The Role of Hyperthermia in the Water Economy of Desert Birds

B. Irene Tieleman1
Joseph B. Williams2*3

1Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; 2Department of Zoology, Ohio State University, Columbus, Ohio 43210

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ABSTRACT

A number of authors have suggested that hyperthermia, the elevation of body temperature (Tb) 2°–4°C above normal, contributes to a reduction in total evaporative water loss (TEWL) in birds. Information about the role of hyperthermia in the water economy of birds is scattered throughout the literature. We purposed to collate the available information on this subject, to reevaluate the benefits and costs of this process, and to assess its net effect on the water economy of birds, especially species living in deserts. In this review, we first consider the current model of heat balance in birds at high ambient temperatures (Ta), and show that, in most studies performed at a high Ta, birds were increasing their Tb, a violation of the assumption of steady state conditions. Next, we incorporate the rate of heat gain into calculations of the dry heat transfer coefficient (h), below and above temperature equality (Ta = Tb). We develop a method to calculate h at Ta = Tb, using l'Hôpital's rule. The combined result of our approach suggests that birds increase their dry heat transfer even when Ta is above Tb, contrary to our prediction. Finally, we explore aspects of hyperthermia that reduce water loss, such as an improved thermal gradient and heat storage, and aspects that may augment water loss, the latter a result of increased respiratory water loss when Tb is elevated. Our analysis of the combination of these three factors suggests that, during acute exposure to high Ta (1 h), birds over a size range of 10–1,000 g save about 50% of their TEWL by becoming hyperthermic. For chronic episodes of high Ta (5 h), small birds save water by hyperthermia but large birds do not.

Introduction

Deserts are harsh regions characterized by intense solar radiation, temperature extremes, low primary productivity, and scarcity of drinking water (Louw and Seeley 1982). For avian species, living in these areas is especially challenging because, unlike many of their mammalian counterparts, birds are diurnal and nonfossorial and, as a consequence, experience the full brunt of the desert environment. Their successful occupation of these rigorous climes is even more remarkable when one considers that birds have relatively high rates of water loss, a feature attributable to processes that accompany high metabolic rates (Aschoff and Pohl 1970). Moreover, high rates of metabolism result in high body temperatures (Tb), averaging around 41°C (Prinzinger et al. 1991), close to the upper lethal limit of 46°C–47°C (Dawson and Schmidt-Nielsen 1964). During periods of heat stress, their water economy must be compromised because birds defend their Tb from exceeding the lethal limit by means of evaporative cooling, a mechanism that mandates substantial water loss.

The physiological capacity of birds to regulate their Tb by evaporative cooling can be exceeded in some natural situations: periods of extreme heat, with air temperatures exceeding 50°C, have caused significant mortality among populations of desert birds (Miller 1963; Serventy 1971). One can imagine that, because of similar episodes of temperature extremes coupled with a pervasive scarcity of drinking water, natural selection has equipped extant populations of desert birds with a suite of behavioral and physiological adaptations that minimize water loss. Early work that compared desert and nondesert species failed to elucidate physiological differences, leading to the consensus that, in general, birds are preadapted to desert life (Chew 1961; Bartholomew and Cade 1963; Dawson and Schmidt-Nielsen 1964; Dawson 1982; Maclean 1996). However, it has recently been shown (Williams 1996) that birds from arid environments have lower total evaporative water loss rates (TEWL) than do birds from more mesic environments, at least when tested in the laboratory at a Ta of 25°C. This finding leads to the possibility that some desert birds have evolved specific adaptations that reduce their TEWL, but the mechanisms that produce this result remain unknown.

The literature contains a number of suggestions for mechanisms that reduce TEWL, the sum of respiratory and cutaneous water losses. A countercurrent heat exchange system in the nasal passages of some species can ostensibly recover significant quantities of water from the exhaled air stream, thus lowering respiratory water loss (Schmidt-Nielsen et al. 1970). During dehydration, adult zebra finches (Taeniopygia guttata)
reduce cutaneous water loss by altering the lipid composition in their epidermis (Menon et al. 1989). A number of authors have suggested that hyperthermia, the elevation of body temperature 2°–4°C above normal, contributes to a reduction in TEWL among birds (Calder and King 1974; Weathers 1981; Dawson 1984; Withers and Williams 1990).

Discussions about the potential benefits of hyperthermia to the water economy of birds have focused on three factors. First, an improved thermal gradient between $T_a$ and ambient air temperature ($T_a$) increases the potential for dry heat loss, thereby decreasing the need for evaporative cooling (Calder and King 1974). Second, heat that is temporarily stored in body tissues during bouts of high $T_a$ could be dissipated by non-evaporative means when the $T_a$ becomes more favorable (Schmidt-Nielsen 1964; Dawson and Bartholomew 1968; Calder and King 1974). And third, Weathers and Schoenbaechler (1976) found that, for some species, $T_a$ increased in the thermoneutral zone (TNZ) while metabolism remained constant. They reasoned that this absence of a Q10 effect would reduce evaporative water loss because ventilation rates and metabolic heat production would be lower. Weathers (1981) used the three factors above to estimate that Pyrrhuloxia (*Cardinalis simuitatus*) reduce their TEWL by 50% as a result of 2.3°C increase in $T_a$ at a $T_a$ of 38°C.

Few studies have focused explicitly on the role of hyperthermia in the water economy of birds. Much of the information that does exist on this issue is scattered throughout the literature, and many of the data were collected in studies of temperature regulation, often more than a decade ago. Moreover, most interpretations of the significance of hyperthermia that we have found in the literature suggest a positive effect on water savings. Few have delved into the complex features of hyperthermia, some of which may negatively impact water loss rates. Consider, for example, that when birds have an elevated $T_a$, exhaled air temperature ($T_e$) will be higher than it would be at normothermic $T_a$. The result is that the exhaled air will contain more water vapor, assuming that air in the lungs is saturated with water (Schmidt-Nielsen et al. 1970; Withers and Williams 1990). Second, if birds become hyperthermic, they may start panting, increasing the volume of exhaled air by as much as five times above volumes for normothermic birds (Bernstein 1987). The combination of higher water vapor density and increased volume of exhaled air results in an augmentation of respiratory water loss, negating some of the hypothesized advantages of hyperthermia. The above considerations prompted us to collate the available information on hyperthermia in birds, to reevaluate the benefits and costs of this process, and to assess its net effect on the water economy of birds, especially species living in deserts.

In this report, we first reevaluate the current model of heat balance in birds at high $T_a$. Next, we examine the variation in $T_a$ over a range of $T_a$’s in desert and nondesert species, testing the hypothesis that desert species have a higher $T_a$ at a given $T_e$. Then, using our model of heat balance, we assess the roles of an improved thermal gradient, of heat storage, of Q10, and of altered respiratory variables in reducing or augmenting water loss in birds. We do so by comparing water loss of birds with an elevated $T_a$ with the hypothetical situation where $T_a$ is normothermic. Finally, we specify the kind of data needed to arrive at a more complete understanding of the process of hyperthermia and of its role in the water economy of desert birds.

