Nasal Respiratory Turbinate Function in Birds

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ABSTRACT
Nasal respiratory turbinate function in five large bird species (115-1,900 g) inhabiting mesic temperate climates. Evaporative water loss and oxygen consumption rates of birds breathing normally (nasopharyngeal breathing) and with nasal turbinates experimentally bypassed (oropharyngeal breathing) were measured. Water and heat loss rates were calculated from lung tidal volumes and nasal and oropharyngeal exhaled air temperatures ($T_{ex}$). Resulting data indicate that respiratory turbinate function is equally adaptive across a range of avian orders, regardless of environment, by conserving significant fractions of the daily water and heat budget. Nasal $T_{ex}$ of birds was compared to that of lizards, which lack respiratory turbinate function. The comparatively high nasal $T_{ex}$ of the lizards in similar ambient conditions suggests that their relatively low metabolic rates and correspondingly reduced lung ventilation rates may have constrained selection on similar respiratory adaptations.

Introduction
Endothermy is characterized by oxygen consumption that is approximately an order of magnitude higher than that of equivalent sized ectotherms (Nagy 1987). Respiratory minute volumes of endotherms are similarly elevated (Schmidt-Nielsen 1984), creating a potential for comparatively higher respiratory evaporative heat and water loss. Unique morphological adaptations of the upper respiratory tract of birds and mammals modify and condition respired air, minimizing what might otherwise be critically elevated rates of ventilation-related heat and water loss (Hillenius 1992). The relatively low oxygen consumption, ventilation rates, and lung tidal volumes of ectotherms probably obviates the necessity for similar adaptations to reduce respiratory water and heat loss (Hill and Wyse 1976; Schmidt-Nielsen 1984; Hillenius 1992; Ruben 1996).

Within the specialized respiratory tract of birds, only the nasal cavities significantly modify tidal air humidity and temperature during periods of routine, or resting, lung ventilation. The lungs and extensive system of nonvascularized air sacs, located throughout the body cavity, are necessarily maintained at, or close to, deep-body temperature and therefore do not participate as major sites of evaporative or condensative heat exchange during normal respiration. The proximity of the trachea to the carotid arterial circulation along most of its length eliminates it as a primary site of heat exchange during respiration, as this would likely result in highly deleterious cyclical fluctuations of brain temperature (Baumel 1993; Ruben et al. 1997). Additionally, in long-necked birds (e.g., the ostrich, Struthio), the simple tubular geometry and high airflow velocities in the trachea suggest that considerable evaporative cooling between airstream and moist respiratory surfaces is unlikely (Schmidt-Nielsen et al. 1969). The buccal region and the oropharyngeal portion of the trachea participate substantially in heat exchange only during panting and gular flutter, specialized respiratory patterns closely associated with heat stress in birds (Crawford and Schmidt-Nielsen 1967; Lasiewski 1972; Weathers and Schoenbacker 1976; Dawson 1981; Peltonen et al. 1988). It is only within the nasal cavities that morphological adaptations have evolved that are tightly linked to heat and water exchange during breathing.

