The Role of Hyperthermia in the Water Economy of Desert Birds

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ABSTRACT

A number of authors have suggested that hyperthermia, the elevation of body temperature (T_b) 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 (T_a), and show that, in most studies performed at a high T_a, birds were increasing their T_b, 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 ($T_a = T_b$). We develop a method to calculate h at $T_a = T_b$, using l'Hôpital's rule. The combined result of our approach suggests that birds increase their dry heat transfer even when T_a is above $T_a = T_b$, 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 T_b is elevated. Our analysis of the combination of these three factors suggests that, during acute exposure to high T_a (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 T_a (5 h), small birds save water by hyperthermia but large birds do not.

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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 (T_b), averaging around 41°C (Prinzinger et al. 1991), close to the upper lethal limit of 46°–47°C (Dawson and Schmidt-Nielsen 1964). During periods of heat stress, their water economy must be compromised because birds defend their T_b 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 T_b 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 T_a 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_b 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_b increased in the thermoneutral zone (TNZ) while metabolism remained constant. They reasoned that this absence of a Q_{10} 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 sinuatus*) reduce their TEWL by 50% as a result of 2.3°C increase in T_b 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_b, exhaled air temperature (T_{ex}) will be higher than it would be at normothermic T_b. 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_b over a range of T_a's in desert and nondesert species, testing the hypothesis that desert species have a higher T_b at a given T_a. Then, using our model of heat balance, we assess the roles of an improved thermal gradient, of heat storage, of Q_{10}, 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_b with the hypothetical situation where T_b 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_b 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_b, 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_b 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):

$$H = M - E - C(dT_b/dt), \qquad (1)$$

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 for the entire bird, is calculated by multiplying the specific heat of tissue by body mass. The time-dependent variable, $C(dT_b/dt)$, can be determined by continuously monitoring T_b at constant T_a, and it should not be confused with calculations of total heat storage that are based on steady state situations. If there is a significant increase in T_b with time, then $C(dT_b/dt)$ is positive.

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_b. 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_{lc} (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 ($C[dT_b/dt]$) is 0 in steady state situations where T_b 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, $C(dT_b/dt)$ may become a significant factor. Although $C(dT_b/dt)$ 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 ± 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_b remained constant, but at 45°C, T_b increased by $0.5° \pm 0.18°C$ 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} °C^{-1} (Calder and King
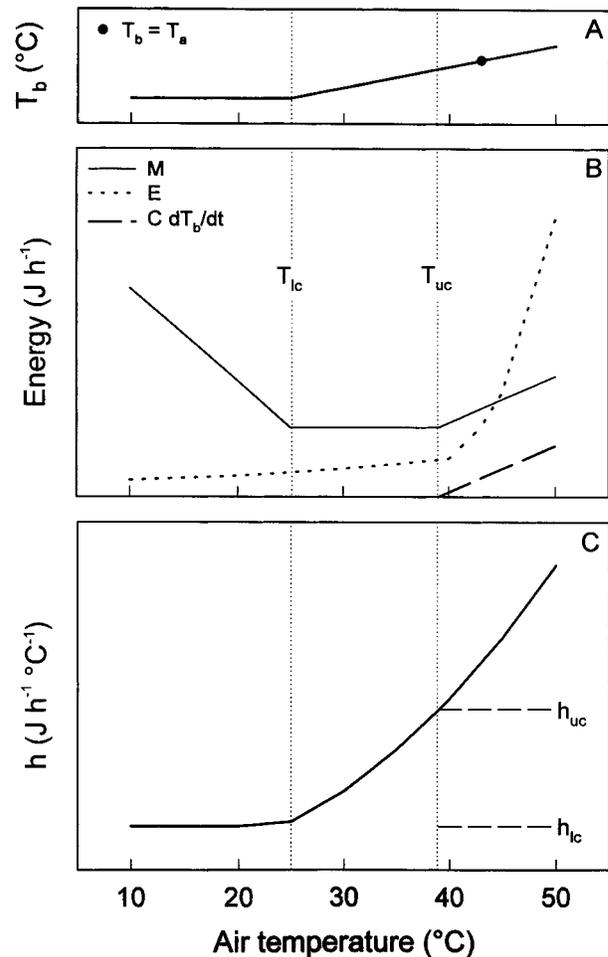

