

# THE FASTING METABOLISM OF SUBADULT MALLARDS ACCLIMATIZED TO LOW AMBIENT TEMPERATURES

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The physiological stress imposed upon a wild animal during the winter months is among the most critical in the organism's life (West 1960; Sturkie 1965; Brocke 1968; Gordon 1968). Kendeigh (1944) stated that temperature is one of the most important environmental factors controlling distribution, migration, abundance, and time and extent of breeding of wild birds under normal outdoor conditions. Lefebvre and Raveling (1967) have related the distribution of two races of the Canada Goose (*Branta canadensis*) in winter to body size and corresponding estimates of heat loss. Temperature as well as other abiotic factors have been correlated to seasonal and daily behavior among avian species by Salt (1952), West (1960), Cox (1961), and Reed and Prince (1974). If ambient temperatures upset the equilibrium between heat production and loss, the animal's behavior must be altered to maintain homeostasis. Fundamentals of energy exchange in endotherms and the literature dealing with avian bioenergetics have been reviewed from many points of view by Irving (1955), Hart (1957), Kleiber (1961), King and Farner (1961), and West (1962).

The Mallard (*Anas platyrhynchos*) has a circumpolar distribution in the Northern Hemisphere and among waterfowl is probably the most abundant species (Delacour 1964). Although there has been no previous attempt to determine the maintenance energy of a Mallard during winter's extreme conditions, a significant correlation was observed between decreasing temperature and decreasing activity for 6000–8000 Mallards wintering in southeastern Michigan (Reed and Prince 1974). In order to clarify this relationship, metabolic responses to temperature should be evaluated. This study was designed to quantify the resting metabolic requirements of the Mallard as a function of temperature.

## MATERIALS AND METHODS

Forty 7-month-old Mallards were used in the experiments. The birds were progeny of "game farm" Mallards obtained from the Max McGraw Wildlife Foundation, Dundee, Illinois. The birds were fed a ration of two parts corn and one part Purina Flight Conditioner ad libitum, and maintained in  $7 \times 3 \times 3$  m outdoor pens containing a heated water supply from October–February. Ambient temperature in the pens was recorded daily.

Prosser and Brown (1950) define  $QO_2$  as milliliters of oxygen (S.T.P.D.) consumed per gram dry weight per hour. In this study,  $QO_2$  refers to milliliters of oxygen (S.T.P.D.) consumed per gram wet weight per hour.  $QO_2$  values were obtained manometrically based on a constant pressure changing volume respirometer, as discussed by Reineke (1961). A  $20 \times 35 \times 40$  cm plexi-glass chamber with five ports was constructed. A 50-cc gas syringe, manometer, copper-constantan thermocouple, air inlet tube, and exhaust were arranged in the five openings of the respirometer. A copper screen bed of indicating Ascarite (sodium hydrate asbestos) was attached to the door of the chamber. A pilot study revealed that at the thermal condition of maximum  $CO_2$  production,  $150 \text{ cm}^2$  of Ascarite were saturated in 4 hr. An air pump was used to ventilate the system during the acclimation period and between each  $QO_2$  determination. It was found that an adult male Mallard could survive in the chamber without the air pump for 4 hr before chronic anoxia became fatal. A mercurial barometer was used to determine atmospheric pressure and the copper-constantan thermocouple with a millivolt recorder monitored ambient temperature ( $T_A$ ).  $T_A$  was controlled by an environmental chamber with a temperature range of  $-30$  to  $50^\circ\text{C} \pm 1^\circ\text{C}$ .

Metabolic rates of the birds were determined from 15 January–15 February. Ducks were fasted for 18 hr before oxygen consumption was determined. Even though a postabsorptive state was relatively assured after 18 hr (Benedict and Lee 1937; Sleeth and Van Liere 1937), a mixed caloric conversion for both fat and protein catabolism of 4.825 Kcal/liter  $O_2$  was used. Weights of both sexes were recorded before and after the fasting period.

The precooled respiratory chamber was darkened during the 2.5-hr acclimation period and during the  $QO_2$  determinations. At the end of this period, the air pump was stopped and the chamber was sealed. Fifty milliliters of air were injected from the gas syringe into the chamber; the length of time required to consume the volume of air, as determined by the manometer, was used to calculate oxygen consumption per gram per hour. One measurement was taken

every 5 min and the measurements were rejected if  $T_A$  fluctuated  $\pm 1^\circ\text{C}$  during the 30-min test period. If a fluctuation of  $\pm 1^\circ\text{C}$  occurred, no measurement was attempted until the  $T_A$  returned to its previous value.