Material and Methods

We found 28 studies that reported laboratory measurements of metabolic rate, evaporative water loss, and $T_a$ of birds at $T_a \geq 45°C$. Most of these investigations used species that weighed <200 g (see appendix); information on larger species is lacking. Two studies reported data up to 44°C; we estimated data in these cases by solving the appropriate equations at 45°C. Six studies did not contain all variables required for calculations of the dry heat transfer coefficient (h) and were not used in our calculations of water savings. All studies used open-circuit respirometry, but different experimental conditions under which measurements were made, along with diverse techniques used to determine $T_a$, metabolism, and evaporative water loss, add variation to the data. We included studies without regard to when measurements were made during the day (α or ρ phase) or year, the length of time animals had been in captivity, or their digestive state (postabsorptive vs. nonpostabsorptive). We excluded studies in which birds were water stressed or in which low air flow rates were used, a situation that can adversely affect rates of TEWL (Lasiewski et al. 1966). Our rationale for selecting data at 45°C was that many desert species experience equivalent $T_a$’s in the field, most species have an elevated $T_a$ at this $T_a$, and considerations of water economy are important for survival at this high $T_a$. In classifying a species as desert or nondesert, we followed the judgment of the original authors.

Statistical analyses were performed using SPSS/PC+ (SPSS 1997) or following Zar (1984). Means are presented ± SD.

Results

Heat Balance in and above the Thermoneutral Zone

An appreciation of the heat balance of birds at high $T_a$’s is important when trying to understand the impact of hyperthermia on the rate of water loss. The classic model of heat balance, originally designed for moderate and cold air temperatures (Scholander et al. 1950; Calder and King 1974), requires reevaluation before it can be applied to situations of heat stress.

Dry Heat Loss. The rate of dry heat loss $H$ (J h⁻¹) of an animal is described by Equation (1) (following Bakken 1976; Gates 1980):
in which \( M \) = metabolic heat production (J h\(^{-1}\)), \( E \) = total evaporative heat loss (J h\(^{-1}\)), and \( C(dT_b/dt) = \) rate of heat gain in or loss from the animal’s body tissue (J h\(^{-1}\)). All three components are functions of \( T_a \) (Fig. 1). Note that \( C \), the specific heat capacity of the entire bird, is calculated by multiplying the specific heat of tissue by body mass. The time-dependent heat capacity for the entire bird, is calculated by multiplying \( C \) on crested larks (Galerida cristata, body mass \( 33 \pm 1.3 \) g, \( n = 6 \)) during exposure of 3–5 h to constant \( T_a \), a much longer period than most researchers use when measuring metabolism at high temperatures. At lower \( T_a \),s, \( T_a \) remained constant, but at 45°C, \( T_a \) increased by 0.5\(^\circ\) ± 0.18°C h\(^{-1}\). This corresponds to a rate of heat gain of 59 ± 19.9 J h\(^{-1}\) per animal (25% of dry heat production \( H \) at \( T_a = 45°C \)), assuming that the specific heat of tissue is 3.35 J g\(^{-1}\) \( ^\circ\)C\(^{-1}\) (Calder and King 1974; Schmidt-Nielsen 1983). Implicit in this calculation is the assumption that core \( T_a \) equals the average \( T_a \) over the bird’s body. While, at low \( T_a \)’s, core \( T_a \) is typically higher than the average \( T_a \), at high \( T_a \)’s, this difference is small (Bartholomew 1982), justifying our assumption that core \( T_a \) = mean \( T_a \).

Although there are no direct measurements of \( C(dT_b/dt) \) at temperature equality (\( T_a = T_b \)), there should be no net dry heat transfer between a bird and its environment at this temperature (\( H = 0 \)). and \( C(dT_b/dt) \) can be calculated as \( C(dT_b/dt) = M - E \). For 22 studies, we tested whether steady state conditions were met by calculating a value for \( C(dT_b/dt) \) at \( T_b = T_a \), using values or equations for \( T_a \) as provided by the individual authors. When plotted as a function of body mass, \( C(dT_b/dt) \) was pos-

\[
H = M - E - C(dT_a/dt),
\]

Metabolic Heat Production. Metabolic heat production (\( M \)) varies with \( T_a \) and for most species, there exists a thermoneutral zone (TNZ) where metabolic rate is minimal and constant over a range of \( T_a \) (Fig. 1B: Scholander et al. 1950; Calder and King 1974). Below the lower critical temperature (\( T_{lc} \)), metabolism increases in response to decreasing \( T_a \) to maintain a constant \( T_a \). Above the upper critical temperature (\( T_{uc} \)), birds often pant or gular flutter, augmenting their ventilation rate as requirements for evaporative cooling increase, and as a consequence, their metabolic rate increases (Calder and King 1974).

Evaporative Heat Loss. Empirical evidence shows that birds have a relatively constant total evaporative heat loss (\( E \)) below the \( T_a \) (Dawson and Bennett 1973; Calder and King 1974; Withers and Williams 1990; Williams et al. 1991; Weathers 1997), whereas in the TNZ, \( E \) gradually increases with increasing \( T_a \). Above the \( T_{uc} \), where a decreasing potential for dry heat loss and an elevation in metabolic rate combine to form an increasing heat load, \( E \) increases rapidly (Fig. 1B). Note that \( E \) is calculated from TEWL (g water d\(^{-1}\)), the sum of respiratory and cutaneous water losses.

Rate of Heat Gain. The rate of heat gain or loss from an animal’s body (\( C(dT_a/dt) \)) is 0 in steady state situations where \( T_a \) does not change with time. The oft applied assumption of steady state seems valid for measurements in the TNZ, but for those made above the TNZ, where heat stress becomes more severe, \( C(dT_a/dt) \) may become a significant factor. Although \( C(dT_a/dt) \) can be quantified by measuring \( T_b \) continuously during measurements, most studies assess \( T_b \) only after the metabolic trial is completed. In a separate study, we have made measurements of \( T_b \) on crested larks (Galerida cristata, body mass \( 33 \pm 1.3 \) g, \( n = 6 \)) during exposure of 3–5 h to constant \( T_a \)’s, a much longer period than most researchers use when measuring metabolism at high temperatures. At lower \( T_a \)’s, \( T_a \) remained constant, but at 45°C, \( T_a \) increased by 0.5\(^\circ\) ± 0.18°C h\(^{-1}\). This corresponds to a rate of heat gain of 59 ± 19.9 J h\(^{-1}\) per animal (25% of dry heat production \( H \) at \( T_a = 45°C \)), assuming that the specific heat of tissue is 3.35 J g\(^{-1}\) \( ^\circ\)C\(^{-1}\) (Calder and King 1974; Schmidt-Nielsen 1983). Implicit in this calculation is the assumption that core \( T_a \) equals the average \( T_a \) over the bird’s body. While, at low \( T_a \)’s, core \( T_a \) is typically higher than the average \( T_a \), at high \( T_a \)’s, this difference is small (Bartholomew 1982), justifying our assumption that core \( T_a \) = mean \( T_a \).

Although there are no direct measurements of \( C(dT_a/dt) \) at temperature equality (\( T_a = T_b \)), there should be no net dry heat transfer between a bird and its environment at this temperature (\( H = 0 \)), and \( C(dT_a/dt) \) can be calculated as \( C(dT_a/dt) = M - E \). For 22 studies, we tested whether steady state conditions were met by calculating a value for \( C(dT_a/dt) \) at \( T_b = T_a \), using values or equations for \( T_a \) as provided by the individual authors. When plotted as a function of body mass, \( C(dT_a/dt) \) was pos-

![Figure 1](image-url)
itive at $T_a = T_i$ in 19 of 22 studies (Fig. 2). If one divides by the specific heat of tissue, $C(dT_i/dt)$ can be converted to the rate of change in $T_i$. For these 22 studies, $T_i$ was increasing at an average rate of $2.1^\circ + 0.67^\circ$ (SE) h$^{-1}$, a value significantly different from 0 ($t = 3.18$, $P < 0.005$). This analysis suggests that steady state conditions may have been violated in some of these studies at high $T_i$’s. In future experiments, we recommend that practitioners continuously monitor $T_i$ when investigating questions concerning heat balance in birds, especially at higher $T_i$’s. The ramifications for the above finding are complex, but one message seems clear: calculations of heat transfer within our data set cannot ignore $C(dT_i/dt)$. However, because there are no direct measurements of $C(dT_i/dt)$ available and because we can only estimate $C(dT_i/dt)$ at $T_a = T_i$, the relationship between $C(dT_i/dt)$ and $T_i$ is not known. In our model, we assume, for simplicity, that $C(dT_i/dt)$ is a linear function defined by two points: $C(dT_i/dt) = 0$ (J h$^{-1}$) at the $T_{i0}$, and $C(dT_i/dt) = M - E$ (J h$^{-1}$) at $T_i = T_b$ (Fig. 1B). Continuous measurements of $T_i$ in future metabolism experiments will test the validity of this model.

