

METABOLIC RATES OF RED-TAILED HAWKS AND GREAT HORNED OWLS¹

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Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) are common raptors in Michigan and throughout most of the United States. Although breeding ranges of both species are very similar, winter ranges of Great Horned Owls remain considerably farther north than Red-tailed Hawks. Both species are very similar in size and their utilization of habitat and prey (Orlans and Kuhlman 1956, McInville and Keith 1974, Petersen 1979, Chaplin et al. 1984). Even their home ranges overlap greatly in many areas (Craighead and Craighead 1969). In fact, the most notable ecological difference between them in addition to winter range differences is the nocturnal vs. diurnal activity period of Great Horned Owls and Red-tailed Hawks.

Little information is known about the metabolism of these species, especially as metabolic rates may relate to their winter ranges. We investigated the metabolic rates of Great Horned Owls and Red-tailed Hawks to provide a comparison of these ecologically similar species. We predict that (1) the metabolic response of Great Horned Owls to decreasing temperature would be less than the metabolic response of Red-tailed Hawks, and (2) Great Horned Owls have lower critical temperatures than Red-tailed Hawks.

METHODS

Six adult Great Horned Owls and six adult Red-tailed Hawks (each species consisted of two females and four males) were obtained from injured animals that were anatomically whole and had normal plumage but could not be returned to the wild. Birds were maintained in captivity for several months prior to the determination of metabolic rates and were housed in an unheated indoor pen open to the outdoors and subject to natural photoperiod and temperature. Small mammals (mice or hamsters) were fed to the birds every other day. Water was available ad libitum. The sex of each bird was determined by internal anatomical examination after all laboratory trials were completed.

Metabolic rates of the birds were determined in March 1986. Oxygen measurements were obtained at six target temperatures (-50°C , -35°C , -20°C , -5°C , 10°C , and 25°C) for each bird. Metabolic measurements at the three highest temperatures and at the two lower temperatures (i.e., -35°C and -20°C) were obtained

on the same day, while measurements at -50°C were obtained on separate days. All trials were done during the daytime. The trial schedules were randomized, and the same bird was not used more than once during a 5-day period. Species were alternated between trials. Each bird was fasted for 24 hr prior to a trial and weighed to the nearest gram prior to being placed in the dark chambers where they could perch but could not move around.

Oxygen consumption was measured in an open circuit system (Hill 1972) using an Applied Electrochemistry S-3A Oxygen Analyzer with Ascarite as the absorbent for carbon dioxide and Drierite as the desiccant. Two polyvinyl chloride metabolic chambers ($35\text{ cm} \times 76\text{ cm} \times 46\text{ cm}$) were simultaneously housed in a Kelvinator ultra cold environment chamber (-76°C to 40°C). Two birds were tested at the same time, with separate oxygen sampling for each metabolic chamber.

When testing a bird at more than one temperature per day, 1 hr was allowed for adjustment after each new target temperature was reached, and temperatures were always lowered for successive tests. After an initial adjustment period of 3 hr for the bird in the metabolic chamber, four 5-min oxygen samples and the ambient temperatures were measured over a 1-hr period. The rate of oxygen consumption was calculated using equation (4) in Hill (1972) based on the average of the oxygen and temperature reading during the sampling period. Conversion of oxygen consumption to watts was made for comparison with other studies using standard units ($1\text{ ml O}_2/\text{g}/\text{hr} = 4.8\text{ cal}/\text{hr}$; $1\text{ cal}/\text{hr} = 1.163 \times 10^{-3}\text{ W}$).

Differences in standard metabolic rate (SMR) between species and sex were compared using an ANOVA. Least squares linear regression was used to evaluate the effect of temperature on metabolic rate. Differences in regression equations between species and within each sex were tested with analysis of covariance (Zar 1973).

Lower critical temperatures (T_c) of each distinct metabolic group were estimated as the point where a horizontal line through the mean metabolic rate at 25°C intersected the regression line for the metabolic rate at temperatures of -50°C , -35°C , -20°C , and -5°C .

