

## Partitioning heat loss from mallard ducklings swimming on the air–water interface

Marilyn R. Banta<sup>1,2</sup>, Aaron J. Lynott<sup>1,3</sup>, Matthew J. VanSant<sup>1</sup> and George S. Bakken<sup>1,\*</sup>

<sup>1</sup>Department of Ecology and Organismal Biology, Indiana State University, Terre Haute, Indiana 47809 USA,

<sup>2</sup>Department of Biological Sciences, University of Northern Colorado, Greeley, Colorado 80639 USA and

<sup>3</sup>South Vermillion High School, 770 West Wildcat Drive, Clinton, Indiana 47842, USA

\*Author for correspondence (e-mail: LSGSB@isugw.indstate.edu)

Accepted 22 September 2004

### Summary

Water birds whose young begin swimming while downy are interesting because hypothermia and mortality are associated with wetting. While wetting is known to increase heat loss, little is known about basic issues, such as the amount of heat lost to air vs water during surface swimming. To partition heat loss to air and water, we measured the body temperature, metabolism and thermal conductance of 2–3-day-old mallard ducklings (*Anas platyrhynchos*) swimming under different combinations of air and water temperature. Ventral down remained dry or was wetted only on the surface, and most ducklings could maintain  $T_b > 39^\circ\text{C}$  for 1 h while swimming on water as cold as  $5^\circ\text{C}$ . Ducklings were at or below thermal neutrality when swimming in water at  $T_w = 30^\circ\text{C}$  even when air

temperature  $T_a = 45^\circ\text{C}$ . Heat loss from ducklings with dry down to air and water was partitioned by fitting data to a heat transfer model of the form  $M = G(T_b - T_w) + K_e(T_b - T_a)$ . For an average 48 g duckling, thermal conductance to water increased with water temperature,  $G = 0.0470(1 + 1.059 \times 10^{-6} T_w^4) \text{ W}^\circ\text{C}^{-1} \text{ animal}$ . Conductance to air was  $K_e = 0.0196 \text{ W}^\circ\text{C}^{-1} \text{ animal}$  for all air temperatures. Thus, a minimum of 70% of metabolic heat production is lost to water, and this fraction increases with increasing temperature.

Key words: thermoregulation, swimming, mallard, *Anas platyrhynchos*, down, waterfowl, metabolism, feather.

### Introduction

Ducklings go to the water and swim while downy. This behavior is interesting because the available data indicate that down is much less resistant to wetting than contour feathers (Nye, 1964; Kooyman et al., 1976; Mendenhall, 1979; Barré and Roussel, 1986; Taylor, 1986; Stephenson, 1997). Indeed, wetting, chilling and exhaustion have been observed to cause 1–5-day-old ducklings (class Ia; Gollop and Marshall, 1954) to die directly from hypothermia (Reed, 1975; Seymour, 1982; Talent et al., 1983; Mauser et al., 1994; Korschgen et al., 1996; Sayler and Willms, 1997). The fraction of total mortality resulting directly from hypothermia is not well known, but reported data for mallard (*Anas platyrhynchos*) and canvasback (*Aythya valisineria*) ducks suggest ranges from 8–9% (Talent et al., 1983; Mauser et al., 1994) to 24–27% (Korschgen et al., 1996), respectively. Wetting and chilling may also cause indirect mortality from reduced growth (Samuel et al., 1995) or increased susceptibility to disease (Mendenhall and Milne, 1985), pesticides (Martin and Solomon, 1991) and predation (Mendenhall and Milne, 1985).

Most observed mortality occurs in class I, and class I dabbling ducklings, such as mallards, normally swim on the

surface and forage by surface skimming and gleaning insects from emergent vegetation for the first week or two after hatching (e.g. Pehrsson, 1979; Ringelman and Flake, 1980). Despite its apparent ecological importance, thermoregulation of downy waterbird chicks during surface swimming has received limited attention (Eppley, 1984; Steen et al., 1989; Sutter and MacArthur, 1992). None of these studies attempted to partition heat loss to air and water, even though a large fraction of North American ducks breed in the pothole prairie area of the central plains, where the continental climate is characterized by widely varying combinations of air and water temperature. The relative importance of air vs water temperature for thermoregulation is largely unknown. Thus, knowledge of how heat loss is partitioned to air and water could significantly improve our understanding of the physiological ecology of hatchling waterfowl.

To address this question, we conducted experiments using swimming 2–3-day-old mallard ducklings exposed to various combinations of air and water temperature. This allowed us to make separate estimates of the heat transfer coefficients to air and to water. These coefficients determine the relative importance of heat loss to air vs water for young ducklings.