Figure 1. Variables as a function of T_a. A, T_b as a function of T_a. B, Metabolic heat production (M, *solid line*), evaporative heat loss (E, *dotted line*), and rate of heat gain ($C[dT_b/dt]$, *dashed line*), as functions of T_a. C, Dry heat transfer coefficient (h, *solid line*) as a function of T_a. The upper broken line indicates the expected maximal h reached at the T_{uc} (see text). The lower broken line indicates the minimal h, at the T_{lc}.

1974; Schmidt-Nielsen 1983). Implicit in this calculation is the assumption that core T_b equals the average T_b over the bird's body. While, at low T_a's, core T_b is typically higher than the average T_b, at high T_a's, this difference is small (Bartholomew 1982), justifying our assumption that core T_b = mean T_b.

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 $T_a = T_b$, using values or equations for T_b as provided by the individual authors. When plotted as a function of body mass, $C(dT_b/dt)$ was pos-

itive at $T_a = T_b$ in 19 of 22 studies (Fig. 2). If one divides by the specific heat of tissue, $C(dT_b/dt)$ can be converted to the rate of change in T_b. For these 22 studies, T_b was increasing at an average rate of $2.1° \pm 0.67°C$ (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_a's. In future experiments, we recommend that practitioners continuously monitor T_b when investigating questions concerning heat balance in birds, especially at higher T_a's. The ramifications for the above finding are complex, but one message seems clear: calculations of heat transfer within our data set cannot ignore $C(dT_b/dt)$. However, because there are no direct measurements of $C(dT_b/dt)$ available and because we can only estimate $C(dT_b/dt)$ at $T_a = T_b$, the relationship between $C(dT_b/dt)$ and T_a is not known. In our model, we assume, for simplicity, that $C(dT_b/dt)$ is a linear function defined by two points: $C(dT_b/dt) = 0$ (J h^{-1}) at the T_{uc}, and $C(dT_b/dt) = M - E$ (J h^{-1}) at $T_a = T_b$ (Fig. 1B). Continuous measurements of T_b in future metabolism experiments will test the validity of this model.

Our analysis of $C(dT_b/dt)$ could be criticized because one may argue that net dry heat transfer is 0 at $T_a = T_{skin}$, the temperature of the skin surface, and not at $T_a = T_b$ (Seymour 1972). However, data that relate T_{skin} 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°–5.1°C 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°C lower than its core T_b, T_{skin} equaled T_b during heat stress (Schmidt-Nielsen et al. 1969). In our analysis of $C(dT_b/dt)$, the assumption that net dry heat transfer is 0 at $T_a = T_b$ gives a conservative estimate of $C(dT_b/dt)$. If T_{skin} were lower than T_b, estimates of $C(dT_b/dt) = M - E$ would be larger than at $T_a = T_b$. For example, if one assumes that dry heat transfer equals 0 at $T_a = T_{skin} = T_b - 2$ (following Seymour [1972] for the temperature of the respiratory passages), our estimate of $C(dT_b/dt)$ would be, on average, 2.6 times larger than when calculated at $T_a = T_b$.