RESULTS

Female Great Horned Owls and Red-tailed Hawks weighed $1,588 \pm 147\text{ g}$ and $1,384 \pm 205\text{ g}$, respectively, and were significantly ($P < 0.05$) greater than $1,229 \pm 106\text{ g}$ and $1,067 \pm 163\text{ g}$ for males, respectively.

SMR of Great Horned Owls was $0.491 \pm 0.133\text{ ml/g}/\text{hr}$ and slightly ($P < 0.10$) lower than $0.739 \pm 0.244\text{ ml/g}/\text{hr}$ for Red-tailed Hawks. Female Great Horned Owls had a significantly lower SMR of 0.343 ± 0.044

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ml/g/hr than males which was 0.566 ± 0.080 ml/g/hr ($P < 0.05$). There was no significant difference in SMR of female (0.808 ± 0.236 ml/g/hr) and male (0.705 ± 0.275 ml/g/hr) Red-tailed Hawks.

A negative linear relationship ($P < 0.001$) existed between temperature and oxygen consumption between -50°C and -5°C for both species (Fig. 1). The rate of increase of oxygen consumption with decreasing temperatures for Red-tailed Hawks (mixed sexes) was significantly higher ($P < 0.01$) compared with the rate for Great Horned Owls. Although there were no differences in slopes of the regression for male and female Great Horned Owls, the elevation of the metabolic rate for males was 0.124 ml/g/hr higher ($P < 0.05$) than for females. Metabolic rates of Red-tailed Hawks differed by sex, with females having a lower slope than males ($P < 0.01$).

Estimated T_{lc} of male and female Great Horned Owls, 17.8°C and 24.9°C , were significantly higher ($P < 0.01$) than 2.1°C and 10.7°C for male and female Red-tailed Hawks, respectively.

DISCUSSION

Benedict and Fox (1927) reported the SMR of Great Horned Owls as 3.10 W with an average weight of 1.45 kg which compares favorably with our values of 3.03 W for female and 3.88 W for male Great Horned Owls with an average weight of 1.59 kg and 1.38 kg, respectively. Kasparie (1983) found that the SMR of Great Horned Owls (mixed sexes, average weight 1.412 kg) was 0.6 cc $\text{O}_2/\text{g}/\text{hr}$ (3.50 W).

Energy expenditure at thermoneutrality for Red-tailed Hawks was 6.24 W for females and 4.20 W for males adjusted for body weights. Wasser (1986) reported that the oxygen consumption for this species with an average weight of $1,475$ g was 0.386 cc $\text{O}_2/\text{g}/\text{hr}$ (2.15 W), while Hayes and Gessaman (1980) gave the value of 0.42 cc $\text{O}_2/\text{g}/\text{hr}$ (2.34 W).

A number of factors may influence the rate of oxygen consumption of an animal including activity, temperature, body size, stage in the life cycle, season and time of day, sex of an animal, and genetic background (Prosser 1973). Few studies have examined the influence of sex on the metabolic rates of wild birds. Male Mourning Doves (*Zenaida macroura*) were found to have higher metabolic rates than females (Riddle et al. 1934), as were male domestic fowl, *Gallus gallus* (Kibler and Brody 1944). No difference was found in the SMR of male and female Wild Turkeys (*Meleagris gallopavo*), despite males being larger than females, although metabolic costs for females below the T_{lc} were greater than for males (Gray and Prince 1988). Female Mallards (*Anas platyrhynchos*) had higher metabolic rates than males (Smith and Prince 1973).