Extant reptiles, birds, and mammals possess one or more pairs of cartilaginous, epithelially covered projections within the nasal cavity known as conchae, or turbinates. In living reptiles these are relatively simple structures associated with olfaction, usually consisting of paired, domelike cartilaginous projections from the lateral walls of the nasal cavity (Matthes 1934; Portmann 1961; Hillenius 1992). Birds and mammals typically possess additional elaborations of the nasal cavity, respiratory turbinates, that are absent in all ectotherms (Hillenius 1992, 1994; Ruben 1996; Wittmer 1995). Unlike the simple conchal structures of reptiles, avian respiratory turbinates are highly convoluted, often scrolled structures, lined with moist mucociliated epithelium (Bang 1961, 1971). Mammalian respiratory turbinates, the maxilloturbinates (referred to as inferior conchae in humans), are ossified, scrolled, lamellar extensions of the lateral walls of the maxillary bone (Hillenius 1992). Avian respiratory turbinates are morphologically and functionally...
analogous, though likely not homologous, to the mammalian maxilloturbinates (Witmer 1995). Respiratory turbinates of birds, also referred to as the anterior and middle conchae, are, like mammalian maxilloturbinates, situated directly in the path of respiratory airflow, greatly increasing the surface area of the nasal epithelial mucosa and simultaneously reducing the effective distance of respiratory air from the mucosal surfaces. Unlike the bony respiratory turbinates of mammals, avian turbinates are usually cartilaginous. These paired structures, as in mammals, extend from the lateral walls of the nasal cavity, where they apparently function as intermittent countercurrent heat exchangers (Schmidt-Nielsen et al. 1969). As inspired air passes through the nasal cavities and over the moist surfaces of the respiratory turbinates, heat and water are exchanged, warming and humidifying the air while simultaneously cooling the epithelium of the turbinates. The efficiency of this evaporative exchange is such that the temperature of the nasal surfaces may occasionally drop below the temperature of the ambient air (Jackson and Schmidt-Nielsen 1964). Inspired air is fully saturated and approaches deep-body temperature by the time it leaves the nasal cavity (Schmidt-Nielsen et al. 1970). These data suggest that during exhalation air is cooled and becomes supersaturated as it passes over the turbinates, condensing and recycling excess moisture within the nasal cavities and minimizing evaporative heat loss. This mechanism apparently allows birds and mammals to recover significant fractions of the water and heat that would otherwise be lost to the environment (Schmidt-Nielsen 1970; Hillenius 1994).

Distinct olfactory conchae not associated with heat exchange are present in many birds. When present, these simple sensory structures are situated in a blind-ended, posterodorsal chamber of the nasal cavity, out of the main path of respired air (Bang 1971). These conchae are probably homologous to structures associated with olfactory reception (e.g., naso- and ethmoturbinals of mammals) found in the nasal cavities of most other living tetrapods (Witmer 1995).

Previous studies on the water economy of birds have focused primarily on respiratory turbinate function of taxa living in extreme environments (Schmidt-Nielsen et al. 1970; Withers and Williams 1990; Morgan et al. 1992; Tielman et al. 1999). However, since respiratory turbinates are present in virtually all extant birds, independent of animal mass or the environment inhabited, their function in the water economy and heat balance of animals from less extreme environments call for closer examination.

Material and Methods

In this study, I assessed turbinate function in resting birds that inhabit primarily temperate, mesic environments. Net respiratory evaporative water loss rates from birds breathing normally (i.e., oropharyngeal breathing) were compared to water loss rates in individuals with the respiratory turbinates experimentally bypassed (oropharyngeal breathing). Water loss rates were calculated from exhaled nasal and oral air temperatures recorded at the external nares and at the oropharynx near the exit to the trachea, respectively. Additionally, temperature of exhaled air of the birds was contrasted with that of comparably sized lizards at similar body temperatures in identical ambient conditions.

Birds used in this study ranged from moderately sized to relatively large species representing five avian orders. All experiments were performed on resting animals at 15°C, an ambient temperature that approximates the daily mean in many temperate regions (Rufner and Bair 1984). A moderate relative humidity (RH; 50% ± 3%) was maintained during all exhaled air temperature recordings to approximate nasal turbinate function in relatively nonstressful mesic environmental conditions.

Animals

Experimental animals include pigeons (Columbiformes; Columbidae: COLUMBIA Livia; 319 ± 45.2 g; n = 5), Japanese quail (Galliformes, Phasianidae: Coturnix coturnix; 117 ± 10.2 g; n = 5), herring gulls (Charadriiformes, Laridae: Larus argentatus; 799 ± 45.1 g; n = 5), American crows (Passeriformes, Corvidae: Corvus brachyrhynchos; 357 ± 21.6 g; n = 6), and Canada geese (Anseriformes, Anatidae: Branta canadensis; 1,857 ± 389.4 g; n = 6). All animal masses are presented mean ± SEM. Gulls were captured on the central Oregon coast. Pigeons and Japanese quail were obtained through local commercial sources. Crows and Canada geese were provided courtesy of local breeders, the Portland Audubon Society, and/or the Oregon State Department of Fish and Wildlife. All animals were adults, as determined by size, age information from their keepers, or, for the guls, by plumage pattern. Birds were maintained in cages or pens with 12L: 12D photoperiod and fed and watered ad lib. at the facilities of the Oregon State Lab Animal Resources. All birds were fasted 8–12 h before experimental protocols to ensure a postabsorptive metabolic state.