Our analysis of $C(dT_i/dt)$ could be criticized because one may argue that net dry heat transfer is 0 at $T_a = T_{min}$, the temperature of the skin surface, and not at $T_a = T_b$ (Seymour 1972). However, data that relate $T_{min}$ to core $T_b$ in heat-stressed birds are scarce, and most work in this area has focused on temperatures of the evaporative surfaces in the respiratory tract, which can be $0.9^\circ$–$5.1^\circ$ lower than core $T_b$ (Lasiewski and Snyder 1969; Schmidt-Nielsen et al. 1969; Seymour 1972). While the temperatures of the evaporative surfaces in the respiratory tract of the ostrich were $2.2^\circ$C lower than its core $T_b$, $T_{min}$ equaled $T_b$ during heat stress (Schmidt-Nielsen et al. 1969). In our analysis of $C(dT_i/dt)$, the assumption that net dry heat transfer is 0 at $T_a = T_b$ gives a conservative estimate of $C(dT_i/dt)$. If $T_{min}$, were lower than $T_i$, estimates of $C(dT_i/dt) = M - E$ would be larger than at $T_a = T_i$. For example, if one assumes that dry heat transfer equals 0 at $T_a = T_{min} = T_i - 2$ (following Seymour [1972] for the temperature of the respiratory passages), our estimate of $C(dT_i/dt)$ would be, on average, 2.6 times larger than when calculated at $T_a = T_i$.

**Heat Balance.** When a bird is in heat balance, the following equation applies (Birkebak 1966; Porter and Gates 1969; McNab 1970; Calder and King 1974; Gates 1980):

$$M - E - C(dT_i/dt) = h(T_b - T_i),$$

(2)

in which $M$, $E$, $C(dT_i/dt)$, and $T_i$ are defined above, and $h =$ dry heat transfer coefficient (J h$^{-1} \cdot ^\circ$C$^{-1}$). Both $T_b$ and $h$ are functions of $T_i$ (Fig. 1).

**Body Temperature.** In the TNZ, birds have average $T_i$’s of $38.5^\circ \pm 0.96^\circ$C ($n = 203$) during the rest phase and $41.0^\circ \pm 0.94^\circ$C ($n = 74$) during the active phase (Prinzinger et al. 1991).

Although these data may suggest that birds maintain their $T_i$ at fairly constant levels in the TNZ, many species showed a marked increase in $T_b$ within and above the TNZ (see also Weathers and Schoenbackler 1976; Weathers 1981), presumably under steady state conditions (Fig. 3). All birds within our data set were hyperthermic at a $T_i$ of $45^\circ$C. Body temperature was, on average, $3.3^\circ \pm 1.28^\circ$C ($n = 23$) higher at $T_i = 45^\circ$C than at the $T_{i0}$. The degree of hyperthermia was independent of body mass as judged by the slope of a regression through the data points ($slope = 2.9 \times 10^{-3}$, SE$_{slope} = 2.10^{-3}$, $r^2 = 0.06$, $P = 0.3$), but we emphasize that our data include birds from 6.4 g to 412 g.

The hypothesis that desert birds increase their $T_b$ above the level of nondesert birds was not supported. Comparison of the mean elevation in $T_b$ at a $T_i$ of $45^\circ$C for desert and nondesert species revealed no difference ($t = 0.7$, df $= 21$, $P = 0.5$).

**Dry Heat Transfer Coefficient.** The dry heat transfer coefficient is a property of the bird influenced by characteristics of insulation, vasodilation, size, and surface to volume ratios. It includes specific heat transfer coefficients for conduction, radiation, and convection and is described by rearranging Equation (2) to

$$h = \frac{M - E - C(dT_i/dt)}{T_b - T_i}.$$
maximum at $T_{w}$ ($h_{w}$, Fig. 1C). Above $T_{w}$, where the thermal gradient $T_{a} - T_{b}$ becomes smaller, the relative importance of $h$ in dissipating heat decreases and evaporative cooling becomes increasingly important in maintenance of $T_{b}$. At $T_{b}$’s above $T_{a} = T_{w}$ where the direction of heat flow is reversed and the bird gains heat from its environment, one might predict a decrease to minimal $h$ ($h_{b}$, Fig. 1C). The values reported for $h$ at $T_{b}$’s above $T_{a} = T_{b}$ show considerable variation in all species. Some studies suggest a decrease to a minimal value ($h_{b}$), while in others there is no apparent trend (Dawson and Schmidt-Nielsen 1966; Hinds and Calder 1973; Weathers and Caccamise 1975; Weathers and Schoenbaechler 1976; Dmi’el and Tel-Tzur 1985; Withers and Williams 1990). These studies did not take into account the rate of heat gain $C(dT_{a}/dt)$, which would explain some of the variation in $h$ (see below).

Calculations of $h$ near $T_{a} = T_{b}$ have been problematical in many studies because small errors in measurements of the variables in Equation (3) can translate into large errors in $h$. We have shown that $C(dT_{a}/dt)$ is a significant factor at $T_{a} = T_{b}$ (Fig. 2). Therefore, the error in $h$ should be reduced by including $C(dT_{a}/dt)$ in calculations of the numerator of Equation (3), $M - E = C(dT_{a}/dt)$. In a commonly used method to calculate $h$ as $(M - E)(T_{b} - T_{a})$, the numerator is usually a positive number when $T_{a} = T_{b}$ because $C(dT_{a}/dt)$ is not included. Algebraic rules dictate that, in this approach, $h$ goes to infinity when $T_{a}$ approaches $T_{w}$ (as in the dashed line of Fig. 4), a result that seems biologically unrealistic.

At $T_{a} = T_{w}$, $h$ has not been calculated because here both numerator and denominator are 0, a mathematical impediment, not a biological problem. We caution readers that despite heat transfer ($1 \text{ h}^{-1}$) being 0 at $T_{a} = T_{w}$, the heat transfer coefficient ($1 \text{ h}^{-1} \text{ °C}^{-1}$), a property of the bird, does not become 0. To calculate $h$ at $T_{a} = T_{w}$ we have applied l’Hôpital’s rule (Apostol 1967), a differentiation technique that provides a polynomial approximation of $h$ when both numerator and denominator are 0. L’Hôpital’s rule assumes that both numerator, $\{M(T_{a}) - E(T_{a}) - C(dT_{a}/dt(T_{a}))\}$, and denominator, $[T_{w}(T_{a}) - T_{a}]$, approach 0 when $T_{a}$ approaches $T_{w}$. The addendum ($T_{w}$) indicates that the given variable ($M, E$, etc.) is a function of $T_{a}$. L’Hôpital’s rule states that, if the quotient of the derivatives tends to a finite limit as $T_{a}$ approaches $T_{w}$, the quotient of the functions approaches the same limit:

$$h(T_{a} = T_{w}) = T_{w} \lim_{\rightarrow} T_{a} \frac{M(T_{a}) - E(T_{a}) - C(dT_{a}/dt(T_{a}))}{T_{a}(T_{a}) - T_{a}} = T_{w} \lim_{\rightarrow} T_{w} \frac{M(T_{a}) - E(T_{a}) - C(dT_{a}/dt(T_{a}))}{T_{w}(T_{a}) - T_{a}} = T_{w} \lim_{\rightarrow} T_{w} \frac{M(T_{a}) - E(T_{a}) - C(dT_{a}/dt(T_{a}))}{T_{w}(T_{a}) - T_{a}}.$$