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):

$$M - E - C(dT_b/dt) = h(T_b - T_a), \qquad (2)$$

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

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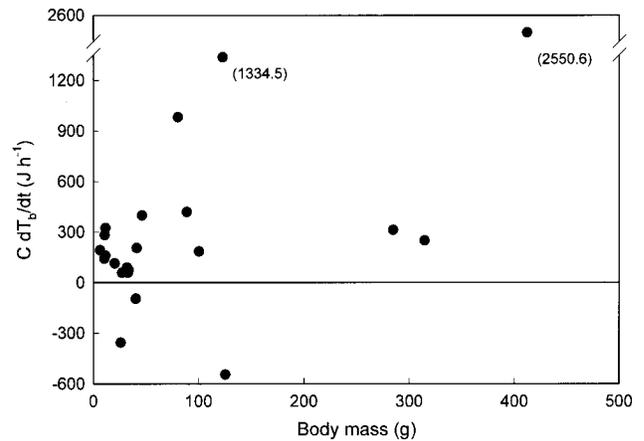

Figure 2. The rate of heat gain [$C(dT_b/dt)$] of birds at $T_a = 45°C$ as a function of body mass.

Although these data may suggest that birds maintain their T_b 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 Schoenbaechler 1976; Weathers 1981), presumably under steady state conditions (Fig. 3). All birds within our data set were hyperthermic at a T_a of 45°C. Body temperature was, on average, $3.3° \pm 1.28°C$ ($n = 23$) higher at $T_a = 45°C$ than at the T_{lc}. 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$_{slope} = 210^{-3}$, $r^2 = 0.06$, $P = 0.3$), 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_a of 45°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

$$h = \frac{M - E - C(dT_b/dt)}{T_b - T_a}. \qquad (3)$$

Below the TNZ, h is often assumed to be minimal (but see McNab 1980). As T_a increases within the TNZ, a bird has to dissipate its metabolic heat by dry heat loss over a decreasing thermal gradient. Therefore, intuitively, one might expect that the bird would continuously make adjustments in feather erection and blood supply to the skin, such that h increases to a
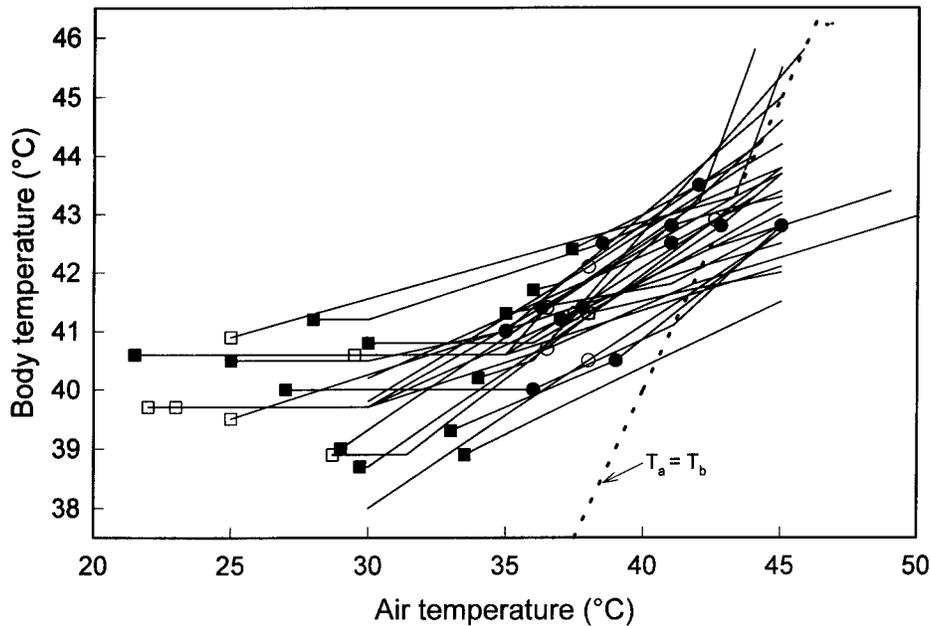
Figure 3. T_b as a function of T_a in and above the TNZ for 26 species. Some lines have an inflection point because authors reported two separate functions for T_b versus T_a. Squares represent the lower critical temperature, circles represent the upper critical temperature, and the dotted line $T_a = T_b$. 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.