The reptile used for expired air temperature experiments in this study was the Australian bearded dragon (Agamidae: Pogona vitticeps). Mean body mass of lizards was 352 ± 21.7 g (n = 5).

Determination of Metabolic and Respiratory Variables

Metabolic rate and lung ventilation parameters of resting birds were recorded simultaneously. Experiments were performed in custom-made cylindrical PVC respirometry chambers placed in a temperature- and humidity-controlled room maintained at 15°C ± 0.3°C and 50% ± 3% RH. Chamber volumes were 59,878 and 7,620 cm³. The smaller chamber was used for experiments on quail, pigeons, and crows. Gulls and geese were tested in the larger chamber. Uniform flow of dry air (converted to STPD) from a pressurized source was maintained and con-
continuously monitored with Cole-Parmer 150-mm high-resolution variable area flowmeters, calibrated daily with a Vitalograph brand spirometer. Flowmeters were positioned between the air source and the metabolic chamber. Flow rates were high enough to ensure the concentration of oxygen in the chamber never fell below 20% during any experimental period (flow rate data for each species is included in Table 1). I recorded chamber temperature \((T_c)\) every 5 min during the experiments with a thermocouple thermometer (Omega Instruments, model HH21) placed in the air outflow port. \(T_c\) was controlled and maintained at \(15^\circ\pm 0.4^\circ\)C during all experiments. RH of air in the chamber during the experiments was determined by placing an Extech model 5070C humidity meter/thermometer (calibrated for each run against a saturated salt solution = 75% ± 3% RH) in the outflow line (Hillenius 1992).

Oxygen consumption was determined using open-circuit respirometry. A sample of the outflow air was passed through a column of drierite and ascarite to remove water and CO\(_2\), respectively, before being drawn through an Applied Electrochemistry S-3A/1 oxygen sensor for determination of fractional oxygen content. The sensor was calibrated against a sample of dried outdoor air before and immediately at the completion of each experiment. Readings from the oxygen sensor during the experiments were recorded at 5-s intervals and recorded to a microcomputer running Datacan V (Sable Systems) through a commercial data acquisition and analysis software (Sable Systems, Datacan V). Sample averaging software was used to increase resolution of tidal volume calculations. \(T_c\) (body temperature and pressure saturated; BTPS) was estimated from ventilation pressure deflections recorded in the respirometer using equation (6) from Malan (1973). Time lag between events in the chambers and the oxygen sensor was determined at each flow rate to coordinate ventilation traces with \(V_o\) recordings. Ventilation frequency \((f)\) was measured directly from the traces. The plethysmograph was calibrated at the end of each run by calculating the mean pressure fluctuation determined from a minimum of 10 injections of a known volume of air into the chamber. The injection rate was controlled to mimic deflection kinetics caused by lung ventilation (Maloney and Dawson 1994). Chamber pressures were measured at the end of each experiment by opening a valve on the outflow line connected to a fluid-in-glass manometer. Flow rates into the respirometer were such that total chamber pressure was never more than 10

