/\text{degree of freedom}$ describing the goodness of the fits of the piloerection data (χ_F^2/f) and the shivering data (χ_S^2/f). The functions used in fitting are given in Eq. (1) and (2) and the resulting parameters in Fig. 3. $N=6$ in each case. For further explanations see Fig. 1

	Animal group	χ_F^2/f	χ_S^2/f
Outdoor	W_o	0.26	0.74
	S_o	0.59	0.14
Indoor	W_i	0.22	0.44
	S_i	0.44	0.32
	CA	0.23	0.10

induced slight differences in ptilomotor responses of pigeons. The response difference can also be seen from time constants in Fig. 3 showing the smallest time constants and thus the fastest ptilomotor response in S_i and CA pigeons.

The piloerection, however, was not enough to eliminate increasing heat loss. The cooling elicited an activation of heat production, manifested by the onset of shivering (Fig. 1). The fitted functions $S(t)$ are shown in Fig. 2 and the resulting parameters together with their errors are again given in Fig. 3. The increase of EMG activity of outdoor pigeons was more rapid in summer than in winter reaching the half maximum value at 2.4 and 3.3 min, respectively. The fastest response was found with CA pigeons achieving the half maximum value within 1.2 min. However, the errors in the time constants were quite large as seen from Fig. 3. Statistically significant differences were found in the magnitude of the EMG activity starting at 10 min from the cold exposure. The EMG values of W_i pigeons were significantly above the ones of CA and W_o pigeons ($P < 0.001$) and also of S_o pigeons ($P < 0.05$).

The mean decrease in T_b within 30 min was 1 °C in S_i pigeons and 0.8 °C in S_o pigeons, and 0.7 °C in W_o , W_i and CA groups (Fig. 1). No significant differences between the groups could be

found in the decreasing patterns of T_b . The mean T_f decreased by 12.4 °C (S_i), 14.6 °C (W_i), 7.4 °C (CA) and by 20.9 and 16.8 °C in S_o and W_o pigeons, respectively. The basal level of T_f in S_i pigeons was found to be significantly ($P < 0.001$) higher than of CA pigeons. T_f of W_o pigeons was significantly lower than T_f of S_o pigeons, starting 10 min from cold exposure ($P < 0.05$ between 10 and 20 min, $P < 0.01$ between 20 and 30 min) contrary to the response of T_f 's in the metabolic chamber (N.S., Table 2). Similarly, T_f of S_o pigeons as measured in dark metabolic chamber at 5 °C was significantly lower than T_f of indoor pigeons according to the Tukey test (Table 2). T_f of W_o pigeons was at the lower level after cold exposure than T_f of indoor pigeons (Table 2). The difference was not significant perhaps because of higher T_f before cold exposure.

Table 2 further shows that there is a trend that outdoor pigeons were able to increase their metabolic rates more than indoor pigeons at 5 °C (N.S. according to the Tukey test). Stabilized T_b of W_o pigeons was 0.4 °C higher than T_b of S_o pigeons (N.S.), while conversely in indoor conditions the mean T_b of S_i pigeons was 0.8 °C higher than T_b of W_i pigeons (N.S.) and 0.9 °C higher than T_b of CA pigeons ($P < 0.05$). EMG activity of indoor pigeons measured in a dark metabolic chamber was 33–131% higher than in outdoor pigeons. The difference was, however, significant only between CA and outdoor pigeons according to the Tukey test. BMR of outdoor pigeons showed no seasonal changes. BMR of W_i pigeons was found to be slightly lower than BMR of CA pigeons ($P < 0.05$). Mean plumage weight (wet) of S_i pigeons was lighter (18%) than the plumage of W_i and CA pigeons showing only slight seasonal changes of plumage thickness. Curiously however, plumage weight was decreased in winter pigeons (W_o) compared with summer pigeons (S_o) in outdoor conditions. The differences between groups were not significant according to the Tukey test. No significant