### Material and methods

#### *Animal care and housing*

Experimental procedures were approved by the Indiana State University Institutional Animal Care and Use Committee 01-08:GB. Fertilized duck eggs (*Anas platyrhynchos* L.) were obtained from a commercial breeder (Whistling Wings, Hanover, IL, USA) and incubated in the laboratory in a commercial incubator (Model 1202, GQF Manufacturing, Savannah, GA, USA). Parents were derived from wild stock (ca. fifth generation). After hatching, ducklings were weighed and placed inside a dry plastic wading pool (1.3 m diameter) equipped with a brooder. When ducklings were approximately 24 h old, they were transferred to a second plastic wading pool (1.3 m diameter) filled with 6–8 cm of water. This pool was also equipped with a brooder. We found that ducklings remained calm and swam better under the experimental conditions with previous swimming experience. High protein poultry starter and water were available *ad libitum*. Ducklings were therefore not post-absorptive when metabolic measurements began. Both pools were housed in environmental chambers at 27°C and a 12L:12D light cycle. We imprinted ducklings on a mallard hen decoy attached to an arm driven by a 3 rpm motor, which towed the decoy around the pools intermittently (1 min on, 4 min off). Ducklings were tested when 2–3 days old (48–87 h post-hatch).

#### *Experimental apparatus*

Ducklings swam in an acrylic respirometry box mounted in a water flow tank (cf. Vogel and LaBarbera, 1978; Fish, 1995). A female decoy identical to the one used for imprinting was positioned just above the water surface in front of the respirometry chamber to guide the ducklings. A trolling motor (MinnKota Endura 50, Johnson Outdoors Inc., Sturtevant, WI, USA) generated a flow of  $\sim 0.25 \text{ m s}^{-1}$ . A purpose-built turbine meter with optical pulse readout was calibrated against a Prandtl-design Pitot tube and used to monitor water velocity during experiments. Fairings and screens were used to create a smooth flow with  $\pm 10\%$  or less velocity variation across the working section. The flow tank was placed in a walk-in environmental chamber. A thermostatically controlled heater and fan in the respirometry box allowed fine control of air temperature within the respirometry box. Water temperature,  $T_w$ , was regulated by a thermostat controlling the flow of refrigerated propylene glycol solution from a recirculating chiller (IcEWagon 30 WCLT, GCI Industrial Refrigeration, Wilmington, DE, USA) through copper heat-exchange tubing in the flow tank. The tank was filled from the city water supply and changed regularly to avoid accumulating contaminants that might increase down wetting (Stephenson and Andrews, 1997; Stephenson, 1997).

The open-circuit respirometry equipment and procedures used in this study generally followed Bakken et al. (1991, 1996, 2002) with some changes in instrumentation. Prior studies have reported that exchange of oxygen between water and air in the animal enclosure is not significant (Woakes and

Butler, 1983; Ancel et al., 2000), and we found no effects in empty chamber trials using nitrogen dilution to simulate metabolism. Nevertheless, we allowed for this possibility by using a reference chamber of the same volume and with the same area exposed to the water in the flow tank. The animal enclosure and reference enclosures were each supplied with dry, CO<sub>2</sub>-free outdoor air at  $1.5 \text{ l min}^{-1}$ . Flow rates were regulated by a mass flow controller (Tylan FC-260, Coastal Instruments, Burgaw, NC, USA), calibrated on-site against a bubble meter (Levy, 1964).

Air leaving the chambers flowed continuously to a sampling manifold adjacent to the oxygen analyzer. We measured the oxygen content of a dry, CO<sub>2</sub>-free  $200 \text{ ml min}^{-1}$  subsample of air leaving the animal and reference chambers during the last 10 s of alternating 1 min intervals. The electrochemical oxygen analyzer (FC-1, Sable Systems, Henderson, NV, USA) equilibrated 20–30 s after switching gas sources. We corrected all O<sub>2</sub> exchange data to STP. Switching allowed pseudo-differential operation that provided continuous baseline correction for changes in building pressure and any oxygen exchange with water in the flow tank.

Oxygen consumption was computed for each consecutive 2 min sample interval during the experiment using standard Z-transform methods to avoid chamber washout issues (Bakken et al., 1981; Bartholomew et al., 1981). Overall respirometry errors from all sources were 2% or less, directly validated by using an infusion pump, which added either nitrogen or oxygen at known rates (Fedak et al., 1981; Bakken, 1991). As our ducklings were not fasting, we converted oxygen consumption to heat production rate  $M$  (W) assuming  $20.9 \text{ J ml}^{-1} \text{ O}_2$ . Data were averaged over the 20 min data collection period to smooth transients, as this procedure gives improved estimates of thermoregulatory demands (Bakken et al., 1981).

We used copper–constantan thermocouples (type TT, Omega Engineering, Stamford, CT, USA) to measure air and water temperatures. All data were recorded with a digital data logger (CR-21X, Campbell Scientific, Logan, UT, USA). Data logger control outputs were used to regulate air and water temperatures, step through a predetermined air temperature sequence and switch the sampling valve.

Each duckling was randomly assigned to one of six water temperatures (5, 10, 15, 20, 25 or 30°C). During two consecutive 30 min runs, each duckling was exposed to two air temperatures in random order, one low (5°C above  $T_w$ ) and the other high (either 15 or 20°C above  $T_w$ ). Metabolic rate was recorded during the last 20 min of each run, so that ducklings had 10 min to adjust to new conditions before data were recorded. Experiments were conducted during active phase with 300 lux illumination. At the end of the trial (on or before 1700 h), each duckling was returned to the holding pool. Any ducklings that had become hypothermic ( $<37^\circ\text{C}$ ) while swimming were first placed in an incubator, where they quickly recovered normal body temperature and behavior.