Table 1: Calculated respiratory and metabolic variables

<table>
<thead>
<tr>
<th>Species</th>
<th>(V_o) (ml min(^{-1}))</th>
<th>(V_T) (ml)</th>
<th>(E_o) (%STP)</th>
<th>(H_2O) Savings (mg d(^{-1}))</th>
<th>Heat Savings (cal d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coturnix coturnix</td>
<td>4.33 ± .3</td>
<td>2.26 ± .27</td>
<td>34.1 ± 1.83</td>
<td>2,666.4 ± 99.5</td>
<td>1,546.7 ± 57.7</td>
</tr>
<tr>
<td>Columba livia</td>
<td>7.91 ± .96</td>
<td>5.24 ± .16</td>
<td>35.2 ± 2.09</td>
<td>5,734.8 ± 555.8</td>
<td>3,282.6 ± 332.4</td>
</tr>
<tr>
<td>Corvus brachyrhynchos</td>
<td>11.59 ± 1.68</td>
<td>7.25 ± 1.10</td>
<td>33.7 ± 2.02</td>
<td>5,087.3 ± 1,029.9</td>
<td>2,950.9 ± 597.4</td>
</tr>
<tr>
<td>Larus argentatus</td>
<td>14.80 ± .92</td>
<td>21.66 ± 1.49</td>
<td>26.9 ± 0.79</td>
<td>9,604.0 ± 384.9</td>
<td>5,568.8 ± 223.3</td>
</tr>
<tr>
<td>Branta canadensis</td>
<td>19.33 ± .93</td>
<td>27.82 ± 1.48</td>
<td>37.7 ± 2.93</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Pogona vitticeps</td>
<td>.86 ± .054*</td>
<td>2.14 ± .13*</td>
<td>14.9*</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

Note. \(V_o\), oxygen consumption; \(V_T\), lung tidal volumes; \(E_o\), oxygen extraction. Flow rates of dry CO\(_2\)-free air in the metabolic chambers were 1.4 L min\(^{-1}\) (quail); 1.4–1.55 L min\(^{-1}\) (pigeons); 2.14 L min\(^{-1}\) (crows); 3.5 L min\(^{-1}\) (gulls); 2.75–2.85 L min\(^{-1}\) (geese).

* Reptilian \(V_o\), \(V_T\) and \(E_o\) values from Bennett (1973).
mmHg, and generally less than 2 mmHg, above ambient atmospheric pressure.

**Expired Air Temperature and Water Loss Rate**

Temperature of expired air was recorded in a temperature- and humidity-controlled room immediately on completion of oxygen consumption and pressure measurements. $T_e$ was maintained at 15.0° ± 0.4°C and RH at 50% ± 3%. Birds were lightly restrained with an elastic and cotton tube placed around their bodies during temperature recordings. When necessary, a hood was placed over the head of the birds to calm the animals during procedures. All birds except geese tolerated the restraints and hoods without any obvious signs of stress.

Temperature of expired air ($T_e$) was measured with a 40-gauge copper-constantan probe and thermocouple thermometer (Omega Instruments, model TAC-386-TC). The tip of the probe was held 1 mm inside the external nares to record temperature of exhaled nasal air (Withers and Williams 1990). Oral $T_e$ values were collected by inserting short lengths of tygon or rubber tubing into the mouths of the animals with one end positioned immediately posterior to the internal nares at the oropharynx, thereby bypassing the upper respiratory tract and turbinates. Birds tolerated these short treatments without signs of apparent stress. Tubing diameter for each bird was adjusted to fit comfortably within the circumference of the buccal cavity. To record oral $T_e$, a thermocouple was inserted into the tube without touching its walls. During both nasal and oral respiratory cycles, the temperature recordings plateaued as equilibrium was reached between the thermocouple and expired air (Withers and Williams 1990). $T_e$ was calculated from the average of at least 10 peak-voltage readings after equilibrium had been established. The thermocouple was calibrated against a mercury thermometer traceable to the U.S. Bureau of Standards. Body temperatures ($T_b$) of the birds were recorded using a thermocouple inserted either deeply within the cloaca or deeply down the gullet of the animals immediately after expired air temperatures were recorded.

It is noted that exhaled oral and nasal air temperatures used to estimate water and heat loss rates were measured on unrestrained birds, while lung tidal volumes and ventilation frequency measurements were taken on unrestrained birds within a darkened metabolic chamber. The effect of restraint on birds increased respiratory frequency and therefore likely increased exhaled air temperature (and water loss rate) over resting values. Therefore, as exhaled air temperature varies with respiratory frequency, the data probably represent overestimates of total respiratory evaporative water loss (REWL) and respiratory evaporative heat loss (REHL), and water and heat savings estimates are likely to be conservative. To minimize the effect of restraint, oral and nasal $T_e$ values were used in calculations only if ventilation frequencies during these two manipulations were within 10% of one another.