Figure 3. $T_{a}$ as a function of $T_{a}$ in and above the TNZ for 26 species. Some lines have an inflection point because authors reported two separate functions for $T_{a}$ versus $T_{a}$. Squares represent the lower critical temperature, circles represent the upper critical temperature, and the dotted line $T_{a} = T_{w}$, If lines do not have symbols for lower or upper critical temperature, original authors did not report these temperatures. Filled symbols represent desert species; unfilled symbols represent nondesert species.
functions that relate the black-throated sparrow in which Weathers (1981) provides duplicate our approach on other species. Consider a study of birds save relatively more water by an improved thermal gradient on water savings, we assumed that all species had.

Weathers (1981) provides functions that relate \( T_s, M, \) and \( E \) to \( T_s \) (Table 1; Fig. 4). To establish the equation for \( C(dT_s/dt) \), we determined temperature equality, \( T_i = T_h = 43.3^\circ C \), for this species, where net dry heat transfer is 0, and we calculated \( C(dT_s/dt) \) at this \( T_i \): 

\[
C(dT_s/dt) = M - E = 13680.0 - 1045.1 = 322.9 \text{ J h}^{-1}.
\]

Fitting a linear function that relates \( C(dT_s/dt) \) to \( T_i \) requires at least two values for \( C(dT_s/dt) \), and for our second value, we assume that \( C(dT_s/dt) \) is 0 at \( T_a = 36.3^\circ C \). The function relating \( C(dT_s/dt) \) to \( T_i \) is given in Table 1. Equation (3) and the functions for \( T_o, M, E, \) and \( C(dT_s/dt) \) given in Table 1 allow one to calculate \( h \) at temperatures above \( T_a \). At \( T_s = T_o \), Equation (3) is undefined, and we have used the derivatives of each function (Table 1) in the previously described method to calculate \( h \) at \( T_s = T_o \):

\[
h(43.3) = T_o \lim_{T_o \to 43.3} \frac{M'(43.3) - E'(43.3) - C(dT_s/dt)'/(43.3)}{T_o'(43.3) - 1} = \frac{94.0 - 259.9 - 46.1}{0.268 - 1} = 289.6 \text{ J h}^{-1}.
\]

We have used our method to calculate the pattern of variation in \( h \) versus \( T_i \) for 22 species; all species showed the same trend in \( h \) above \( T_i \). We summarized the results of our calculations in a general model for \( h \) (Fig. 1C). Apparently, small birds do not reduce their dry heat uptake at \( T_i \)'s above their \( T_o \)'s by decreasing \( h \).

**Thermal Gradient**

The rate of dry heat transfer \([h(T_h - T_i)]\) is a linear function of the thermal gradient \((T_h - T_i)\) between a bird and its surroundings if the insulation is held constant. Because heat flows from higher to lower temperatures, hyperthermia increases the dry heat loss if \( T_s < T_h \) and decreases the dry heat uptake if \( T_s > T_h \) (Calder and King 1974).

Calder and King (1974) hypothesized that the importance of hyperthermia in increasing heat loss or retarding heat gain is inversely related to body size. The amount of water saved as a result of an improved thermal gradient can be estimated from the rate of dry heat transfer when comparing a bird with a hypothetical normothermic \( T_i \) with its actual hyperthermic \( T_i \). We tested the hypothesis of Calder and King (1974) that smaller birds save relatively more water by an improved thermal gradient by calculating \( h \) at \( T_i = 45^\circ C \) for each species. We rearranged Equation (2) to

\[
E = M - C(dT_s/dt) - h(T_h - T_i)
\]

and assumed that \( M, C(dT_s/dt), \) and \( h \) were constant at this temperature. At \( T_i = 45^\circ C \), \( T_i \) is elevated by \( 0.7^\circ -5.2^\circ C \) above normothermic \( T_i \). In order to examine only the effect of the thermal gradient on water savings, we assumed that all species had.

![Figure 4](image-url)

Figure 4. The dry heat transfer coefficient \( (h, \text{ in J h}^{-1} \text{C}^{-1}) \) as a function of \( T_s \) in (A) the black-rumped waxbill, (B) the black-throated sparrow, and (C) the monk parakeet. The dotted line represents \( h \) when calculated as \((M - E)(T_h - T_i)\), a commonly used approach. The unfilled squares represent \( h \) above the \( T_o \) when calculated with Equation (3), see text. The unfilled circle represents \( h \) at \( T_i = T_o \), and is calculated by using \( \text{l'Hôpital's rule} \) (see text). The solid line represents \( h \) as a function of \( T_s \) above the \( T_o \).

We applied this technique to our calculations of \( h \) at \( T_i = T_o \) when there is no dry heat transfer and both \( T_h - T_i \) and \( M - E - C(dT_s/dt) \) are 0 (Fig. 4).

Because this is a new method for calculating \( h \) at \( T_i = T_o \), we provide an example for our colleagues who may want to duplicate our approach on other species. Consider a study of the black-throated sparrow in which Weathers (1981) provides functions that relate \( T_o, M, \) and \( E \) to \( T_s \) (Table 1; Fig. 4). To establish the equation for \( C(dT_s/dt) \), we determined temperature equality, \( T_i = T_h = 43.3^\circ C \), for this species, where net dry heat transfer is 0, and we calculated \( C(dT_s/dt) \) at this \( T_i \): 

\[
C(dT_s/dt) = M - E = 13680.0 - 1045.1 = 322.9 \text{ J h}^{-1}.
\]

Fitting a linear function that relates \( C(dT_s/dt) \) to \( T_i \) requires at least two values for \( C(dT_s/dt) \), and for our second value, we assume that \( C(dT_s/dt) \) is 0 at \( T_a = 36.3^\circ C \). The function relating \( C(dT_s/dt) \) to \( T_i \) is given in Table 1. Equation (3) and the functions for \( T_o, M, E, \) and \( C(dT_s/dt) \) given in Table 1 allow one to calculate \( h \) at temperatures above \( T_a \). At \( T_s = T_o \), Equation (3) is undefined, and we have used the derivatives of each function (Table 1) in the previously described method to calculate \( h \) at \( T_s = T_o \):

\[
h(43.3) = T_o \lim_{T_o \to 43.3} \frac{M'(43.3) - E'(43.3) - C(dT_s/dt)'/(43.3)}{T_o'(43.3) - 1} = \frac{94.0 - 259.9 - 46.1}{0.268 - 1} = 289.6 \text{ J h}^{-1}.
\]

We have used our method to calculate the pattern of variation in \( h \) versus \( T_i \) for 22 species; all species showed the same trend in \( h \) above \( T_i \). We summarized the results of our calculations in a general model for \( h \) (Fig. 1C). Apparently, small birds do not reduce their dry heat uptake at \( T_i \)'s above their \( T_o \)'s by decreasing \( h \).