Most raptors, including the two species we studied, have reverse sexual dimorphism (females are bigger than males). Although sexes of Red-tailed Hawks did not significantly differ in SMR, female Great Horned Owls had a lower SMR than males. The heavier female Great Horned Owl appears to be a more efficient user of energy which could be important in light of the early reproductive chronology of the species. Sex did influence the rate of energy consumption below the T_{lc} of Red-tailed Hawks, with the smaller males utilizing in-

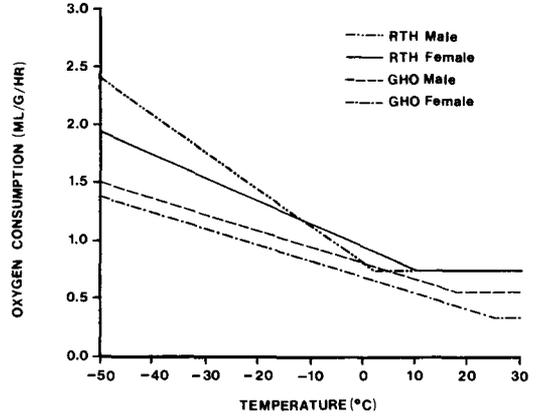


FIGURE 1. Oxygen consumption of male ($n = 4$, $Y = 0.809 - 0.034T \pm 0.005$, $r^2 = 0.73$) and female ($n = 2$, $Y = 0.954 - 0.020T \pm 0.003$, $r^2 = 0.85$) Red-tailed Hawks (RTH) and male ($n = 4$, $Y = 0.815 - 0.14T \pm 0.001$, $r^2 = 0.84$) and female ($n = 2$, $Y = 0.691 - 0.014T \pm 0.001$, $r^2 = 0.90$) Great Horned Owls (GHO) in relation to temperature.

creasingly more energy per gram than females. T_{lc} of Red-tailed Hawks was the reverse of that predicted for the species compared to Great Horned Owls. This appears to be caused by the lower SMR and thus heat production of Great Horned Owls which required the owls to utilize additional energy for thermoregulation at a higher temperature than the Red-tailed Hawks.

Great Horned Owls display an energetic advantage over Red-tailed Hawks in northern climates. They have a lower SMR and, more importantly, a lower rate of energy production with decreasing temperature which keeps the thermoregulatory energy budget of Great Horned Owls well below that of Red-tailed Hawks. This allows the nonmigratory Great Horned Owl to endure severe winter conditions more efficiently than Red-tailed Hawks.

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ANALYSIS OF A DIALECT BOUNDARY IN CHACO VEGETATION IN THE RUFIOUS-COLLARED SPARROW¹

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Key words: Dialects; vocalizations; Rufous-collared Sparrow; *Zonotrichia capensis*.

Examinations of the relationship between culturally transmitted traits, like bird song, and ecological attributes are particularly important in the study of avian song dialects. Correlation between habitat and bird song is the foundation of the genetic adaptation hypothesis developed by Nottebohm (1972). In the genetic adaptation hypothesis, a dialect functions as a recognition signal among individuals of a local population which is adapted to a particular habitat and which is genetically distinct from neighboring populations in different habitats (Payne 1981). Such ecological correlates may also reflect adaptation of song characteristics to acoustic properties of different habitats (the acoustic adaptation hypothesis, e.g., Wiley and Richards 1982). There are a number of studies in which correlations between bird song and habitat have been examined. For example Baker et al. (1982) found no relationship between four dialects in *Zonotrichia leu-*

cophrys nutalli and the coastal scrub vegetation of their study area, although the dialect populations appeared to be genetically differentiated to some degree. Hunter and Krebs (1979) suggested that differences in territorial songs of *Parus major*, the Great Tit, between dense forest and open woodland were, in part, due to differences in acoustic characteristics of their respective habitats.

The occurrence of vocal dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, has been well documented (Nottebohm 1969, 1975; King 1972; Handford and Nottebohm 1976). The typical song of *Z. capensis* consists of an introductory theme with between one and five whistled notes, followed by a trill, a series of similar, brief notes (Nottebohm 1975). Nottebohm (1975) and Handford (1981, 1988) have demonstrated a consistent association between the rate of the terminal trill (the dialect-discriminating variable) and vegetation over a large area in northwestern Argentina. However, there have been few fine-grained analyses of dialect boundaries (Nottebohm 1975, Handford and Nottebohm 1976). In these studies, dialect boundaries were usually sharply demarcated and located in areas where vegetation types changed rapidly.

Here we provide a detailed description of a dialect

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