Lizards were maintained in terraria equipped with heat lamps before all recordings. $T_e$ of the lizards was maintained at 36.5°C to approximate the preferred body temperature ($T_{pref}$) of 37°C (Bennett 1973) and to provide a similar $T_e/T_b$ gradient to that of the birds for appropriate comparison of $T_e$. Nasal $T_e$ values for lizards were recorded as it was for birds. As with the birds, all measurements were taken in a temperature- and humidity-controlled room ($T_e$ = 15°C, RH = 50%). Lizard $T_e$ was measured by insertion of a thermocouple deeply in the cloaca immediately before and at the end of each $T_e$ recording.

**Respiratory Water and Heat Savings**

Heat savings produced by nasopharyngeal breathing relative to oropharyngeal breathing for quail, pigeons, gulls, and crows (at $T_e$ = 15°C, RH = 50%) were estimated from the calculated volume of H$_2$O reclaimed from exhaled air. The volume of H$_2$O condensed during exhalation in the nasal passages and turbinates was estimated as the difference of the volume of H$_2$O lost per minute with turbinates experimentally bypassed, and the volume of H$_2$O lost per minute during nasopharyngeal breathing, assuming saturation of exhaled air (Schmidt-Nielsen et al. 1970). Water loss rates for nasal and oral breathing were calculated from saturation water vapor–partial pressure values at respective exhaled air temperatures (Hillenius 1992, 1994). Daily respiratory heat savings were calculated from 24-h lung ventilation volumes (Table 1) and the latent heat of evaporation (584 cal g$^{-1}$ H$_2$O) assumed to have been recovered on the respiratory turbinates surfaces during exhalation. Total daily heat production was estimated from 24-h VO$\sub{2}$ using the average caloric equivalent of 4.85 kcal L$^{-1}$ O$_2$ (Schmidt-Nielsen 1990).

**Data Analysis**

Variables are given mean ± SEM. VO$\sub{2}$ values (see Table 1) for birds were accepted if they were within 10% of the lowest continual 5 min of VO$\sub{2}$ recorded for that animal during each individual run (Maloney and Dawson 1994). Mean values of exhaled nasopharyngeal and oropharyngeal air temperatures recorded for each species were compared using paired t-tests. Results were considered significantly different if $P<0.05$.

Lung tidal volumes used to determine minute volume are given BTPS. Lung tidal volumes used for calculation of oxygen extraction efficiency (EO$_{O_2}$) are given STPD. EO$_{O_2}$ was calculated as

$$EO_{O_2}(\%) = \frac{100 \times \dot{V}O_2}{FEO_2 \times V_l \times f}$$

where FEO$_2$ is the fractional concentration of oxygen in chamber excurrent air, $V_l$ = tidal volume, and $f$ = frequency of respiration.

Net daily water loss rates for bird species for both experi-
mental (oropharyngeal) and control (nasopharyngeal) were calculated as the difference between water added to ambient air (15°C, 50% RH) during inhalation to reach saturation at $T_{b}$, minus water recovered at $T_{ex}$ (Schmidt-Nielsen et al. 1970; Tielman et al. 1999).

Results

Mean values for respiration frequencies, body temperatures, and exhaled narial and oropharyngeal air temperatures were measured from four relatively large bird species and compared with exhaled narial air and body temperatures of the agamid lizard *Pogona viticeps* (Table 2). Exhaled air temperature data from resting birds was obtained from four of the five species used in this study. No exhaled oropharyngeal air temperatures were obtained for lizards (*Pogona*). Oropharyngeal water loss data for the lizards were estimated by assuming that oropharyngeal exhaled air temperatures were approximately equal to body temperature. These data probably represent a slight over-estimation of oropharyngeal water loss rates, as limited cooling of exhaled air undoubtedly took place in the trachea of lizards. Values for oxygen consumption ($V_{O2}$), lung tidal volumes ($V_{T}$), oxygen extraction coefficients ($E_{O2}$), and daily water and caloric savings generated by condensation in the nasal passages and turbinate system were calculated for four of the birds in this study (Table 1). No reliable exhaled air temperature data could be obtained for *Branta*, as the geese would not submit to handling, including hooding or placement of the thermocouple at the external nares, without exhibiting signs of extreme stress (panting, elevated respiratory frequencies, flailing of the head, etc.). Oxygen extraction coefficients for resting lizards were assumed to be 14.9% (Bennett 1973).