Table 2. Mean \pm SE of body weight (W_b , kg), metabolic rate^c (\dot{M} , W/kg), body temperature^c (T_b , °C), foot temperature^c (T_f , °C), electromyogram activity^c (EMG, μ V) and thermal conductance^f (C , cal (g·h·°C)⁻¹) at 5 °C, and mean \pm SE of basal metabolic rate (BMR, W/kg at 26 °C) and plumage weight^g (W_p , mg/cm²) of outdoor and indoor pigeons in winter and summer. $N=6$. For further explanations see Fig. 1

		W_b (kg)	\dot{M} (W/kg)	T_b (°C)	T_f (°C)	EMG (μ V)	C (cal(g·h·°C) ⁻¹)	BMR (W/kg)	W_p (mg/cm ²)
Outdoor	W_0	0.34 \pm 0.011	13.7 \pm 0.68	39.6 \pm 0.31	15.5 \pm 2.48	42 \pm 9.8 ^d	0.34 \pm 0.016	8.8 \pm 0.61	30.8 \pm 1.11 ^e
	S_0	0.34 \pm 0.005	14.0 \pm 0.79	39.2 \pm 0.36	12.5 \pm 1.58	42 \pm 3.6	0.35 \pm 0.059	8.8 \pm 0.54	37.0 \pm 1.91 ^e
Indoor	W_i	0.34 \pm 0.080	13.6 \pm 0.60	39.2 \pm 0.32	18.1 \pm 2.02	63 \pm 6.3 ^d	0.34 \pm 0.014	7.0 \pm 0.55 ^a	37.8 \pm 2.03 ^d
	S_i	0.34 \pm 0.010	13.4 \pm 0.85	40.0 \pm 0.18 ^a	16.7 \pm 1.55	56 \pm 9.8	0.32 \pm 0.021	8.1 \pm 0.78 ^d	32.0 \pm 1.45 ^d
	CA	0.34 \pm 0.010	13.3 \pm 0.41	39.1 \pm 0.21 ^a	17.0 \pm 1.72	97 \pm 11.9 ^b	0.33 \pm 0.011	9.1 \pm 0.36 ^a	37.8 \pm 0.91

^a Figures within one column, bearing superscript^a are significantly different ($P < 0.05$ according to t -test)

^b $P < 0.05$ CA vs. W_0 and S_0 according to the Tukey test

^c measured in dark metabolic chamber at 5 °C

^d $N=5$

^e $N=4$

^f Thermal conductance $C = \frac{\dot{M}}{T_b - T_a}$ (see Calder and King 1974)

^g The surface area of birds $A = 10 M^{0.67}$, M = body weight in grams (see Calder and King 1974)

differences in thermal conductance (C) between groups were observed. The lowest value of C was found in S_i pigeons.

Discussion

As shown previously with small wild birds by Hart (1962) and West (1965) the current findings were also not able to present any clear evidence on seasonal adaptation in thermoregulatory effectors of pigeons to static cold conditions (Table 2). Furthermore, our results show no marked seasonal variation in the dynamics of ptiloerection and shivering. Outdoor pigeons seem to resort slightly more to ptiloerection and also to shivering in summer than in winter when exposed in the cold (Figs. 1, 2), however, regulating their T_b 's at the same level (Fig. 1, Table 2). Similarly S_i and CA pigeons fluffed only slightly faster than W_i pigeons (Fig. 3). According to the dynamic experiment it would appear that CA pigeons shivered less than W_i and S_i pigeons (Figs. 2, 3), having however higher BMR than W_i pigeons and lower T_b than S_i pigeons (Table 2).

Unfortunately, static values show that in the metabolic chamber the EMG activity of CA pigeons was higher than the EMG activity in W_i and S_i pigeons (Table 2). This discrepancy may be due to different light conditions in Exp. 1 (light) against Exp. 2 and 3 (dark). Our recent results (unpublished) show that pigeons shiver more strongly in a dark than in a lighted metabolic chamber. From our experience the activity of birds is lower in dark than in light. Thus, to obtain standard

metabolic values we decided to perform metabolic measurements in the dark, although we did not know in advance the influence of light conditions on results. On the other hand, the visual observation of ptiloerection needs some illumination. Similarly, contrasting results in T_f 's of W_0 and S_0 pigeons during dynamic and static measurements were obtained (Fig. 1, Table 2). This is perhaps because of differences in pre-exposed T_f 's between groups. Furthermore, it is clear that T_f changes are dependent on the bird's behaviour, i.e. if it is sitting on its feet or not.