#### *Thermographic measurement of body temperature*

Body temperature was estimated from the thermographic

temperature of a shaved area of scalp directly over the brain. Creating this bare spot may result in a slight increase in convective heat loss to air. However, thermography was particularly useful in our study because it avoids both abdominal surgery and cloacal thermocouples, either of which could disrupt the structure of the down in contact with water and increase wetting (Fabricius, 1956; Nye, 1964). Mallard ducklings are dependent on air retained in the down for insulation when swimming, and quickly become hypothermic when the down is saturated (G.S.B., unpublished data; Nye, 1964).

We recorded overhead thermograms of the duckling using a radiometric thermal imager with an 80° lens attachment (FLIR ThermoCam PM575, FLIR Systems, North Billerica, MA, USA) placed in an opening in the top of the metabolism enclosure. Images (0.1°C resolution over a –20 to 350°C range) were recorded every 5 s or 10 s and transmitted to a laptop computer and stored on the hard drive. These images were then analyzed with proprietary software (IRwin Research 2.1, FLIR Systems, North Billerica, MA, USA) to obtain apparent scalp temperature (Fig. 1A). These temperatures were corrected for zero drift and the transmission of the 80° lens attachment to obtain true scalp temperatures (Fig. 1B). A preliminary series of experiments on  $N=30$  ducklings of the same age swimming in the same apparatus were used to generate a regression model that predicted cloacal temperature (measured with a thermocouple) with a standard deviation of less than 1°C (Fig. 1C). Averaging values derived from multiple images gave  $T_b$  with a 95% accuracy of  $\pm 1^\circ\text{C}$  or better.

#### Data analysis

For heat transfer analysis, the duckling is divided into two areas, aerial and aqueous, and analyzed using a two-dimensional heat transfer model (Bakken, 1981). The operative temperature acting on the aerial surface of the duckling,  $T_e$ , is equal to air temperature  $T_a$  in our experimental enclosures (Bakken, 1976; appendix C). Thus, the equation has the form:

$$M - E - C \, dT_b / dt = K_e (T_b - T_a) + G (T_b - T_w), \quad (1)$$

where  $M$  (W/animal) is metabolic heat production,  $E$  (W/animal) is evaporative cooling,  $C$  is heat storage capacity (J/°C-animal),  $T_b$  (°C) is body temperature,  $T_w$  (°C) is water temperature,  $T_a$  (°C) is air temperature, and  $t$  (s) is time. The overall thermal conductance to water is  $G$  (W/°C-animal), and that to the aerial environment is  $K_e$  (W/°C-animal). Both  $K_e$  and  $G$  may be functions of  $T_w$ ,  $T_a$ , or both. We used only data from animals with a stable body temperature, so that the heat storage term  $C \, dT_b/dt$  could be neglected. Evaporative cooling cannot be measured on swimming animals and is not easily estimated. Equation 1 therefore reduces to:

$$M = K_e (T_b - T_a) + G (T_b - T_w). \quad (2)$$

The thermal conductances can be obtained using multiple linear regression with  $(T_b - T_a)$  and  $(T_b - T_w)$  as the independent variables and  $K_e$  and  $G$  as the regression coefficients. Because evaporative cooling may occur even when ambient air is

saturated, the actual thermal conductances are smaller than these estimates, but the ratio of heat loss to air vs water is unaffected.

We used SYSTAT 7.0 for all statistical analyses (Wilkinson, 1996). We used a preliminary linear regression model to test possible experimental covariates (mass, order of air temperatures, date, gender, time since hatching, area of down showing surface wetting, and measures of swimming performance). We screened the data for potential outliers (data points with large Z-transformed residuals), which may result from experimental problems or data copying errors (Draper and Smith, 1981).

Previous studies have found that metabolic rate may have a nonlinear dependence on body mass, and most thermoregulatory metabolism studies have found thermal conductance to have a nonlinear dependence on ambient temperature. Therefore, we examined partial residual plots for such effects and, where appropriate, constructed and tested models with nonlinear terms.

## Results

### Body temperature

Ducklings did not become wetted to the skin if they had prior swimming experience, unless they tried to dive out of the experimental chamber. Some ducklings splashed water on the lens during the run that blocked the imager's view and prevented  $T_b$  measurement. Eliminating ducklings that dove or splashed water on the lens left a total of  $N=33$  ducklings ( $N=66$  measurements). We found no outliers among these data.

Calibrated thermographic body temperatures have been plotted in Fig. 2. Ducklings that had no wetting or slight surface wetting that did not penetrate to the skin were able to defend a normothermic body temperature of  $39.5 \pm 0.8^\circ\text{C}$  for 1 h in water as cold as  $5^\circ\text{C}$  as long as their down was not penetrated by water. Body temperature increased to an average of  $41.5 \pm 0.5^\circ\text{C}$  in  $30^\circ\text{C}$  water. Typical body temperatures for 3-day-old mallard ducklings are  $40\text{--}42^\circ\text{C}$ , and  $T_b=39^\circ\text{C}$  is considered to be the minimum homeothermic value (Ostnes and Bech, 1997).