**Thermal Gradient**

The rate of dry heat transfer \([h(T_h - T_i)]\) is a linear function of the thermal gradient \((T_h - T_i)\) between a bird and its surroundings if the insulation is held constant. Because heat flows from higher to lower temperatures, hyperthermia increases the dry heat loss if \( T_s < T_h \) and decreases the dry heat uptake if \( T_s > T_h \) (Calder and King 1974).

Calder and King (1974) hypothesized that the importance of hyperthermia in increasing heat loss or retarding heat gain is inversely related to body size. The amount of water saved as a result of an improved thermal gradient can be estimated from the rate of dry heat transfer when comparing a bird with a hypothetical normothermic \( T_i \) with its actual hyperthermic \( T_i \). We tested the hypothesis of Calder and King (1974) that smaller birds save relatively more water by an improved thermal gradient by calculating \( h \) at \( T_i = 45^\circ C \) for each species. We rearranged Equation (2) to

\[
E = M - C(dT_s/dt) - h(T_h - T_i)
\]

and assumed that \( M, C(dT_s/dt), \) and \( h \) were constant at this temperature. At \( T_i = 45^\circ C \), \( T_i \) is elevated by \( 0.7^\circ -5.2^\circ C \) above normothermic \( T_i \). In order to examine only the effect of the thermal gradient on water savings, we assumed that all species had.
a normothermic $T_n$ of 3°C below their actual $T_a$ at 45°C. Then we solved Equation (4) for evaporative heat loss of the hypothetical normothermic birds, $E_n$. The difference between the measured hyperthermic evaporative heat loss $E_a$ and $E_n$ yielded the maximal amount of water saved by the 3°C elevation in $T_n$ at 45°C (appendix contains all the variables that we used).

At a $T_n$ of 45°C, water savings as a result of an improved thermal gradient varied with body mass:

$$\log \text{water saved (mg h}^{-1}) = 1.98 + 0.47 \log \text{mass (g)} \quad (5)$$

(SE$_{slope} = 0.092$, $n = 22$, $r^2 = 0.57$; Fig. 5A). The analysis supports the hypothesis that, as a result of the improved thermal gradient, smaller species save more water relative to body mass than do larger species when hyperthermic.

An expression for TEWL at a $T_n$ of 45°C as a function of body mass has not been published. To compare our calculations of water savings to TEWL, we first regressed TEWL at a $T_n$ of 45°C against body mass:

$$\log \text{TEWL (mg h}^{-1}) = 2.13 + 0.56 \log \text{mass (g)} \quad (6)$$

(SE$_{slope} = 0.061$, $n = 28$, $r^2 = 0.77$; Fig. 5A). The similarity of slopes for the Equations (5) and (6) ($t = 1.21$, df = 46, 0.20 < $P$ < 0.50) suggests that water saved as a result of an improved thermal gradient is a constant proportion of TEWL at $T_n = 45°C$, independent of body mass.

**Heat Storage**

Another contribution of hyperthermia to water savings occurs when heat is temporarily stored in body tissues during bouts of high $T_a$, and later passively dissipated by nonevaporative means when $T_a$’s have become more favorable (Schmidt-Nielsen 1964; Dawson and Bartholomew 1968; Calder and King 1974). The amount of water that is saved depends on the specific heat of tissue (Calder and King 1974), heat of vaporization of water (1 mg water = 2.426 J; Schmidt-Nielsen 1983), the difference between hyperthermic and normothermic $T_n$ and body mass. These variables allow one to calculate the theoretical maximum savings of water assuming that all the heat stored is subsequently lost by nonevaporative avenues. The amount of water saved (heat stored) is independent of the duration of the hyperthermic state.

Based on allometric equations for heat storage and resting metabolism, Calder and King (1974) hypothesized that the significance of heat storage in the water economy of birds increased with body size. Our analysis supports this hypothesis.

Figure 5. Water savings (mg h$^{-1}$) at 45°C. A. Water savings as a result of an improved thermal gradient for birds that have a standardized elevation in $T_n$ of 3°C, as a function of body mass (symbols as in fig. 3). TEWL (mg h$^{-1}$) at 45°C is represented by the dotted line. B. Water savings (mg, dashed line) as a function of body mass for birds that have a standardized elevation in $T_n$ of 3°C. The solid line represents the increased respiratory evaporative water loss (REWL) (mg h$^{-1}$) at a $T_n$ of 45°C as a result of a 3°C increase in $T_a$. The dotted line represents TEWL (mg h$^{-1}$) at 45°C.

**Table 1: Heat balance equations and their derivatives for the black-throated sparrow**

<table>
<thead>
<tr>
<th>Heat Balance Equation</th>
<th>Derivative$^*$</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_n(T_a) = 31.66 + 0.268 \times T_a$</td>
<td>$T_n'(T_a) = 0.268$</td>
<td>For $T_a &gt; 29°C$</td>
</tr>
<tr>
<td>$M(T_n) = -2700.4 + 94.0 \times T_n$</td>
<td>$M'(T_n) = 94.0$</td>
<td>For $T_a &gt; 36.3°C$</td>
</tr>
<tr>
<td>$E(T_n) = 22.02 \times 10^{-7} \times 10^{10\text{log} T_n}$</td>
<td>$E'(T_n) = 5.475 \times 10^{-3} \times 10^{10\text{log} T_n}$</td>
<td>For $T_a &gt; 33.5°C$</td>
</tr>
<tr>
<td>$C(dT_n/dt)(T_n) = -1672.6 + 46.1 \times T_n$</td>
<td>$C(dT_n/dt)'(T_n) = 46.1$</td>
<td>For $T_a &gt; 36.3°C$</td>
</tr>
</tbody>
</table>


Note. $M, E, C(dT_n/dt)$ are in units of J h$^{-1}$, $T_n$ in degrees centigrade.

$^*$ If $f(x) = c \times a^x$, then $f'(x) = c \times a^x \times b \times \ln a$. 

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When we standardized the elevation in $T_b$ as 3°C, water savings as a result of heat storage at a $T_e$ of 45°C varied proportionally with body mass (Fig. 5B):

$$\log \text{water saved (mg)} = 0.62 + 1.0 \log \text{mass (g)}. \quad (7)$$

The unity of the slope indicates that mass-specific water savings as a result of heat storage do not vary with body size. However, Equation (7) had a significantly higher slope than Equation (6), which relates TEWL and body mass ($t = 72$, $df = 52$, $P < 0.001$), indicating that larger species save a larger proportion of their TEWL by heat storage than do smaller species.

$Q_{10}$ Effect

Within the TNZ, some species increase their $T_b$ as $T_e$ increases without a concomitant increase in metabolic heat production. This apparent lack of a $Q_{10}$ effect has been proposed as a factor that contributes to the water economy of hyperthermic birds (Weathers and Schoenbaechler 1976; Weathers 1981). The $Q_{10}$ effect describes the effect of temperature on chemical reaction rates and typically varies between 2 and 3 for biochemical reactions (Schmidt-Nielsen 1983). Weathers and Schoenbaechler (1976) suggested that if $Q_{10} = 2.5$, one might expect oxygen consumption to increase in the TNZ when $T_b$ increases (as in Fig. 3). The absence of an increase in oxygen consumption was predicted to contribute to a lower TEWL because the reduced metabolic heat production requires dissipation of a smaller quantity of heat and the increase in respiratory water loss, which would have been associated with an increase in ventilation if oxygen consumption had increased, does not occur (Weathers and Schoenbaechler 1976).