The importance of ptilomotion as a defense mechanism against heat loss in birds has been demonstrated (see Kendeigh et al. 1977). Prevention of feather fluffing was found to increase the heat loss 15–30% in some small birds and pigeons at 0 °C. Quantitative measurements of feather posture over a range of T_a from 5 to 45 °C have been made in the barbary dove by McFarland and Baher (1968). Their curve of FI tallies is similar to our pre-exposure mean scores of FI in pigeons at 28 °C. Similar to the results of Wallgren (1954) in two bunting species and to those of McFarland and Baher (1968) in barbary doves, the degree of ptiloerection in our experiments continued to increase as the T_a fell far below the lower critical temperature; the maximum (FI=12) was reached only by S_0 pigeons. Supposedly the thermal conductance of the bird is not minimized at the lower critical temperature (see also Calder and King 1974; Hill et al. 1980) as predicted by Scholander et al. (1950). This was supported by infrared radiographic studies by Hill et al. (1980), which showed

a decrease of thermal conductance (C) of the plumage by 12–17% when T_a fell from 10 to -16 °C. The decrease of C resulting from the increasing degree of ptiloerection can not be quantified with the methods of the present study. However, our calculations show indirectly that C is smallest in S_i and CA pigeons after cold exposure (see Table 2). Both groups also had the most intense and rapid increase in ptiloerection (Fig. 2 and 3). Plumage weight was found to increase (18%) in winter and during cold-acclimation compared with S_i pigeons. The unsynchronized molting of the different groups might have affected the results. However, the values agree with the predicted plumage weight (wet) obtained from the equation of Turček (1966) ($W_p = 36.4 \text{ mg/cm}^2$).

In agreement with the results of Hart (1962) and West (1965) we found no significant seasonal differences in muscle EMG activity. However, the dynamic response was fastest in CA pigeons (Fig. 3). W_0 pigeons may compensate reduced shivering and FI responses to cooling by better vasoconstriction (Fig. 1). The influence of cold-acclimation seems to be different showing that also other environmental factors, such as changes in photoperiodism, are involved in the acclimatization process. Because only slight variation in EMG responses and no variation in BMR, \dot{M} and T_b at 5 °C were found, it can be suggested that the same electrical activity of shivering produces more heat in winter-acclimatized birds than in summer-acclimatized ones, as was implied by Hart (1962), and as also shown in cold-acclimated rats (Ivanov 1980). An increase in \dot{V}_{O_2} per unit electrical activity is also observed as a result of cold-adaptation in mammals and birds (Slonim 1971). The increased thermogenic capacity is further revealed by increased lipid supplies and by the amount of glycogen in the breast muscles and in the bird's increased ability to use these reserves in winter (Hart 1962; Carey et al. 1978; Southwick 1980).

The increased sympathetic and thyroid activity in winter (Kendeigh and Wallin 1966; Ljunggren 1968; Koban and Feist 1982) is supposedly reflected in metabolism, including enhanced metabolic capacity of winter-acclimatized birds. Schwan and Williams (1978) found slightly augmented BMR in winter-acclimatized ravens, while \dot{M} was not significantly different at T_a 's ranging from $+35$ to -80 °C. According to our results, no significant seasonal fluctuation could be found. Paradoxically the mean BMR of W_i pigeons was lower than in S_i pigeons. The mean BMR's fit well with the values predicted for domestic birds (including pigeons) in the equation of Brody (1945)

(BMR = 7.0 W/kg), and those predicted for non-passerine birds in the equation of Prinzinger and Hänsler (1980) (BMR = 7.3 W/kg).

In conclusion it can be stated that although seasonal acclimatization in birds is known to involve many physiological adaptation processes, any significant changes in response velocities of ptiloerection and shivering were not observed in the present study.

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