### Metabolic rate and heat loss to air and water

Various regression procedures, including forward and backward stepwise analysis and all-possible-models, found mass to be the only significant covariate. The average mass of ducklings in this study was  $48 \pm 5.7$  g, and this range of variation was too small to allow us to assign an exponent to the mass dependence. It is not clear that there is a universal 'best' intraspecific exponent for the variation of metabolic rate with mass. Thus, we express the variation of  $M$  with mass as a linear function of the deviation of individual mass from the mean ( $m-48$ ). Over a small range of mass variation, this model is indistinguishable from an otherwise similar model using any reasonable mass exponent.

Thermal conductance typically increases as a curvilinear function of ambient temperature (e.g. Bakken et al., 1991,

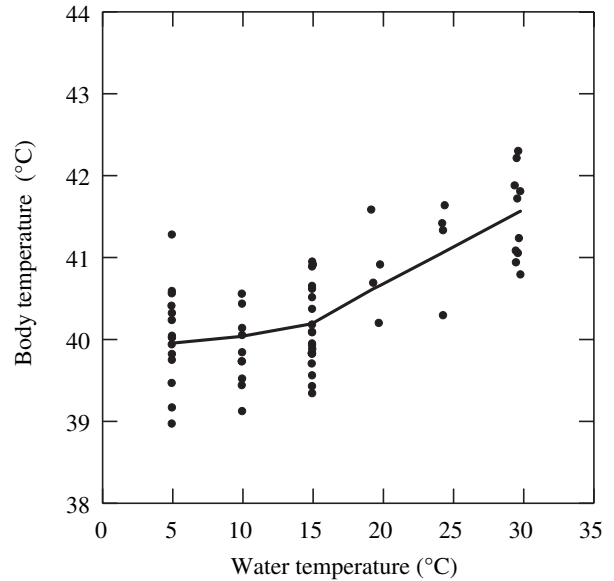
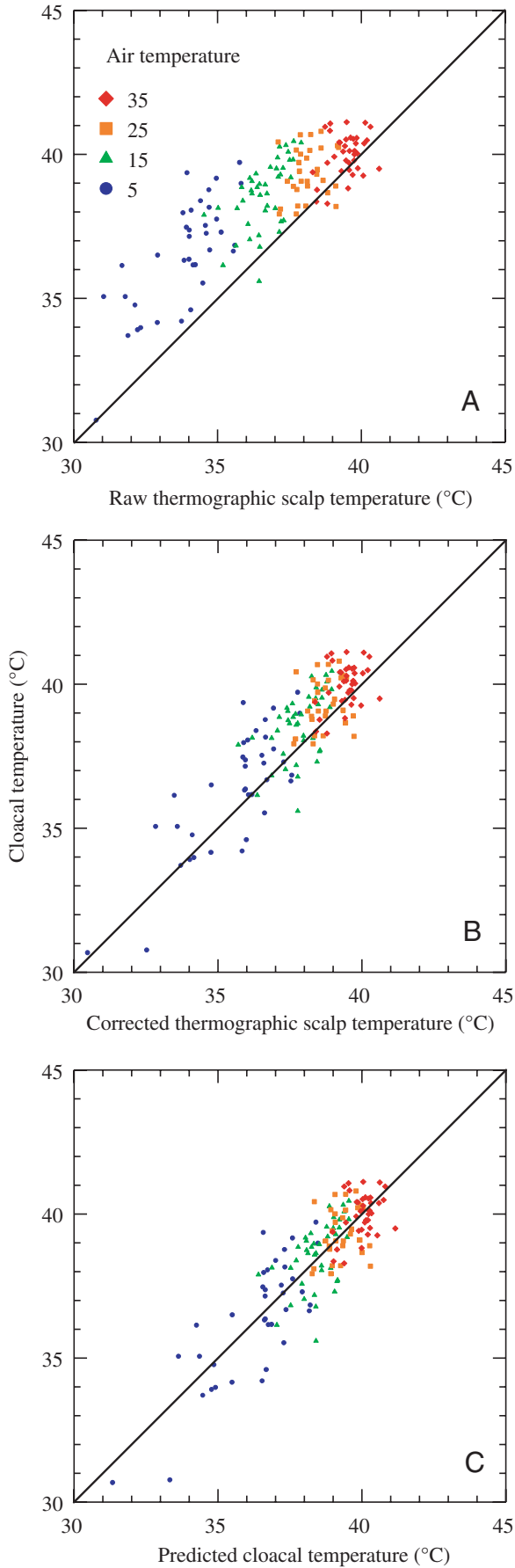


Fig. 2. Body temperature measured by calibrated thermography of a shaved spot on the scalp directly over the brain. This method agreed with cloacal temperature within  $<1^{\circ}\text{C}$  and avoided the restraint and increased wetting of the down associated with the use of cloacal thermocouples. Body temperature decreased as water temperature decreased to  $\sim 15^{\circ}\text{C}$ , and then stabilized. The line is a LOWESS smoother (Cleveland, 1985) showing the trend.