Control (nasopharyngeal) and experimental (oropharyngeal) respiratory evaporative water loss rates of bird and lizard species were estimated from exhaled air temperatures, assuming saturation (Fig. 1). Caloric savings calculated from the volume of condensed water recovered in the nasal passages due to cooling of saturated exhaled air are expressed as a percentage of the animal's daily energy budget (Fig. 2). Comparison of avian and reptilian water loss values per cubic centimeter oxygen consumed is graphically depicted (Fig. 3).

Discussion

Turbinate Function

Nasal $T_{ex}$ values of resting birds used in this study were significantly lower ($P<0.001$) than oral $T_{ex}$ (Table 2). Nasopharyngeal breathing resulted in substantially lower rates of respiratory and heat loss than oropharyngeal breathing in all birds that had the upper respiratory tract experimentally bypassed (Table 1). These data, coupled with previous reports of respiratory turbinate-mediated reductions in REWL (Schmidt-Nielsen et al. 1970; Brent et al. 1984; Withers and Williams 1990; Maloney and Dawson 1994) provide evidence for broad distribution within class Aves of an effective countercurrent heat-exchange mechanism in the nasal cavities, at

| Table 2: Measured values of physiological variables of experimental animals |
|---|---|---|---|---|---|---|
| | $n$ | Mass (g) | $F_{res}$ (min$^{-1}$) | $T_{b}$ (°C) | Nasal $T_{ex}$ (°C) | Oral $T_{ex}$ (°C) | t-Statistic |
| *Coturnix coturnix* (Japanese quail) | 5 | 117 ± 10.2 | 26.1 ± 1.98 | 40.5 ± .21 | 20.4 ± .4 | 37.0 ± .3 | 44.01* |
| *Columbia livia* (pigeon) | 5 | 319 ± 45.2 | 21.9 ± 1.44 | 40.7 ± .13 | 21.4 ± .5 | 38.2 ± .5 | 34.93* |
| *Corvus brachyrhynchos* (American crow) | 5 | 357 ± 21.56 | 23.7 ± 1.08 | 41.1 ± .18 | 21.9 ± .9 | 36.6 ± .4 | 20.10* |
| *Larus argentatus* (Herring gull) | 6 | 799 ± 45.11 | 12.6 ± .71 | 39.4 ± .23 | 19.4 ± .7 | 35.9 ± .3 | 30.20* |
| *Branta canadensis* (Canada goose) | 6 | 1,857 ± 389.4 | 9.1 ± .35 | 40.1 ± .24 | NA | NA | NA |
| *Pogona viticeps* (Bearded dragon) | 5 | 352 ± 21.7 | 15.6| 36.5 ± .43 | 31.3 ± .67 | NA | NA |

Note. $F_{res}$, respiration frequency; $T_{b}$, body temperature; $T_{ex}$, exhaled narial temperature; $T_{ex}$, oropharyngeal temperatures. Exhaled air temperatures unavailable for *Branta*. Exhaled oropharyngeal temperatures unavailable for *Pogona*. All measured values are mean ± SEM.

* Estimated respiration frequency for *Pogona* from Bennett 1973.

* t-statistics given are for $P<0.0001$.  

Figure 1. Absolute rates of respiratory evaporative water loss (REWL; mean ± SEM) for four species of birds representing four orders and a lizard (Pogona). Values calculated from exhaled air temperature, assuming saturation of respiratory air with water vapor. Hatched columns (nose) represent REWL rates of animals during routine nasopharyngeal breathing (using nasal respiratory turbinates). Hatched columns (mouth) represent REWL rates with respiratory turbinates experimentally bypassed (oropharyngeal breathing). All experiments performed at $T_a = 15^\circ C$, RH = 50%.

least during periods of rest or routine activity. Significantly, none of the avian species used in this study are highly specialized for life in extreme thermal or xeric environments. This suggests a range of crucial physiological functions of the avian upper respiratory tract and turbinate complex, including, but not limited to, specific adaptations for life in deserts or extremely cold high-latitude environments. In addition, it has been demonstrated that birds maintain brain temperature below body temperature via specialized vasculature in the head, the ophthalmic rete (Crowe and Withers 1979; Pinshow et al. 1982). Venous circulation associated with countercurrent heat exchange in the nasal passages and respiratory turbinates is known to contribute to ophthalmic rete-mediated cooling of the brain in a variety of resting birds (Bernstein et al. 1978).