Five birds of each sex were randomly chosen and subjected to one of four temperature zones centering around  $-8^\circ\text{C}$ ,  $0^\circ\text{C}$ ,  $10^\circ\text{C}$ , and  $20^\circ\text{C}$ . No bird was used twice. Any movement by the bird in the chamber was readily detected by fluctuations in the manometer fluid level, and measurements were accepted only if the animal was quiet. Condensation or ice was present in the chamber after 3 hr at all of the test temperatures, indicating that the atmosphere was saturated with water vapor and thus simplifying the conversion of the volume of oxygen from ambient temperature-pressure-saturated (A.T.P.S.) to standard temperature-pressure-dry (S.T.P.D.). In a saturated system,  $P_{H_2O}$  equals the aqueous vapor pressure; therefore, aqueous vapor pressure at the specific  $T_A$  was subtracted from the barometric pressure to standardize the volume of air.  $QO_2$  was determined from 10:30 to 11:00 for females and 14:00 to 14:30 for males.

Body weight data were analyzed with a two-way analysis of variance (Steel and Torrie 1960) using the model  $X_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \epsilon_{ij}$  where  $X_{ij}$  equals the individual duck weight,  $\mu$  equals the parametric mean,  $\alpha_i$  equals the  $i^{\text{th}}$  treatment effect ( $i = 1 \dots a$ ), with the treatments representing the weight before and after the 18-hr fast,  $\beta_j$  equals the  $j^{\text{th}}$  block effect ( $j = 1 \dots b$ ) with the blocks representing sex,  $\alpha\beta_{ij}$  represents the interaction of sex and weight loss, and  $\epsilon_{ij}$  equals the random, experimental error (independently and normally distributed about zero mean and with a common variance). The effects of temperature on  $QO_2$  and caloric values were determined using the polynomial regression routine discussed in Cooley and Lohnes (1971). Standard linear and quadratic models were sufficient to explain these effects. Treatment separations without the added effects of temperature for differences between sexes were accomplished with an analysis of covariance (Steel and Torrie 1960) using the model  $Y_{ij} - \beta(X_{ij} - \bar{x}_{..}) = \mu + \alpha_i + \epsilon_{ij}$  where  $Y_{ij}$  equals the oxygen consumption of an individual duck,  $\beta(X_{ij} - \bar{x}_{..})$  equals the adjustment for regression of oxygen consumption on temperature,  $\mu$  equals the parametric mean,  $\alpha_i$  equals the  $i^{\text{th}}$  treatment effect ( $i = 1 \dots a$ ) with the treatments representing male and female oxygen consumption, and  $\epsilon_{ij}$  equals the random, experimental error (independently and normally distributed about zero mean and with a common variance). This model provides for the known relationship with temperature, allowing an analysis of variance on adjusted treatment means. It is assumed that temperature is a fixed variable and measured without error, that the regression of oxygen consumption on temperature is linear, and that the error is random and in an independent, normal distribution about zero mean with a common variance. Unless otherwise stated, in all cases where statistical significance is indicated  $P < 0.001$ . Analyses were conducted on the CDC 6500 computer at the Michigan State University computer center.

RESULTS

Average body weights of 7-month-old male and female Mallards were significantly different before and after the 18-hr fast (table

TABLE 1. Body weights ( $\bar{x} \pm \text{S.E.}$ ) before and after an 18-hr fast.

Sex	n	Av. wt. (g) before fast	Av. wt. (g) after fast	Av. wt. (g) lost
Female	20	1084 $\pm$ 21 <sup>a</sup>	1012 $\pm$ 20 <sup>c</sup>	71 $\pm$ 5 <sup>e</sup>
Male	20	1248 $\pm$ 25 <sup>b</sup>	1166 $\pm$ 22 <sup>d</sup>	72 $\pm$ 6 <sup>e</sup>

Any two values in a row or column having the same superscript (a, b, c, d, e) are not significantly different.

1). The males and females responded similarly to fasting and experienced a weight loss of 6.5% and 5.7% of the total body weight, respectively. The temperature during the period of fast in the outdoor pens varied from  $-30$  to  $10^\circ\text{C}$ . No mortality was observed. There was no relationship between maximum, minimum, or average daily temperatures during the period of fast and weight loss.

Several times the black cover over the respiratory chamber was lifted briefly to observe behavior. At lower temperatures, the birds would exhibit gross muscular activity, but eventually settle into the resting position. Once at rest, shivering was observed.