maximum at T_{uc} (h_{uc}, Fig. 1C). Above T_{uc}, where the thermal gradient $T_b - T_a$ becomes smaller, the relative importance of h in dissipating heat decreases and evaporative cooling becomes increasingly important in maintenance of T_b. At T_a's above $T_a = T_b$, 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_{lc}, Fig. 1C). The values reported for h at T_a's above $T_a = T_b$ show considerable variation in all species. Some studies suggest a decrease to a minimal value (h_{lc}), 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 $C(dT_b/dt)$, 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 $C(dT_b/dt)$ is a significant factor at $T_a = T_b$ (Fig. 2). Therefore, the error in h should be reduced by including $C(dT_b/dt)$ in calculations of the numerator of Equation (3), $M - E - C(dT_b/dt)$. 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 $C(dT_b/dt)$ is not included. Algebraic rules dictate that, in this approach, h goes to infinity

when T_a approaches T_b (as in the dashed line of Fig. 4), a result that seems biologically unrealistic.

At $T_a = T_b$, 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 (J h^{-1}) being 0 at $T_a = T_b$, the heat transfer coefficient (J h^{-1} °C^{-1}), a property of the bird, does not become 0. To calculate h at $T_a = T_b$, 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, $\{M(T_a) - E(T_a) - C[dT_b/dt(T_a)]\}$, and denominator, $[T_b(T_a) - T_a]$, approach 0 when T_a approaches T_b. The addendum (T_a) 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_b, the quotient of the functions approaches the same limit:

$$h(T_a = T_b) = T_a \lim_{\to} T_b \frac{M(T_a) - E(T_a) - C(dT_b/dt)(T_a)}{T_b(T_a) - T_a}$$

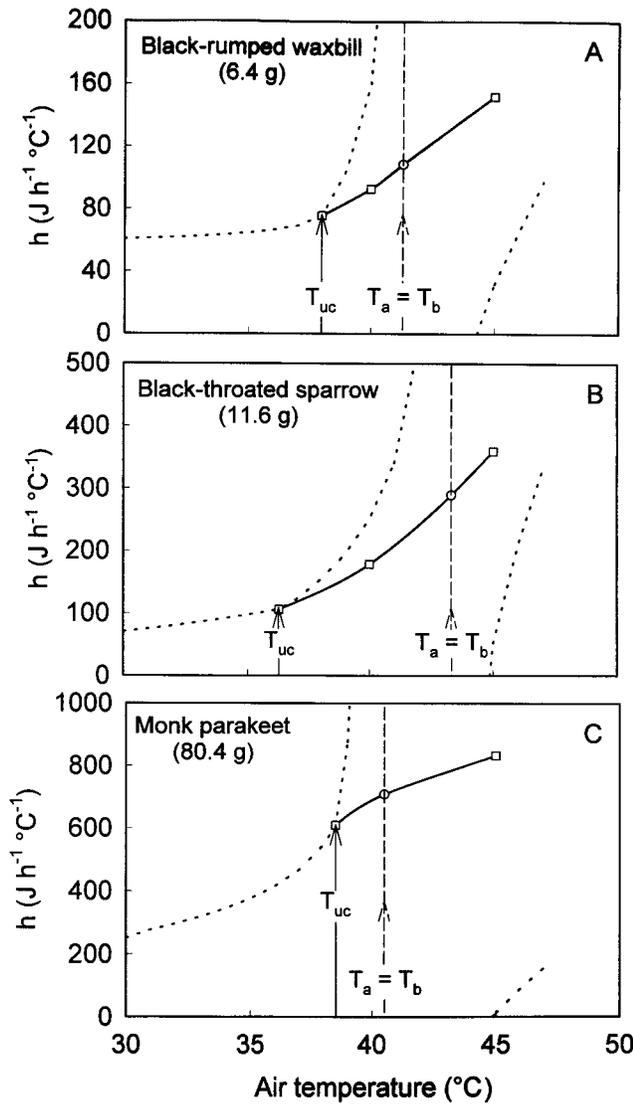$$= T_a \lim_{\to} T_b \frac{M'(T_a) - E'(T_a) - C(dT_b/dt)'(T_a)}{T_b'(T_a) - 1}.$$

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

We applied this technique to our calculations of h at $T_a = T_b$ when there is no dry heat transfer and both $T_b - T_a$ and $M - E - C(dT_b/dt)$ are 0 (Fig. 4).