1999). To test for this, we made rough estimates of the heat transfer coefficients  $K_e$  and  $G$  in Equation 2 by first fitting a linear model and plotting model residuals  $vs T_w$ . These showed the expected curvilinear increase of duckling thermal conductance with  $T_w$ . There is no theoretical expectation for the exact form of the increase of conductance with temperature. Therefore, we first tested a variety of 2nd to 5th order polynomial models for  $G$ , as heat loss to the water is the dominant avenue of heat loss. All such models gave a significantly better fit than a linear model ( $P$  to enter or remove  $<0.0001$ ), but  $r^2$  varied little among the curvilinear models (range  $0.988 > r^2 > 0.986$ ). With no clear statistical basis for selecting a particular curvilinear model, we arbitrarily used the model that gave the largest  $r^2$  and best visual fit,  $G = G_o(1 + bT_w^4)$ . Here,  $G_o$  is the minimum thermal conductance at low water temperatures, and  $b$  is a regression coefficient. A similar analysis found that the best-fit model for conductance

Fig. 1. Cloacal body temperature predicted by thermographic measurements of scalp temperature. (A) Cloacal temperature  $vs$  raw thermographic values. The effect of absorption and emission in the  $80^{\circ}$  lens attachment are evident. (B) Cloacal temperature thermographic temperature corrected for lens effects. True radiometric scalp temperature averages about  $1^{\circ}\text{C}$  lower than cloacal temperature. (C) Measured cloacal temperature  $vs$  cloacal temperature predicted by a regression to the data in Fig. 1B. In all cases, data points are from a single image, and overall precision can be improved by calculating the mean of data from several images.



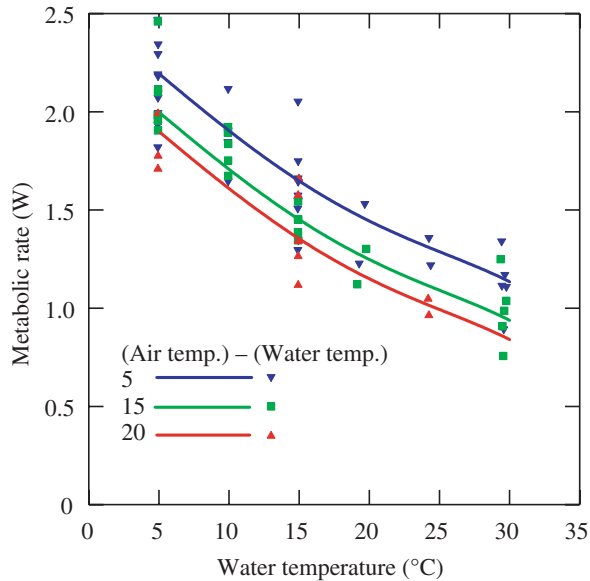


Fig. 3. Metabolic rate of 2–3-day-old ducklings vs water temperature, adjusted to the average mass of 48 g. The slope of the lines indicates the effect of water temperature on metabolic rate. The spacing of the lines indicates the additional effect of air temperatures. The lines are drawn using the heat transfer model in Equation 3. Even with 30°C water temperature and 45°C air temperature, there is no indication that the thermal neutral zone has been reached.

to air,  $K_e$ , was a simple constant. Incorporating the best-fit values of the regression coefficients:

$$M = 0.0139 (m - 48) + 0.0470 (1 + 1.059 \times 10^{-6} T_w^4) (T_b - T_w) + 0.0196 (T_b - T_a), \quad (3)$$

where  $F_{4,62}=1302$ , adj.  $r^2=0.98$ ,  $P \ll 0.0001$ , S.E.E.=0.187 W. Note that this model does not include a constant, which results in inflated values of  $F$  and  $r^2$  compared with models with constants (Wilkinson, 1996). However, the standard error of the estimate (S.E.E.) is not affected and, thus, provides the best indication of the ability of the model to predict the metabolic rate of a given duckling. Briefly, the ‘standard error of the estimate’ is the standard deviation of the model residuals. (The residuals are the distances between measured values of  $M$  and the corresponding values predicted by the model, i.e. Equation 3.) Thus, it represents the precision with which the model is able to predict the value of an individual measurement.

This model is plotted together with the mass-adjusted data in Fig. 3. The main effect, the variation in heat loss to the water as a function of water temperature, is indicated by the slope of the lines. The additional effect of variation in  $T_a$  is indicated by the vertical separation of the lines. Even at a water temperature of 30°C and an air temperature of 45°C, metabolic rate data give no evidence of a thermal neutral zone.

To visualize the variation of  $G$  with  $T_w$ , we calculated partial residuals of this model with respect to  $(T_b - T_w)$  and divided by  $T_b - T_w$  to obtain individual estimates of  $G$ . These estimates are plotted in Fig. 4, together with the conductance model from

