THERMAL ADAPTIVENESS OF PLUMAGE COLOR IN SCREECH OWLS

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CLINAL variation in the relative proportions of red and gray plumage phases in Screech Owls (*Otus asio*) was analyzed by Owen (1963) and Marshall (1967). This variation was well known prior to Owen's work, but was misinterpreted (Baird, et al. 1874, Hasbrouck 1893, Allen 1893).

Laurel VanCamp and Charles Henny (MS) have 30 years of data on a northern Ohio Screech Owl population. They observed an overwinter decline (from about 25% to 15%) in the proportion of red phase birds in the winter of 1951–52. This decline was correlated with a severe winter of above normal snowfall and below average temperatures. They examined banding and recovery data and found overwinter survival of red and gray birds to be the same except for this one severe winter when 44% more red phase birds were lost than gravs (VanCamp and Henny MS). Differential mortality was reported by Gullion and Marshall (1968) for red and gray phase Ruffed Grouse (Bonasa um*bellus*) where snow conditions for roosting is apparently the critical factor for grouse overwinter survival and is related to predation. Snowroosting has not, to our knowledge, been observed in Screech Owls. VanCamp and Henny (MS) discuss the observations of Ruffed Grouse and Screech Owls and suggest that possible thermoregulatory differences between red and gray phase birds could account for differential overwinter survival.

Our objective was to test for differences between color phase in oxygen uptake at several ambient temperatures. We hypothesized that oxygen uptake would be greater by red phase birds, especially at lower temperatures.

METHODS AND MATERIALS

Ten Screech Owls were captured at nest sites in northern Ohio during February 1975 and shipped via air express to Utah. Transit time was less than 12 h. Two birds died within 1 day of arrival, the remaining eight birds (4 red and 4 gray) were housed in cardboard boxes ($25 \times 25 \times 25$ cm) equipped with a perch bar and wood shavings on the floor. The birds were kept in the laboratory at a constant temperature of $22^{\circ} \pm 1^{\circ}$ C and 24 h light. Their diet consisted of day-old chickens with an occasional quail (*Coturnix coturnix*) chick.

Oxygen consumption (V_{0_2}) was measured in an open flow system (about 2.5 1/min, STP) using the appropriate formula of Depocas and Hart (1957). All birds of the same color phase were measured on the same day in random order within color phase. The birds were weighed to the nearest 0.1 g and placed in

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Fig. 1. Oxygen consumption (V_{0_2}) versus ambient temperature (T_a) for red and gray phase Screech Owls. Regression equations are $V_{0_2} = 3.06-0.08T_a$, r = 0.88 and $V_{0_2} = 2.92-0.05T_a$, r = 0.62 for red and gray phase owls respectively. Slopes are significantly different at P = 0.001.

the metabolism chamber (a wide-mouthed 1 gal glass jar) in a walk-in temperature control box between 0900 and 1000. At least 1 h was allowed for adjustment to the chamber temperature and for the birds to calm down after being handled. Half-hour records of oxygen concentration in the outlet air (Vo₂) were made for each bird. The temperature was then reset and a 1-h wait followed establishment of the new temperature before measurements were made again as described above.

TABLE 1

Analysis of Variance for the Model $V_{0_2} = C + B + T + BT + e^1$

Source	df	Sum of Squares	Fratio	α
Mean	1	819.070		
Color	1	0.304	0.463	NS (0.01)
\mathbf{Bird}	6	3.942	3.634	0.005
Temperature	3	42.929	60.268	0.001
$C \times \tilde{T}$	3	4.573	6.431	0.005
B×T	18	4.274	1.313	NS (0.01)
Error	67	12.115		· - · · · · · · · · · · · · · · · · · ·
${ m Total} m r^2=0.822$	99	887.210		

 1 Model terms are C = color, B = bird, and T = temperature.

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TABLE 2	2
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Color phase	Temperature (°C)				
	-10	-5	5	15	
Red $4.07 \pm 0.12(8)$		$3.48 \pm 0.15(8)$ 2.67 $\pm 0.10($	$2.67 \pm 0.10(8)$	$1.87 \pm 0.12(8)$	
Gray	$3.52 \pm 0.12(8)$	$2.72 \pm 0.15(8)$	$3.00 \pm 0.11(8)$	$1.98 \pm 0.12(4)$	

MEAN OXYGEN CONSUMPTION OF RED AND GRAY PHASE Screech Owls versus Ambient Temperature¹

¹ Oxygen consumption is in $ml/g \cdot h \pm standard$ error (sample size).

 V_{0_2} was measured at -10°, -5°, 5°, and 15°C. These data were analyzed by the analysis of variance model $V_{0_2} = C + B + T + C \times T + B \times T + e$, where C is color phase, B is individual bird and T is temperature. Comparisons were made to test for any difference in V_{0_2} response at different temperatures between the two color phases.