Because this is a new method for calculating h at $T_a = T_b$, 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_b, M, and E to T_a (Table 1; Fig. 4). To establish the equation for $C(dT_b/dt)$, we determined temperature equality, $T_a = T_b = 43.3$°C, for this species, where net dry heat transfer is 0, and we calculated $C(dT_b/dt)$ at this T_a: $C(dT_b/dt) = M - E = 1368.0 - 1045.1 = 322.9$ J h^{-1}. Fitting a linear function that relates $C(dT_b/dt)$ to T_a requires at least two values for $C(dT_b/dt)$, and for our second value, we assume that $C(dT_b/dt)$ is 0 at $T_{uc} = 36.3$°C. The function relating $C(dT_b/dt)$ to T_a is given in Table 1. Equation (3) and the functions for T_b, M, E, and $C(dT_b/dt)$ given in Table 1 allow one to calculate h at temperatures above T_{uc}. At $T_a = T_b$, Equation (3) is undefined, and we have used the derivatives of each function (Table 1) in the previously described method to calculate h at $T_a = T_b$:

$$h(43.3) = \lim_{T_a \to 43.3} \frac{M'(43.3) - E'(43.3) - C(dT_b/dt)'(43.3)}{T_b'(43.3) - 1}$$

$$= \frac{94.0 - 259.9 - 46.1}{0.268 - 1} = 289.6 \text{ J h}^{-1}.$$

We have used our method to calculate the pattern of variation in h versus T_a for 22 species; all species showed the same trend in h above $T_a = T_b$. 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_a's above their T_b's by decreasing h.

Thermal Gradient

The rate of dry heat transfer $[h(T_b - T_a)]$ is a linear function of the thermal gradient $(T_b - T_a)$ 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 $T_a < T_b$ and decreases the dry heat uptake if $T_a > T_b$ (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_b with its actual hyperthermic T_b. 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 $T_a = 45$°C for each species. We rearranged Equation (2) to

$$E = M - C(dT_b/dt) - h(T_b - T_a) \tag{4}$$

and assumed that M, $C(dT_b/dt)$, and h were constant at this temperature. At 45°C, T_b is elevated by 0.7°–5.2°C above normothermic T_b. In order to examine only the effect of the thermal gradient on water savings, we assumed that all species had

a normothermic T_b of 3°C below their actual T_b 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_h and E_n, yielded the maximal amount of water saved by the 3°C elevation in T_b at 45°C (appendix contains all the variables that we used).

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

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

($\text{SE}_{slope} = 0.092$, $n = 22$, $r^2 = 0.57$; 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_a 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_a of 45°C against body mass:

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

($\text{SE}_{slope} = 0.061$, $n = 28$, $r^2 = 0.77$; 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 $T_a = 45$°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_b 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
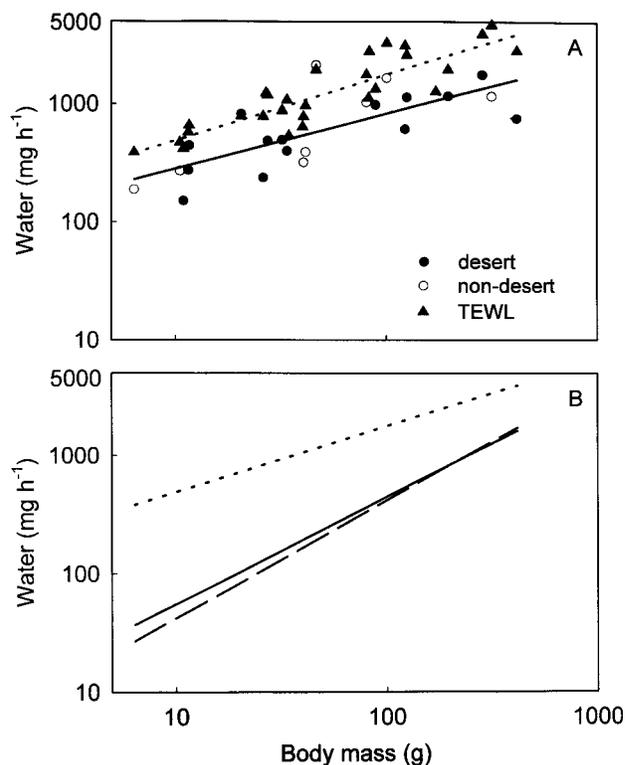