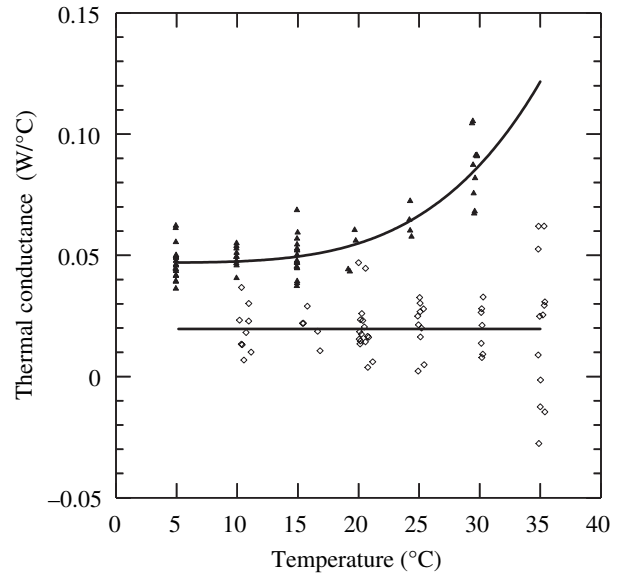


Fig. 4. Plot of the thermal conductance to water (filled symbols) and corresponding conductance model (upper curve) and the thermal conductance to air (open symbols) and corresponding thermal conductance model (lower line). Both conductance models are taken from Equation 3. The horizontal axis is the temperature of the corresponding medium. The scatter in the conductance to air at 35°C results from uncertainties in the small difference between body and air temperature.

Equation 3,  $G=0.0450(1+1.059 \times 10^{-6} T_w^4)$ . The measured thermal conductance to air, computed similarly, is also plotted in Fig. 4, together with the conductance model from Equation 3,  $K_e=0.0188$ .

## Discussion

### Body temperature

With prior swimming experience, nearly all of our 2–3-day-old mallard ducklings could maintain  $T_b > 39^\circ\text{C}$  for at least 1 h while swimming in clean water as cold as 5°C. Body temperature increased to the 40–41.5°C range when  $T_w > 25^\circ\text{C}$  (Fig. 2). Reported body temperatures for ducklings of various species exposed to thermal neutral conditions are 40–42°C (Koskimies and Lahti, 1964; Nye, 1964; Ostnes and Bech, 1997; Nichelmann and Tzschentke, 2002), and  $T_b=39^\circ\text{C}$  is considered to be the minimum homeothermic value (Ostnes and Bech, 1997). The variation of  $T_b$  with water temperature in our swimming 2–3-day-old ducklings is similar to the variation of  $T_b$  with air temperature reported for 5-day-old domestic muscovy ducklings (*Cairina moschata*; fig. 6 in Nichelmann and Tzschentke, 2002).

The use of infrared thermography to make remote measurement of  $T_b$  using calibrated scalp temperatures (Bakken et al., 2005) was particularly valuable in our study because it avoided the problem that indwelling cloacal thermocouples disrupt the down structure and increase the probability of serious wetting.

Overall, the lower limit for the temperature tolerance of swimming ducklings with minimal or no wetting of the down was 5°C or less (Fig. 2). This is similar to the 0–10°C low air temperature limit reported for dabbling ducks in prior studies (e.g. Koskimies and Lahti, 1964; Untergasser and Hayward, 1972; Bakken et al., 1999). The effectiveness of air within the down as insulation from water contact, coupled with very low blood flow to the tibiotarsus and feet (Kilgore and Schmidt-Nielsen, 1975) apparently accounts for the similar low temperature tolerances of swimming and non-swimming ducklings.

#### Heat transfer properties

As shown in Fig. 4, our ducklings had a low and constant conductance to the air,  $K_o=0.0188$  W/°C-animal at all air temperatures ( $T_a$ ). Conductance to the water is approximately constant for  $T_w<20^\circ\text{C}$  at  $G=0.0450$  W/°C-animal. Thus, assuming  $T_w=T_a$ , Equation 3 predicts that 70% of total metabolic heat production is lost to the water under cold (<15°C) conditions. This estimate is conservative, as our ducklings maintained air within the ventral plumage and heat loss to air may have been increased by trimming the down for scalp thermography. Thermal conductance, and thus heat loss to water, increased at higher temperatures. Presumably this is the result of increasing blood flow to the feet. The increase in heat loss from ducklings appears to begin (Fig. 4) at the same or somewhat higher temperatures (18–23°C), as does the increase in heat loss from feet to water in adult mallards (18°C; Kilgore and Schmidt-Nielsen, 1975).

Comparison with other studies of birds swimming on the air–water interface is difficult because these used constant air temperatures close to water temperature and therefore could not partition heat loss between air and water (e.g. Prange and Schmidt-Nielsen, 1970; Eppley, 1984; Steen et al., 1989; Sutter and MacArthur, 1992; de Vries and van Eerden, 1995). We can make limited comparisons by noting that the overall conductance of our 2–3-day-old ducklings swimming with little or no down wetting, assuming  $T_a=T_w\cong 10^\circ\text{C}$ , is 0.065 W/°C-animal. This is 1.5–1.6 times the conductance of 1–2-day-old mallard ducklings in 10°C air (Bakken et al., 1999). This increase in conductance is comparable to that of adult mallards resting in water, which have a metabolic rate 1.4 times that in air at the same temperature (Prange and Schmidt-Nielsen, 1970). The metabolic rate of 1–2-day-old eider ducklings (*Somateria mollissima*) at 0°C shows a 1.4-fold increase when their feet are in salt water (Steen et al., 1989). Eider ducklings are larger (50–75 g) than mallards of similar age, have dense down, and are notably cold hardy. Consequently, it is surprising that the ratio is only slightly better than for our mallards. A possible explanation is that they were tested in 0°C salt water, and may have begun to increase blood flow to their feet to prevent freezing as do adult mallards (Kilgore and Schmidt-Nielsen, 1975).