RESULTS

The results of the analysis of variance are presented in Table 1. The model accounts for 82.2% of the variation in V_{O_2} . Individual bird, temperature, and color \times temperature interaction are significant. There is no significant bird \times temperature interaction, and color is not significant by itself. Fig. 1 depicts the relationship between V_{O_2} and ambient temperature (T_a) for red and gray owls. The mean V_{O_2} for the two color phases at each of the four temperatures is presented in Table 2. The 95% confidence limits for the means at -5° and -10° do not overlap.

The effect of T_a on body temperature is shown in Table 3. There is no significant difference between the mean difference in body temperature for red and gray owls.

		Tem] (Tomporatura		
Individuals		25°	5°	change	
Red	1	37.0	35.8	-1.2	
	2	39.0	36.0	-3.0	
3 4 Mean	3	38.0	35.0	-3.0	
	4	39.0	36.0	-3.0	
	Mean	38.3	35.7	-2.6	
Gray	1	39.1	34.5	-4.6	
	2	37.3	34.0	-3.2	
	3	36.0	34.5	-1.5	
4	4	38.0	36.0	-2.0	
	Mean	37.6	34.8	-2.8	
0	verall mean	37.9	35.2	-2.7	

TABLE 3

BODY TEMPERATURE	(T_b) V	/ERSUS	Ambient	Temperature	(T_a)
FOR R	ED AND	GRAY	Screech	Owls	

Mean body weights for the red and gray owls over the duration of the study were 173 (n = 32) and 159 (n = 28) respectively. These means are significantly different at $\alpha = 0.05$ but not at $\alpha = 0.01$.

DISCUSSION

We conclude that red phase Screech Owls have significantly higher metabolic requirements below -5° C than do gray phase owls. This higher metabolic requirement, coming at a time when heavy snowfall reduces hunting efficiency, could cause a differential mortality between the color phases. It is important to note that our test temperatures are realistic when compared with the field observations of VanCamp and Henny (MS). During the winter when they noted the red phase mortality they recorded 17 consecutive days of 10 cm plus of snow cover with 6 days of 25 cm or more, and 8 consecutive days below 0° C with a low of -23° C during December.

The conditions under which we measured oxygen uptake preclude the possibility that the differences between color phases were due to differential absorption of radiant energy as demonstrated for light and dark birds by Lustick (1969). Our tests were run under fluorescent lights (G.E. F96T12[·]CW[·]HO) placed at least 1.5 m above the birds, and the birds were shaded from the direct light by the jar tops. The differences may be due to differences in plumage conductance or fundamental physiological differences genetically linked with color phase.

VanCamp and Henny (MS) discount differential predation as an important factor responsible for change in color phase ratios in the Screech Owls. Our data support this conclusion in that they suggest a simpler, more direct explanation for the observed population change.

The effect of body weight on metabolic rate has long been recognized and must be accounted for in studies of energy metabolism. In this study the larger red owls ($\alpha = 0.05$) had significantly higher weight specific metabolic weights in direct contrast to the expected result if a body weight effect was measured, as the larger birds should have had a lower weight specific metabolic rate. This adds further support to our hypothesis, as we were able to show metabolic differences between the color phases in spite of an opposite acting body weight effect.

The significant variability from bird to bird (Table 1) and lability of body temperature (Table 3) were problems in this study. More acclimation to the test conditions could have reduced the first problem, although the significant color \times temperature interaction in the face of high bird variability can be interpreted favorably. Lability of body temperature has been previously reported in Screech Owls by Ligon (1969). He reported a range of 37°C at 10°C to about 41°C at 35°C. These values are consistent with ours (Table 3). We do not know the extent to which the depression of body temperature might reduce oxygen uptake by the van't Hoff effect, but the body temperature depression was the same for both color phases. Our rates of oxygen uptake differ from those reported for Screech Owls by Ligon (1969) where our study temperatures overlap. It must be supposed that our birds were not truly at a resting state and we were seeing the effects of some activity or unrest. While this difference may tend to cloud the issue, what is important is that both color phases were measured under the same conditions. A true resting metabolic rate was not the goal of this study.

Two population phenomena need to be incorporated into our hypothesis or at least explained. Red phase Screech Owls make up as low a proportion of the population in the Gulf Coast states as they do in the northern limits of their range. In the middle latitudes the red phase birds predominate (Owen 1963). This suggests an intolerance of hot, humid regions similar to that noted for cold climates. The absence of red phase birds in the West is likewise not explained by our hypothesis. Without physiological data for birds from these areas, we can merely suggest that environmental differences may exist in humidity or temperature that account for the population distributions. Few ecological phenomena are explainable on the basis of a single factor, and other factors will be operating in conjunction with the metabolic differences we demonstrated in this paper to control color phase distribution.

SUMMARY

We measured oxygen consumption rates of 8 Screech Owls (4 red and 4 gray phase) at 4 environmental temperatures, -10° , -5° , 5° , and 15° C. These data demonstrated a significant difference in oxygen uptake between color phases at -10° and -5° C. This supports our hypothesis that red phase Screech Owls are restricted in their northern distribution by color-related metabolic differences from the gray phase birds. The problems of low red phase occurrence in the Gulf Coast states and their absence from the Western states remain to be studied.

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