We question whether one should expect small changes in $T_b$ to alter metabolic rate, a complex phenomenon regulated by numerous factors in endothermic birds. The $Q_{10}$ effect has traditionally been used in studies on ectothermic or poikilothermic animals under experimental conditions where changes in $T_c$ coincide with, and are predictable from, changes in $T_e$ (Snyder and Nestler 1990). In contrast to ectotherms, the $T_b$ of endotherms is the result of regulatory processes for heat loss and heat production that are still poorly understood. Several authors have shown that apparent $Q_{10}$'s in mammals and birds undergoing hibernation or daily torpor are artifacts produced by changes in the heat transfer coefficient (Snyder and Nestler 1990), the thermal gradient (Heldmaier and Ruf 1992), or both, and have no relevance to the metabolic state of the animal (Snyder and Nestler 1990; Heldmaier and Ruf 1992). Active thermoregulatory control of metabolic rate of birds in the TNZ implies that there is no a priori reason to assume that metabolic rate is governed by passive temperature effects. The laws of thermodynamics remain valid for single biochemical processes in endotherm tissues, but the integrated control of an endotherm overrides direct temperature effects. Therefore, we do not expect metabolic rate to increase when $T_b$ increases in the TNZ in birds. As a result, we do not regard $Q_{10}$ as a factor of hyperthermia that is involved in water savings of birds within the TNZ.

Respiratory Variables: Temperature and Volume of the Exhaled Air

In the previous sections, our analysis supported the idea that hyperthermia can save water by means of an improved thermal gradient and heat storage. However, changes in respiratory variables that accompany the transition from normothermia to hyperthermia in birds may impact their water economy negatively. An elevation in the temperature of the exhaled air ($T_{ex}$), which increases the air’s capacity to carry water vapor, and an increase in minute volume ($V_i$), which enlarges the total volume of exhaled air, combine to increase respiratory evaporative water loss (REWL) in hyperthermic birds compared to normothermic birds. We used the available data on respiratory variables that are usually reported in relation to gas exchange within the lungs and a few simplifying assumptions to predict REWL in hyperthermic and normothermic birds at a $T_e$ of 45°C. Though birds do not typically remain normothermic at a $T_e$ of 45°C, we used these hypothetical values as a baseline for comparison. Few studies have focused on the relationship between $T_{ex}$, REWL, and respiratory variables, such as tidal volume, ventilation frequency, and $T_r$. Therefore, we emphasize that the results presented here are based on few data. Our aim is to encourage future work in this field.

Most birds experiencing $T_e$'s below 35°C exhale air at a temperature linearly related to, but consistently greater than, the temperature of the inhaled air (Schmidt-Nielsen et al. 1970; Kaiser and Bucher 1985; Withers and Williams 1990). At $T_e$'s around 35°C, the upper limit of current data, $T_{ex}$ and $T_r$ converge. In our calculations at a $T_e$ of 45°C, we assumed that both hyperthermic ($T_b = 44°C$) and normothermic ($T_b = 41°C$) birds exhaled air that was evaporatively cooled 2°C below $T_e$ to $T_{ex}$'s of 42°C and 39°C, respectively.

The assumption that exhaled air is saturated with water vapor is commonly applied in studies of respiratory water loss (Schmidt-Nielsen et al. 1970; Withers and Williams 1990; but see Withers et al. 1981). We calculated the saturation point $\rho = \rho_{H_2O}(4.62 \times 10^{-4})(T_{ex} + 273)\exp(-273/T_\text{sat})$ (Campbell 1977) to be 48.50 g m⁻³ for normothermic birds and 56.34 g m⁻³ for hyperthermic birds, using values for water vapor pressure $p_{H_2O}$ in saturated air (List 1971).

The product of breathing frequency and tidal volume determines $V_i$ (mL min⁻¹). Based on 22 species, Maloney and Dawson (1994) determined an allometric equation for $V_i$ (mL min⁻¹) of resting birds, presumably with normothermic $T_r$'s:
Table 2: The net effect of hyperthermia on the water balance of 10-, 100-, and 1,000-g hypothetical birds that were hyperthermic during periods of 1 h and 5 h

<table>
<thead>
<tr>
<th>Bird Mass (g)</th>
<th>Improved Thermal Gradient (g water)</th>
<th>Heat Storage (g water)</th>
<th>Increased REWL (g water)</th>
<th>Net Savings (g water)</th>
<th>TEWL (g water)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 h:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>.28</td>
<td>.04</td>
<td>-.05</td>
<td>.27</td>
<td>.49</td>
</tr>
<tr>
<td>100</td>
<td>.83</td>
<td>.42</td>
<td>-.46</td>
<td>.79</td>
<td>1.78</td>
</tr>
<tr>
<td>1,000</td>
<td>2.45</td>
<td>4.16</td>
<td>-3.63</td>
<td>2.98</td>
<td>6.46</td>
</tr>
<tr>
<td>5 h:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>1.41</td>
<td>.04</td>
<td>-.27</td>
<td>1.18</td>
<td>2.45</td>
</tr>
<tr>
<td>100</td>
<td>4.16</td>
<td>.42</td>
<td>-2.31</td>
<td>2.27</td>
<td>8.89</td>
</tr>
<tr>
<td>1,000</td>
<td>12.27</td>
<td>4.16</td>
<td>-18.18</td>
<td>-1.75</td>
<td>32.28</td>
</tr>
</tbody>
</table>

Note. Calculations are based on an increase in $T_b$ from 41° to 44°C at $T_a$ of 45°C.

a Savings by improved thermal gradient calculated from Equation (5).
b Savings by heat storage calculated from Equation (7).
c Costs of increased REWL gradient calculated from Equation (12).
d Total evaporative water loss at 45°C calculated from Equation (6).

log $V_i = 0.38 + 0.69 \log$ mass (g). \hspace{1cm} (8)

Calder and King (1974) reported an equation for $V_i$ of heat-stressed, presumably hyperthermic, panting birds ($n = 5$):

log $V_i = 0.57 + 0.85 \log$ mass (g). \hspace{1cm} (9)

We have multiplied Equation (8) by the water vapor content of saturated air ($T_a = 39°C$) to obtain REWL (mg water h$^{-1}$) of normothermic birds ($T_h = 41°C$) at a $T_a$ of 45°C as a function of body mass:

log REWL$_{\text{normothermic}} = 0.84$ + 0.69 log mass (g). \hspace{1cm} (10)

To estimate REWL of hyperthermic birds at a $T_a$ of 45°C, we have multiplied Equation (9) by the water vapor content of saturated air at 42°C, to obtain the equation:

log REWL$_{\text{hyperthermic}} = 1.10$ + 0.85 log mass (g). \hspace{1cm} (11)

The increased REWL as a result of hyperthermia was given by the difference between the Equations (10) and (11):

log REWL$_{\text{increased}} = 0.83$ + 0.91 log mass (g). \hspace{1cm} (12)

Changes in respiratory variables resulted in a higher mass-specific increase in REWL for smaller birds when they became hyperthermic than for larger birds as suggested by the slope <1. However, at a $T_a$ of 45°C, the increased REWL represents a larger proportion of their TEWL (Eq. [6]) for larger birds than for smaller birds (Fig. 5B).

Discussion

Net Effect of Hyperthermia: All Factors Combined

In this review, we have partitioned the effects of hyperthermia on water loss into categories of an improved thermal gradient, of heat storage, and of altered respiratory variables, and we have generated allometric equations that describe the effect of each category on water loss. The first two categories tend to reduce TEWL; the latter augments REWL. In order to assess the net effect of hyperthermia, we summed the contributions of each category to examine the net water savings for a hypothetical 10-, 100-, and 1,000-g bird. As before, a $T_a$ of 41°C for a normothermic and 44°C for a hyperthermic bird and a $T_a$ of 45°C. Further, we compared the net water savings for birds that were hyperthermic for 1 h and 5 h, the latter period representing a maximal exposure to heat stress that birds might experience in nature on a given day. For a hyperthermic bout of 1 h, our calculations reveal that net water savings for all three body sizes is positive (Table 2). Whereas, for a hyperthermic bout of 5 h, our analyses predict that large birds actually lose more water by becoming hyperthermic than they would if they remained normothermic.