Water Flux

It may be more meaningful to analyze REWL savings not only in absolute terms, but also as a fraction of the total volume of water that the animal processes through its body each day (water flux). Values for daily water flux in captive birds scale allometrically, according to the equation

$$\log \text{daily water flux (mL d}^{-1}) = -0.059 + 0.694 \log \text{mass (g)}$$

(Nagy and Petersen 1988). Predicted water flux values (g d$^{-1}$)

![Water and Heat Savings](Figure 2. The percentage savings of daily caloric expenditure resulting from cooling of exhaled air and condensation of water in the nasal passages during nasopharyngeal breathing in four species of birds. Respiratory heat savings (mean ± SEM) over a 24-h period were calculated from the difference in the volume of water present in saturated exhaled air at temperatures recorded at the oropharynx and the external nares, assuming the latent heat of evaporation = 584 cal g$^{-1}$ H$_2$O. Water vapor-saturation density values from standard tables.)

Water and Heat Savings

Average exhaled air temperatures measured at the oropharynx for the four avian species in this study averaged 3.5$^\circ$C lower than deep-body temperature, compared with an average reduction of 19.6$^\circ$C for temperatures measured at the external nares, supporting the prediction that the trachea is not a major site of heat exchange during routine lung ventilation. Conversely, the relatively low exhaled air temperatures recorded at the external nares demonstrated that the nasal passages of the four avian species for which data were available participated significantly in respiratory heat exchange. In contrast, nasal $T_a$ of lizards averaged only 5.2$^\circ$C less than deep-body temperature. This reduction is comparable with the average reduction of oropharyngeal $T_a$, relative to $T_b$, from birds in this study.

Respiratory turbinate-linked cooling of expired air in the nasal passages resulted in a net reduction of REWL of 55% (crows), 69% (pigeons), 70% (quail), and 71% (gulls). Heat recovered in the nasal passages and associated respiratory turbinates during normal, nasopharyngeal breathing, even at a moderate $T_a$ ($15^\circ$C) and RH (50%), provided a daily caloric savings of 3.5% (crows), 6.1% (pigeons), 5.7% (quail), and 5.6% (gulls) of total daily heat production over mouth-breathing birds (Fig. 2). While nasal breathing conserves significant amounts of heat and water in moderate ambient conditions, bypassing the turbinate complex with specialized respiratory behaviors (i.e., mouth breathing/panting and gular flutter) provides birds with an efficient means of dumping excess metabolic heat during periods of heat stress.
though specific aspects of the morphology of the avian nasal sources to replace the lost calories. 

Display little anatomical variation within closely related avian families (Bang 1971), respiratory turbinate structures often negate production commensurate with increased metabolic heat production required to compensate for additional REWL, this increased water production would probably be minimized or negated by increased REWL during active foraging for dietary sources to replace the lost calories.

Figure 3. Calculated rates of respiratory evaporative water loss (REWL; mean ± SEM) per cubic centimeter O2 consumed of four avian and one reptilian species. Data were obtained from exhale air temperatures of resting animals, under control (nasopharyngeal breathing) and experimental (oropharyngeal breathing) conditions. \( T_r = 15°C, RH = 50\% \)

for the species in this study were quail, 23.8; pigeons, 47.8; gulls, 90.4; and crows, 51.6. The absolute water savings at 15°C achieved by nasopharyngeal breathing over oropharyngeal breathing for each species, calculated as the percentage of total water flux, resulted in 11.2%, 12.0%, 10.6%, and 9.9% of total predicted daily water flux, respectively. The 24-h percentage saving estimates given above are conservative values based on the lowest average ventilatory volumes and \( V_o \), values recorded during each experimental run. This portion of the animal's daily water balance is essentially “free” water, potentially contributin to a direct reduction in energy expended by wild birds flying to or searching for water. Although birds without turbinates would likely experience elevated rates of metabolic water production commensurate with increased metabolic heat production required to compensate for additional REWL, this increased water production would probably be minimized or negated by increased REWL during active foraging for dietary sources to replace the lost calories.