Heat transfer from adult carcasses of an assortment of water birds in simulated swimming postures showed a greater ratio of overall conductance in water to conductance in air, ranging

from 2.0 to 2.5 (de Vries and van Eerden, 1995). The substantial difference between live animal and carcass studies suggests that carcass studies may not be useful predictors of live animal responses.

Class Ia dabbling ducklings, i.e. 1–5-day-old ducklings (such as mallards), normally swim on the surface and forage by surface skimming and gleaning insects from emergent vegetation (e.g. Pehrsson, 1979; Ringelman and Flake, 1980). Although water temperature has the largest effect on metabolic rate, ambient air temperature significantly modifies heat loss. Thus, environmental factors, weighted by the time spent swimming, must be included in environmental energetics studies of young dabbling ducklings.

We thank Clay Higginbotham for many hours of work on apparatus construction and assistance with the experiments. This research was supported by NSF grants IBN 99-82076 and DBI 99-70209 to G.S.B., and by Indiana State University. Experimental procedures were approved by the Indiana State University Institutional Animal Care and Use Committee 01-08:GB.

#### References

- Ancel, A., Starke, L. N., Ponganis, P. J., Van Dam, R. and Kooyman, G. L. (2000). Energetics of surface swimming in Brandt's cormorants (*Phalacrocorax penicillatus* Brandt). *J. Exp. Biol.* **203**, 3727–3731.
- Bakken, G. S. (1976). A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* **60**, 337–384.
- Bakken, G. S. (1981). A two-dimensional operative-temperature model for thermal energy management by animals. *J. Thermal Biol.* **6**, 23–30.
- Bakken, G. S. (1991). Time-resolved respirometry: equations for the simultaneous measurement of all respiratory gases and the calibration of oxygen consumption using variable inert gas flow rates. *J. Thermal Biol.* **16**, 313–315.
- Bakken, G. S., Buttemer, W. A., Dawson, W. R. and Gates, D. M. (1981). Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. *Ecology* **62**, 311–318.
- Bakken, G. S., Murphy, M. T. and Erskine, D. J. (1991). The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. *Physiol. Zool.* **64**, 1023–1049.
- Bakken, G. S., Reynolds, P. S., Kenow, K. P., Korschgen, C. E. and Boysen, A. F. (1996). Thermoregulatory effects of radiotelemetry transmitters on mallard ducklings. *J. Wildlife Management* **60**, 669–678.
- Bakken, G. S., Reynolds, P. S., Kenow, K. P., Korschgen, C. E. and Boysen, A. F. (1999). Metabolic response to air temperature and wind in day-old mallards and a standard operative temperature scale. *Physiol. Biochem. Zool.* **72**, 656–665.
- Bakken, G. S., Van Sant, M. J., Lynott, A. J. and Banta, M. R. (2005). Predicting small endotherm body temperatures from scalp temperatures. *J. Therm. Biol.* **30** (in press).
- Bakken, G. S., Williams, J. B. and Ricklefs, R. E. (2002). Metabolic response to wind of downy chicks of Arctic-breeding shorebirds (Scolopacidae). *J. Exp. Biol.* **205**, 3435–3443.
- Barré, H. and Rousset, B. (1986). Thermal and metabolic adaptation to first cold-water immersion in juvenile penguins. *Am. J. Physiol.* **251**, R456–R462.
- Bartholomew, G. A., Vleck, D. and Vleck, C. M. (1981). Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. *J. Exp. Biol.* **90**, 17–32.
- Cleveland, W. S. (1985). *The Elements of Graphing Data*. Monterey, CA: Wadsworth.
- de Vries, J. and van Eerden, M. R. (1995). Thermal conductance in aquatic birds in relation to the degree of water contact, body mass, and body fat:

- energetic implications of living in a strong cooling environment. *Physiol. Zool.* **68**, 1143-1163.
- Draper, N. R. and Smith, H.** (1981). *Applied Regression Analysis*, Second Edition. New York: John Wiley & Sons.
- Eppley, Z.** (1984). Development of thermoregulatory abilities in Xantus' murrelet chicks *Synthliboramphus hypoleucus*. *Physiol. Zool.* **57**, 307-317.
- Fabricius, E.** (1956). Vad gör fåglarnas kroppsbeklädnad vattenavvisande? (What makes the plumage of birds waterproof?). *Zoologisk Revy* **18**, 71-83.
- Fedak, M. A., Rome, L. and Seeherman, H. J.** (1981). One-step N<sub>2</sub>-dilution technique for calibrating open-circuit VO<sub>2</sub> measuring systems. *J. App. Physiol.* **51**, 772-776.
- Fish, F. E.** (1995). Kinematics of ducklings swimming in formation: consequences of position. *J. Exp. Zool.* **273**, 1-11.
- Gollop, J. B. and Marshall, W. H.** (1954). *A Guide for Aging Duck Broods in the Field*. Northern Prairie Wildlife Research Center, Jamestown, ND: Mississippi Flyway Council Technical Section, U.S. Fish and Wildlife Service. <http://npwrc.usgs.gov/resource/tools/ageduck/ageduck.htm>.
- Kilgore, D. L. and Schmidt-Nielsen, K.** (1975). Heat loss from ducks' feet immersed in cold water. *Condor* **77**, 475-517.
- Kooyman, G. L., Gentry, R. L., Bergman, W. P. and Hammel, H. T.** (1976). Heat loss in penguins during immersion and compression. *Comp. Biochem. Physiol. A* **54**, 75-80.
- Korschgen, C. E., Kenow, K. P., Green, W. L., Johnson, D. H., Samuel, M. D. and Sileo, L.** (1996). Survival of radio-marked canvasback ducklings in northwestern Minnesota. *J. Wildl. Manage.* **60**, 120-132.
- Koskimies, J. and Lahti, L.** (1964). Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. *Auk* **81**, 281-307.
- Levy, A.** (1964). The accuracy of the bubble meter method for gas flow measurements. *J. Sci. Instr.* **41**, 449-453.
- Martin, P. A. and Solomon, K. R.** (1991). Acute carbofuran exposure and cold stress: interactive effects in mallard ducklings. *Pesticide Biochem. Physiol.* **40**, 117-127.
- Mauser, D. M., Jarvis, R. L. and Gilmer, D. S.** (1994). Survival of radiomarked mallard ducklings in northeastern California. *J. Wildl. Manage.* **58**, 82-87.
- Mendenhall, V. M.** (1979). Brooding of young ducklings by female eiders *Somateria mollissima*. *Ornis Scandinavica* **10**, 94-99.
- Mendenhall, V. M. and Milne, H.** (1985). Factors affecting duckling survival of eiders, *Somateria mollissima* in northeast Scotland. *Ibis* **127**, 148-158.
- Nichelmann, M. and Tzschentke, B.** (2002). Ontogeny of thermoregulation in precocial birds. *Comp. Biochem. Physiol. A* **131**, 751-763.
- Nye, P.** (1964). Heat loss in wet ducklings and chicks. *Ibis* **106**, 189-197.
- Ostnes, J. E. and Bech, C.** (1997). Ontogeny of deep-cold sensitivity in pekin ducklings *Anas platyrhynchos*. *J. Comp. Physiol. B* **167**, 241-248.
- Pehrsson, O.** (1979). Feeding behavior, habitat utilization, and feeding efficiency of mallard ducklings (*Anas platyrhynchos* L.) as guided by a domestic duck. *Viltrevy* **10**, 193-218.
- Prange, H. D. and Schmidt-Nielsen, K.** (1970). The metabolic cost of swimming in ducks. *J. Exp. Biol.* **53**, 763-777.
- Reed, A.** (1975). Reproductive output of black ducks in the St. Lawrence Estuary. *J. Wildlife Management* **39**, 243-255.
- Ringelman, J. K. and Flake, L. D.** (1980). Diurnal visibility and activity of blue-winged teal and mallard broods. *J. Wildlife Management* **44**, 822-829.
- Samuel, M. D., Goldberg, D. R., Thomas, C. B. and Sharp, P.** (1995). Effects of *Mycoplasma anatis* and cold stress on hatching success and growth of mallard ducklings. *J. Wildl. Dis.* **31**, 172-178.
- Saylor, R. D. and Willms, M. A.** (1997). Brood ecology of mallards and gadwalls nesting on islands in large reservoirs. *J. Wildlife Management* **61**, 808-815.
- Seymour, N. R.** (1982). Mortality of duckling attributed to separation from mother and subsequent protracted exposure to low ambient temperature. *Auk* **99**, 383-384.
- Steen, J. B., Grav, H., Borch-Johnsen, B. and Gabrielsen, G. W.** (1989). Strategies of homeothermy in eider ducklings (*Somateria mollissima*). In *Physiology of Cold Adaptation in Birds* (ed. C. Bech and R. E. Reinertsen), pp. 361-370. New York: Plenum Press.
- Stephenson, R.** (1997). Effects of oil and other surface-active organic pollutants on aquatic birds. *Environ. Conserv.* **24**, 121-129.
- Stephenson, R. and Andrews, C. A.** (1997). The effect of water surface tension on feather wettability in aquatic birds. *Canadian J. Zool.* **75**, 288-294.
- Sutter, G. C. and MacArthur, R. A.** (1992). Development of thermoregulation in a precocial aquatic bird, the American coot (*Fulica americana*). *Comp. Biochem. Physiol. A* **101**, 533-543.
- Talent, L. G., Jarvis, R. L. and Krapu, G. L.** (1983). Survival of mallard broods in south-central North Dakota. *Condor* **85**, 74-78.
- Taylor, J. R. E.** (1986). Thermal insulation of the down and feathers of pygoscelid penguin chicks and the unique properties of penguin feathers. *Auk* **103**, 160-168.
- Untergasser, G. and Hayward, J. S.** (1972). Development of thermoregulation in ducklings. *Canadian J. Zool.* **50**, 1243-1250.
- Vogel, S. and LaBarbera, M.** (1978). Simple flow tanks for research and teaching. *BioScience* **28**, 638-643.
- Wilkinson, L.** (1996). *Statistics: Systat 6.0 for Windows*. Chicago, Illinois: SPSS.
- Woakes, A. J. and Butler, P. J.** (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. Exp. Biol.* **107**, 311-329.