In order to make interspecific comparisons, we have standardized net water savings due to hyperthermia by expressing these savings relative to TEWL at the same $T_a$ and for the same
three hypothetical bird sizes (Fig. 6). During a hyperthermic bout of 1 h, all three bird sizes saved an amount of water equal to around 50% of their TEWL (Fig. 6A). If these same-sized birds are hyperthermic for a period of 5 h, the amount of water saved as a proportion of TEWL was inversely related to body mass (Fig. 6B). During 5 h of hyperthermia, larger birds are predicted to lose more water than they would if they maintained their \( T_a \) at normothermic levels. This finding is the result of the decreased contribution of heat storage to the net water savings. Heat storage is independent of time, and its positive contribution to water savings is averaged over the duration of the hyperthermic bout, whereas the negative contribution to water savings of the altered respiratory variables and the positive contribution to water savings of the improved thermal gradient are dependent on the duration of the hyperthermic bout.

Our calculations indicate that smaller birds that are hyperthermic for periods up to at least 5 h save water as a net result of hyperthermia, whereas larger birds only save water as a result of hyperthermia when the hyperthermic bout is short and actually increase their TEWL when they are hyperthermic for longer periods. These results suggest the hypothesis that large birds should maintain their \( T_a \) at or near normothermic levels at high \( T_e \) 's. In support of this hypothesis, the ostrich (100 kg, \( Struthio camelus \)), maintained a normothermic \( T_a \) during exposure to a \( T_e \) of 51°C for a period of 7.5 h (Crawford and Schmidt-Nielsen 1967).

This article contains the first equation that relates TEWL at a \( T_e \) of 45°C to body mass. An earlier allometric equation (Williams 1996) for TEWL at a \( T_e \) of 25°C was based on a phylogenetic analysis of 102 bird species from both arid and mesic environments that were measured in the laboratory. Comparison of TEWL at \( T_e \) 's of 25°C and of 45°C (Eq. [6]) reveals that smaller birds augment their TEWL by a larger factor than do larger birds in response to high \( T_e \) 's. A 10-g bird increases its TEWL at a \( T_e \) of 45°C by as much as eight times, whereas a 100-kg bird, the size of an ostrich, increases its TEWL less than three times when \( T_e \) increases from 25°C to 45°C. Larger birds have a smaller surface to volume ratio, which reduces the mass-specific heat load from the environment, and a lower mass-specific metabolic rate, which reduces the internal heat load. A smaller mass-specific total heat load requires less evaporative cooling and can result in lower TEWL rates.

**Summary and Prospectus**

In this article, we reviewed the variation in hyperthermia in desert and nondesert birds, and we attempted to assess the role of hyperthermia in the water economy of desert species. Within our data set, there existed no evidence that the degree of hyperthermia at a \( T_e \) of 45°C differed between desert and non-desert birds. Our search of the literature has revealed that precious few data exist on \( T_e \) 's at high \( T_e \) 's, especially for mesic species, and more data are needed.

In order to assess the role of hyperthermia in the water economy of desert birds, we evaluated the contributions of an improved thermal gradient, of heat storage, and of altered respiratory variables to net water savings. The contribution of the improved thermal gradient can be estimated from the complete heat balance of a bird. We have shown that, at \( T_a = T_m \), the rate of heat gain \( C(dT_e/dt) \) is a significant factor and should be incorporated in the heat balance equation at high \( T_e \) 's. Therefore, during metabolic measurements at high \( T_e \) 's, continuous measurements of \( T_m \) are of critical importance to our understanding of the heat balance of birds at high \( T_e \) 's. Furthermore, at the \( T_e \) 's where \( C(dT_e/dt) \) is a significant factor, \( T_m \) is continuously increasing and is likely to influence metabolism and evaporation.

The contribution of the altered respiratory variables to the net effect of hyperthermia on the water economy of birds, as discussed in this article, should be viewed in light of the scarcity of data on the relationship between respiratory variables and
The Role of Hyperthermia in the Water Economy of Birds

First, the allometric equations for minute volumes of resting and panting birds (Eq. [8] and [9]) are based on sample sizes of 22 and five birds, respectively. An extension of these data sets and a reevaluation of the allometric equations would be welcome. Second, respiratory variables are usually reported in relation to $T_a$, whereas, to understand their effect on REWL in hyperthermic birds, respiratory variables should be related to $T_b$ and to REWL. Third, we found few data on $T_e$ at high $T_a$. More measurements on $T_e$, especially at $T_a$’s close to and above $T_e = T_a$ are necessary to gain understanding how respiration at high $T_a$’s affects water loss.

Hyperthermia not only impacts the water economy of birds but also a suite of other factors—energy balance (Seymour 1972), protein stability, and tissue functioning (Marder et al. 1989). This implies that an elevated $T_b$ may be the result of an optimization process in which the optimal $T_b$ is the result of simultaneously minimizing water loss, energy expenditure, and protein damage. Insights in the latter two factors are poor, and future work is desired to come to an integrated understanding of the role of hyperthermia in birds.

Acknowledgments

We thank W. Weathers for providing original data and G. Bakken for stimulating discussions about heat transfer. Discussions with F. Weissing helped our understanding of l’Hôpital’s rule. The article was improved by comments from W. Weathers, G. Bakken, S. Daan, and two anonymous reviewers on previous versions of the manuscript. Financial support was provided by the Stichting Groninger Universiteitsfonds to B.I.T. and by Ohio State University to J.B.W.

Appendix

Table A1: Body mass, metabolic heat production ($M$), total evaporative heat loss ($E$), rate of heat gain ($C[\frac{dT_b}{dt}]$), dry heat transfer coefficient ($h$), and body temperature ($T_b$) at 45°C of birds from desert and non-desert environments