Figure 5. Water savings (mg h^{-1}) at 45°C. A, Water savings as a result of an improved thermal gradient for birds that have a standardized elevation in T_b of 3°C, as a function of body mass (symbols as in fig. 3). TEWL (mg h^{-1}) at 45°C is represented by the dotted line. B, Water savings (mg, *dashed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

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.

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

Heat Balance Equation	Derivative[a]	Temperature
$T_b(T_a) = 31.66 + .268 \times T_a$	$T_b'(T_a) = .268$	For $T_a > 29$°C
$M(T_a) = -2700.4 + 94.0 \times T_a$	$M'(T_a) = 94.0$	For $T_a > 36.3$°C
$E(T_a) = 22.02 \times 10^{-3} \times 10^{.108 T_a}$	$E'(T_a) = 5.475 \times 10^{-3} \times 10^{.108 T_a}$	For $T_a > 33.5$°C
$C(dT_b/dt)(T_a) = -1672.6 + 46.1 \times T_a$	$C(dT_b/dt)'(T_a) = 46.1$	For $T_a > 36.3$°C

Source. Weathers 1981.

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

[a] If $f(x) = c \times a^{bx}$, then $f'(x) = c \times a^{bx} \times b \times \ln a$.

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

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

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 ($t = 7.2$, 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_a 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_b coincide with, and are predictable from, changes in T_a (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_a of 45 °C. Though birds do not typically remain normothermic at a T_a of 45°C, we used these hypothetical values as a baseline for comparison. Few studies have focused on the relationship between T_b, REWL, and respiratory variables, such as tidal volume, ventilation frequency, and T_{ex}. 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_a'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_a's around 35°C, the upper limit of current data, T_{ex} and T_a converge. In our calculations at a T_a 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_b 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 $\rho(\text{g H}_2\text{O m}^{-3}) = \rho_{\text{H}_2\text{O}}/(4.62 \times 10^{-4})(T_{ex} + 273)\lim_{T_a \to 43.3}$ (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 $p_{\text{H}_2\text{O}}$ 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_b'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

Bird Mass (g)	Improved Thermal Gradient (g water)[a]	Heat Storage (g water)[b]	Increased REWL (g water)[c]	Net Savings (g water)	TEWL (g water)[d]
1 h:					
10	.28	.04	−.05	.27	.49
100	.83	.42	−.46	.79	1.78
1,000	2.45	4.16	−3.63	2.98	6.46
5 h:					
10	1.41	.04	−.27	1.18	2.45
100	4.16	.42	−2.31	2.27	8.89
1,000	12.27	4.16	−18.18	−1.75	32.28

Note. Calculations are based on an increase in T_b from 41°–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).

$$\log V_I = 0.38 + 0.69 \log \text{mass (g)}. \qquad (8)$$

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

$$\log V_I = 0.57 + 0.85 \log \text{mass (g)}. \qquad (9)$$

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

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

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:

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

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

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

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, we assumed a T_b 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_b 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_b at or near normothermic levels at high T_a's. In support of this hypothesis, the ostrich (100 kg, *Struthio camelus*), maintained a normothermic T_b during exposure to a T_a of 51°C for a period of 7.5 h (Crawford and Schmidt-Nielsen 1967).