There was a significant linear relationship between increasing oxygen consumption and decreasing ambient temperature for both sexes (fig. 1). Although there is no significant difference between the regression coefficients, covariance analysis of the regression lines showed a significant difference in the elevation of the lines. The males consumed larger quantities of oxygen per gram body

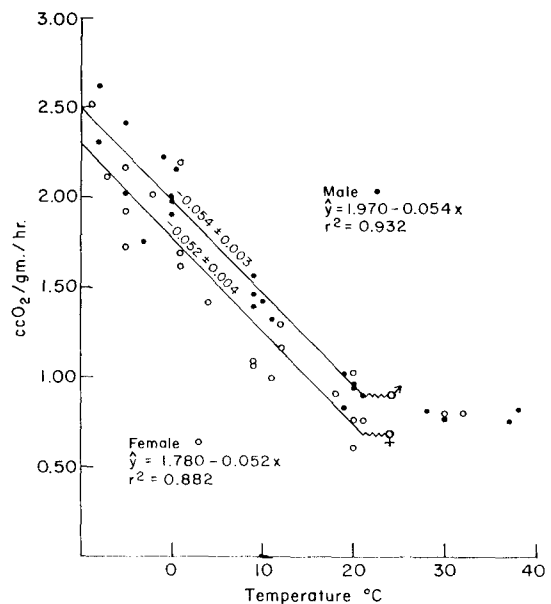


FIGURE 1. Metabolic rates of male and female Mallards under varied temperatures expressed in cc  $O_2$ /g/hr. Six  $QO_2$  values (above  $25^\circ\text{C}$ ) are shown, but are not included in the regression analysis.

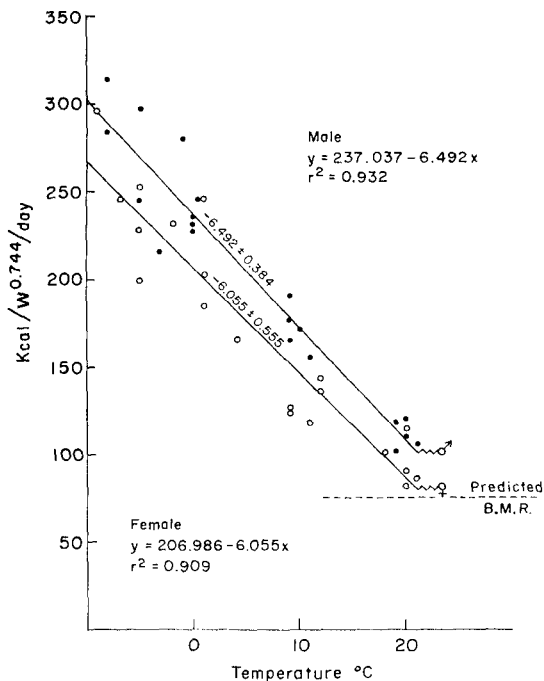


FIGURE 2. Metabolic rates of male and female Mallards under varied temperatures expressed in  $\text{Kcal}/\text{wt}^{0.744}/\text{day}$ . Predicted B.M.R. calculated by the equation  $M = KWt^{0.744}$  from King and Farner (1961).

weight over the temperature range than females. The coefficient of variation for  $\text{QO}_2$  values of five males at  $-8^\circ\text{C}$ ,  $0^\circ\text{C}$ ,  $10^\circ\text{C}$ , and  $20^\circ\text{C}$  was 15, 6, 6, and 7%, respectively, and 14, 17, 9, and 16% for five females at each of the respective temperature zones. The high coefficients of determination ( $r^2$ ) imply that a large percentage of the variation in  $\text{QO}_2$  can be explained by the independent variable, temperature. During a pilot study, oxygen consumption for an additional four males and two females was determined at temperatures ranging from  $28$ – $38^\circ\text{C}$  (fig. 1). A mean of  $0.77 \pm 0.02$  cc  $\text{O}_2/\text{gm}/\text{hr}$  was similar to the  $\text{QO}_2$  at  $22.1^\circ\text{C}$  for the males and  $19.4^\circ\text{C}$  for females, suggesting that the lower critical temperature is in the vicinity of  $20^\circ\text{C}$ .