**Turbinates as an Index of Metabolic Status**

The independent evolution of endothermy (Kemp 1988) and complex nasal respiratory turbinate structures in birds and mammals, coupled with the absence of similar structures in all ectothermic tetrapods, suggests their fundamental correlation with, and apparent physiological importance for, maintenance of endothermy, regardless of the environment inhabited. Notably, though specific aspects of the morphology of the avian nasal cavity and associated turbinates vary between orders and families of birds (Bang 1971), respiratory turbinate structures often display little anatomical variation within closely related avian taxa (i.e., at the family level), independent of the physical environment inhabited. For example, investigations of turbinate structure in pheasant galliform birds indicates a consistent nasal morphology that is virtually indistinguishable between species that inhabit tropical equatorial (guinea fowl), desert (chukar partridge), mesic-xeric (California quail), or high-latitude arctic environments (ptarmigan; N. R. Geist, unpublished observations). These observations are consistent with results of investigations of closely related species of songbirds from different habitats that demonstrate little or no physiological difference in respiratory turbinate-mediated heat and water savings (Schmidt-Nielsen et al. 1970). It is therefore reasonable to assume that the respiratory evaporative heat and water savings, as well as other physiologically important corollary functions (i.e., brain cooling) associated with respiratory turbinates, are likely to have an adaptive physiological value over a broad range of environmental conditions. Even the relatively simple respiratory turbinates of pigeons used in this study produced a significant reduction of respiratory water and heat loss under the experimental conditions.

The few cases within Aves in which turbinates are greatly reduced are clearly secondary losses associated with unique behavioral patterns. For example, many pelicaniform birds have either entirely occluded (e.g., pelicanids, sulids) or highly constricted nostrils (e.g., phaethonids and frigatids) as adults and effectively bypass the upper respiratory tract (Bang 1971), rendering the respiratory turbinates essentially useless as respiratory heat exchangers. This nasal morphology is correlated to the unique plunge-diving habits typical of this order. The presence of open nostrils in plunge divers would likely result in damage to the delicate respiratory-turbinate complex. As a result, most pelicaniforms, including all adult sulids, phalacrocoracids, frigatids, and pelicanids, display only the most rudimentary development of respiratory turbinates in association with their restricted external nasal openings (MacDonald 1960). Significantly, these marine birds possess salt glands (Bang 1971; Schmidt-Nielsen 1980) and are probably able to compensate for increased REWL associated with secondary reduction of respiratory turbinates by increased consumption of salt water.

The absence of respiratory turbinates in ectothermic vertebrates and their presence in birds and mammals further supports their intrinsic physiological importance in maintenance of high endothermic metabolic rates. Living ectothermic amniotes (i.e., amphibians and reptiles) have relatively minimal capacities for sustained aerobic activity and correspondingly low lung ventilation rates that probably constrained the selection for analogous mechanisms of respiratory heat exchange (Hill and Wyse 1976). The low metabolic and lung ventilation rates of extant reptiles typically result in low rates of respiratory water loss relative to similarly sized birds, even when air is exhaled at body temperature.

The widespread heat and water savings provided by respiratory turbinates in virtually all birds and mammals, regardless
of habitat, suggest a crucial physiological role in the main­
ance of endothermic metabolism. The evolution of the res­
piratory turbinate complex in Aves was, nevertheless, likely a
key preadaptation, enabling birds to successfully invade and
exploit extreme habitats, such as deserts and high-latitude en­
vvironments. These data strongly reinforce previous studies sug­
gesting that the development of complex respiratory turbinates
was selectively associated with the acquisition of homeothermic
endothermy during avian evolution (Hillenius 1992; Ruben et
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