<table>
<thead>
<tr>
<th>Species</th>
<th>Category</th>
<th>Body Mass (g)</th>
<th>$M$ (J h$^{-1}$)</th>
<th>$E$ (J h$^{-1}$)</th>
<th>$C[\frac{dT_b}{dt}]$ (J h$^{-1}$)</th>
<th>$h$ (J h$^{-1}$ C$^{-1}$)</th>
<th>$T_b$ (°C)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand partridge ($Ammoperdix heyi$)</td>
<td>d</td>
<td>172</td>
<td>...</td>
<td>3,104</td>
<td>...</td>
<td>...</td>
<td>44.6</td>
<td>Frumkin et al. 1986</td>
</tr>
<tr>
<td>Chukar ($Alectoris chukar$)</td>
<td>d</td>
<td>412</td>
<td>9,478</td>
<td>6,899</td>
<td>3,316</td>
<td>615</td>
<td>43.8</td>
<td>Frumkin et al. 1986</td>
</tr>
<tr>
<td>Common quail ($Coturnix coturnix$)</td>
<td>n</td>
<td>100.6</td>
<td>5,259</td>
<td>7,993</td>
<td>358</td>
<td>1,344</td>
<td>42.7</td>
<td>Weathers 1981</td>
</tr>
<tr>
<td>Gambel’s quail ($Callipepla gambelii$)</td>
<td>d</td>
<td>125.5</td>
<td>3,739</td>
<td>6,313</td>
<td>−1,094</td>
<td>925</td>
<td>43.4</td>
<td>Weathers 1981</td>
</tr>
<tr>
<td>Greater roadrunner ($Geococcyx californianus$)</td>
<td>d</td>
<td>284.7</td>
<td>6,917</td>
<td>9,534</td>
<td>549</td>
<td>1,439</td>
<td>42.8</td>
<td>Calder and Schmidt-Nielsen 1966</td>
</tr>
<tr>
<td>Budgerigar ($Melopsittacus undulatus$)</td>
<td>d</td>
<td>33.7</td>
<td>2,220</td>
<td>2,627</td>
<td>142</td>
<td>323</td>
<td>43.3</td>
<td>Weathers and Schoenbaechler 1976</td>
</tr>
<tr>
<td>Monk parakeet ($Myiopsitta monachus$)</td>
<td>n</td>
<td>80.4</td>
<td>4,263</td>
<td>4,308</td>
<td>3,186</td>
<td>829</td>
<td>41.1</td>
<td>Weathers and Cacacamise 1975</td>
</tr>
<tr>
<td>Common poorwill ($Phalaenoptilus nuttallii$)</td>
<td>d</td>
<td>40</td>
<td>683</td>
<td>1,557</td>
<td>...</td>
<td>...</td>
<td>41.5</td>
<td>Bartholomew et al. 1962</td>
</tr>
<tr>
<td>Rock pigeon ($Columba livia$)</td>
<td>n</td>
<td>314.6</td>
<td>9,539</td>
<td>11,414</td>
<td>399</td>
<td>948</td>
<td>42.6</td>
<td>Calder and Schmidt-Nielsen 1966, 1967</td>
</tr>
<tr>
<td>Spinifex pigeon ($Geophaps plumifera$)</td>
<td>d</td>
<td>89</td>
<td>1,519</td>
<td>3,272</td>
<td>0</td>
<td>797</td>
<td>42.8</td>
<td>Withers and Williams 1990</td>
</tr>
<tr>
<td>Spinifex pigeon ($Geophaps plumifera$)</td>
<td>d</td>
<td>82.3</td>
<td>1,725</td>
<td>2,737</td>
<td>...</td>
<td>...</td>
<td>42.7</td>
<td>Dawson and Bennett 1973</td>
</tr>
<tr>
<td>Diamond dove ($Geopelia cuneata$)</td>
<td>d</td>
<td>34.4</td>
<td>1,160</td>
<td>1,306</td>
<td>...</td>
<td>...</td>
<td>45.4</td>
<td>Schleucher et al. 1991</td>
</tr>
<tr>
<td>Inca dove ($Scardafella inca$)</td>
<td>n</td>
<td>40.4</td>
<td>1,408</td>
<td>1,899</td>
<td>−129</td>
<td>259</td>
<td>43.6</td>
<td>Lasiewski and Seymour 1972; MacMillen and Trost 1967</td>
</tr>
<tr>
<td>Species</td>
<td>Category</td>
<td>Body Mass (g)</td>
<td>$M$ (J h$^{-1}$)</td>
<td>$E$ (J h$^{-1}$)</td>
<td>$C(dT_b/dt)$ (J h$^{-1}$)</td>
<td>$h$ (J h$^{-1}$ C$^{-1}$)</td>
<td>$T_b$ (°C)</td>
<td>Source</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>----------</td>
<td>---------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>---------------------------</td>
<td>---------------------------</td>
<td>------------</td>
<td>---------------------------------------------</td>
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<tr>
<td>Double-banded sandgrouse</td>
<td>d</td>
<td>196.7</td>
<td>2,634</td>
<td>4,766</td>
<td>1,184</td>
<td>947</td>
<td>41.5</td>
<td>Hinsley 1992; Thomas and Maclean 1981</td>
</tr>
<tr>
<td>Tristram’s starling</td>
<td>d</td>
<td>123</td>
<td>7,232</td>
<td>7,582</td>
<td>395</td>
<td>496</td>
<td>43.5</td>
<td>Dmi’el and Tel-Trur 1985</td>
</tr>
<tr>
<td>Common starling</td>
<td>n</td>
<td>83</td>
<td>7,083</td>
<td>6,788</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>Dmi’el and Tel-Trur 1985</td>
</tr>
<tr>
<td>Dune lark</td>
<td>d</td>
<td>27.3</td>
<td>2,597</td>
<td>2,887</td>
<td>65</td>
<td>394</td>
<td>44.1</td>
<td>J. B. Williams, unpublished data</td>
</tr>
<tr>
<td>Horned lark</td>
<td>d</td>
<td>26</td>
<td>1,551</td>
<td>1,907</td>
<td>$-357$</td>
<td>191</td>
<td>45</td>
<td>Trost 1972</td>
</tr>
<tr>
<td>Black-rumped waxbill</td>
<td>n</td>
<td>6.4</td>
<td>850</td>
<td>944</td>
<td>363</td>
<td>152</td>
<td>42</td>
<td>Cade et al. 1965</td>
</tr>
<tr>
<td>Zebra finch</td>
<td>d</td>
<td>11.5</td>
<td>1,501</td>
<td>1,394</td>
<td>218</td>
<td>221</td>
<td>44.5</td>
<td>Cade et al. 1965</td>
</tr>
<tr>
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<td>10.9</td>
<td>1,137</td>
<td>1,009</td>
<td>210</td>
<td>103</td>
<td>44.2</td>
<td>Willoughby 1969</td>
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<tr>
<td>Cassin’s finch</td>
<td>n</td>
<td>26.8</td>
<td>2,089</td>
<td>2,995</td>
<td>...</td>
<td>...</td>
<td>43</td>
<td>Weathers 1981; Weathers et al. 1980</td>
</tr>
<tr>
<td>House finch</td>
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<td>1,782</td>
<td>1,924</td>
<td>125</td>
<td>666</td>
<td>44.6</td>
<td>Weathers 1981</td>
</tr>
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<td>1,528</td>
<td>1,595</td>
<td>401</td>
<td>360</td>
<td>43.7</td>
<td>Weathers 1981</td>
</tr>
<tr>
<td>Variable seedeater</td>
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<td>1,142</td>
<td>160</td>
<td>236</td>
<td>44.4</td>
<td>Weathers 1997</td>
</tr>
<tr>
<td>Red-winged blackbird</td>
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<td>3,823</td>
<td>4,735</td>
<td>471</td>
<td>1,728</td>
<td>44.2</td>
<td>Weathers 1981</td>
</tr>
<tr>
<td>Cardinal</td>
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<td>2,364</td>
<td>2,354</td>
<td>390</td>
<td>316</td>
<td>43.8</td>
<td>Hinds and Calder 1973</td>
</tr>
<tr>
<td>Pyrrhuloxia</td>
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<td>32</td>
<td>1,773</td>
<td>2,136</td>
<td>159</td>
<td>401</td>
<td>43.7</td>
<td>Hinds and Calder 1973</td>
</tr>
</tbody>
</table>

Note. Body mass, $M$, $E$, and $T_b$ are calculated from the equations or values in the original papers; $C(dT_b/dt)$ and $h$ are calculated as described in this article. *Species names according to Sibley and Monroe (1990).  
$^b$d = desert, n = nondesert.
The Role of Hyperthermia in the Water Economy of Birds


Maloney S.K. and T.J. Dawson. 1994. Ventilatory accommodation of oxygen demand and respiratory water loss in a large bird, the emu (Dromaius novaehollandiae), and a re-examination of ventilatory allometry for birds. Comp Biochem Physiol B 164:473–481.

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