A caloric value of 4.825 Kcal/liter  $\text{O}_2$  was used to convert oxygen consumption to Kcal of heat produced. Energy produced per day was then divided by the metabolic body size ( $W^{0.744}$  King and Farner 1961) so comparisons of metabolic rates could be made independent of body weight (fig. 2). For both sexes the theoretical, inverse, linear relation between the amount of energy produced and decreasing temperature was observed. The  $r^2$  values remained high, and the sexual dimorphism in metabolism at all of the test

temperatures remained evident. Using the body weights of our Mallards, a predicted basal metabolic rate of  $74.3 \text{ Kcal}/W^{0.744}/\text{day}$  was calculated (fig. 2) according to King and Farner's formula (1961) which assumes no sex difference in basal metabolism. The conversion of oxygen consumption from the data above  $25^\circ\text{C}$  to energy gave a value of  $91.1 \text{ Kcal}/W^{0.744}/\text{day}$ . When energy production was expressed as Kcal/day, a significant ( $0.01 < P < 0.025$ ) quadratic effect of temperature was observed for the females [ $y = 203.42 - 8.153 (\pm 0.839)x + 0.134 (\pm 0.54)x^2$ ,  $r^2 = 0.932$ ], while the relationship remained linear for the males [ $y = 265.705 - 7.529 (\pm 1.323)x$ ,  $r^2 = 0.933$ ]. Because no quadratic effect was observed for the females when the data were expressed as  $\text{Kcal}/W^{0.744}/\text{day}$ , it is assumed that random experimental differences in female body weight were responsible for the curvilinear relationship.

## DISCUSSION

Both male and female Mallards appeared to maintain homeostasis at low ambient temperatures in the same manner. The importance of metabolic determinations of wintering Mallards above  $25^\circ\text{C}$  is questionable. This, plus acute thermal polypnea causing pressure differentials in a constant pressure apparatus, precluded more than six  $\text{QO}_2$  determinations above  $25^\circ\text{C}$ . Although the values were comparable to those at  $20^\circ\text{C}$ , more information is needed to confidently mark a zone of thermoneutrality. Individual variation in heat production below  $0^\circ\text{C}$  suggests a differential ability to adapt as lower temperature extremes are approached.

Physical thermoregulatory mechanisms create the maximum effectiveness of insulation at the lower critical temperature of the theoretical zone of thermoneutrality. Below the lower critical temperature, the rate of heat loss (thermal conductance) remains constant (Gordon 1968). Although thermal conductivity is inversely related to thickness of subcutaneous fat and density and insulative properties of the plumage, it may vary with several other factors such as blood circulation and evaporation rates (Gordon 1968). A comparison of weight and weight-specific conductance is made for several avian species in table 2. A curvilinear relation appears to exist between increasing body weight and decreasing thermal conductance. The relatively low thermal conductivity of  $0.053$  cc  $\text{O}_2/\text{gm}/\text{hr}/^\circ\text{C}$  for the Mallard suggests that it is capable of surviving in a variety of

TABLE 2. Thermal conductance of several avian species.

Species	Weight (g)	Thermal Cond. cc O <sub>2</sub> /g/hr/°C	Reference
Black-chinned Hummingbird ( <i>Archilochus alexandri</i> )	3.3	0.500	Lasiewski 1963
Black-capped Chickadee ( <i>Parus atricapillus</i> )	10.6	0.283	Herreid and Kessel 1967
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	25.8	0.183	Herreid and Kessel 1967
Cardinal ( <i>Cardinalis cardinalis</i> )	40.0	0.100	Dawson 1958
Evening Grosbeak ( <i>Hesperiphona vespertina</i> )	58.0	0.100	Dawson and Tordoff 1959
Blue Jay ( <i>Cyanocitta cristata</i> )	81.0	0.045	Misch 1960
Northwestern Crow ( <i>Corvus caurinus</i> )	306	0.060	Irving et al. 1955
Blue-winged Teal (female) ( <i>Anas discors</i> )	362	0.052	Owen 1970
Willow Ptarmigan ( <i>Lagopus lagopus</i> )	708	0.029	Herreid and Kessel 1967
Mallard (female) ( <i>Anas platyrhynchos</i> )	1012	0.054	Present study
Mallard (male) ( <i>Anas platyrhynchos</i> )	1166	0.054	Present study
Brant ( <i>Branta bernicla</i> )	1130	0.019	Irving et al. 1955
Sandhill Crane ( <i>Grus canadensis</i> )	2755	0.019	Herreid and Kessel 1967

thermal extremes. High thermal conductance values greatly increase the cost of thermoregulation at low ambient temperatures and may be an important factor in limiting the distribution of endotherms (Lasiewski 1963).

Fasting metabolic rates at low ambient temperatures are applicable to the activities of wintering populations of Mallards. Reed and Prince (1974) observed that a wintering flock of Mallards may feed only once a day, during the afternoon. They also noted a relationship between decreasing mean temperature for the 3 previous days and a decrease in activity on an open body of water. Energy spent on frequent feeding flights and warm weather activities must be used for chemical thermoregulation by wintering populations. The lack of a relationship between temperature and weight loss in an 18-hr interval could also be related to field observations of Reed and Prince (1974). Although they observed no relationship between temperature and activity on the same day, there was a relationship between decreasing activity and decreasing mean temperature on the previous day and the previous 3-day period. This sug-

gests that more than an 18-hr period at low ambient temperatures is needed to observe a weight loss as a function of temperature in a bird the size of the Mallard.

We recognize that time and sex are confounded by a period of 4 hr in this experiment. A diurnal rhythm in the metabolism of birds has been reported by Aschoff and Pohl (1970) and West (1962). Aschoff and Pohl (1970) reported that resting metabolism during the activity-time is 25% higher than during rest-time. The activity-time in their study occurred from 06:00–18:00 in a darkened chamber. Our test times of 11:00–11:30 for females and 14:00–14:30 for males are within this time period and differences due to a diurnal rhythm should not be apparent. Our predicted basal metabolic rate, based on six birds tested over 25°C, of 91.1 Kcal/W<sup>0.744</sup>/day is similar to that reported by Aschoff and Pohl (1970) for nonpasserines of 91.0 Kcal/W<sup>0.729</sup>/day. We believe that the mallards in this experiment were in the activity-time phase of the diurnal rhythm and that the differences observed in metabolic rates were due primarily to sex. A difference in

metabolic rates between sexes has been shown previously for several avian species (Herzog 1930; Benedict 1938; Quirring and Bade 1943). Sturkie (1965) notes that a sex difference in heat production may depend upon the age of the birds and is not always evident when heat production is related to body weight. In this study, the metabolic differences between sexes cannot be explained by a weight difference alone. When heat production is expressed as a ratio with metabolic body size, the regression lines are still significantly different. The sex difference in metabolic rates suggests that males can produce more energy in the form of heat per gram body weight than the females. Thus, with a similar food supply, males should be able to withstand lower ambient temperatures before homeostasis is jeopardized. This difference in metabolism plus the males' larger size provides an explanation for the greater percentage of males in wintering populations in the northern part of the Mallard's winter range as reported by Bellrose et al. (1961) and Reed and Prince (1974).

Sudgen (1971) determined metabolizable energy (M.E.) expressed as Kcal/day for 12 male and 12 female 5-month-old Mallards at 20°C. M.E. values include the heat increment of feeding above the postabsorptive level (S.D.A.). Once the S.D.A. is subtracted from M.E. and adjusted to the body weight of the Mallards used in this study, net energy values are comparable with the values obtained manometrically. For example, based on approximate analysis of Manitou Wheat, the S.D.A. was estimated to be 14.5% of the total diet for both males and females (Brody 1945; Kleiber 1961). The net energy (M.E. - S.D.A.) from the wheat diet was 145.07 Kcal/day for males and 101.93 Kcal/day for females. The average net energy was estimated for our Mallards at 20°C to be 121.50 Kcal/day and 97.89 Kcal/day for males and females, respectively. The calorogenic effect of food, based on the Manitou Wheat data, would increase the ability to physically thermoregulate during the time digestion occurs, and the lower critical temperature would be lowered to the vicinity of 10°C. With the ability to physically thermoregulate between 10°C and 20°C, the chemical energy once used for metabolic thermogenesis below 20°C could then be used for other activities. This may be related to the initiation of breeding in the spring, which usually occurs when mean ambient temperatures are in the 8-15°C range.

## SUMMARY

The caloric requirements of 20 male and 20 female subadult Mallards were determined at low ambient temperatures. The fasted, acclimatized birds were exposed to a -10 to 20°C range, and the time required to consume 50 cc of oxygen at each test temperature was determined manometrically. The average weight of males was 154 g greater than females. There was no relationship between weight loss and ambient temperature during an 18-hr fast prior to metabolic determinations. A significant linear relationship between increasing oxygen consumption and decreasing ambient temperature was observed for both sexes. Although there was no significant difference in the regression coefficients between sexes, there was a significant difference in the elevations of the regression lines, with the metabolic rate being greater for males than for females. When heat production was divided by the metabolic body size ( $W^{0.744}$ ), a sex difference in metabolism unrelated to body weight was still evident. The greater metabolic rate and body weight of the males suggests that they can tolerate lower temperature extremes than the females. The lower critical temperature was near 20°C for a fasted bird. When the calorogenic effect of food was estimated, the lower critical temperature decreased to an estimated 10°C range; the temperature that commonly occurs when breeding is initiated in the spring.

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