TEWL at 45°C versus 25°C

This article contains the first equation that relates TEWL at a T_a of 45°C to body mass. An earlier allometric equation (Williams 1996) for TEWL at a T_a 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_a'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_a's. A 10-g bird increases its TEWL at a T_a 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_a 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_a of 45°C differed between desert and non-
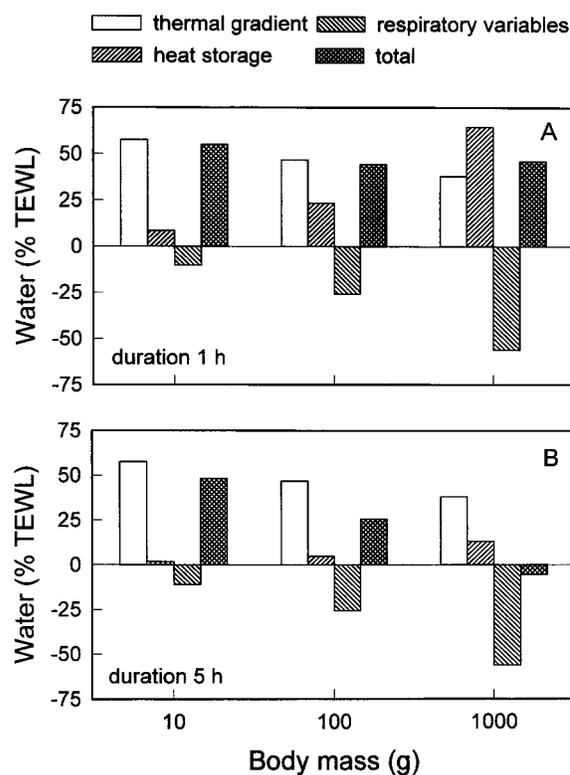

Figure 6. The relative contributions of the improved thermal gradient, heat storage, and increased REWL to the total effect of hyperthermia on the water balance of various sizes of birds. *A*, Duration of the hyperthermic state is 1 h. *B*, Duration of the hyperthermic state is 5 h.

desert birds. Our search of the literature has revealed that precious few data exist on T_b's at high T_a'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 $T_a = T_b$, the rate of heat gain $C(dT_b/dt)$ is a significant factor and should be incorporated in the heat balance equation at high T_a's. Therefore, during metabolic measurements at high T_a's, continuous measurements of T_b are of critical importance to our understanding of the heat balance of birds at high T_a's. Furthermore, at the T_a's where $C(dT_b/dt)$ is a significant factor, T_b 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

REWL. First, the allometric equations for minute volumes of resting and panting birds (Eqq. [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_{ex} at high T_a. More measurements on T_{ex}, especially at T_a's close to and above $T_a = T_b$ 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

Appendix

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

Species[a]	Category[b]	Body Mass (g)	M (J h^{-1})	E (J h^{-1})	$C(dT_b/dt)$ (J h^{-1})	h (J h^{-1} C^{-1})	T_b (°C)	Source
Sand partridge (*Ammoperdix heyi*)	d	172	...	3,104	...	...	44.6	Frumkin et al. 1986
Chukar (*Alectoris chukar*)	d	412	9,478	6,899	3,316	615	43.8	Frumkin et al. 1986
Common quail (*Coturnix coturnix*)	n	100.6	5,259	7,993	358	1,344	42.7	Weathers 1981
Gambel's quail (*Callipepla gambelii*)	d	125.5	3,739	6,313	−1,094	925	43.4	Weathers 1981
Greater roadrunner (*Geococcys californianus*)	d	284.7	6,917	9,534	549	1,439	42.8	Calder and Schmidt-Nielsen 1966
Budgerygar (*Melopsittacus undulatus*)	d	33.7	2,220	2,627	142	323	43.3	Weathers and Schoenbaechler 1976
Monk parakeet (*Myiopsitta monachus*)	n	80.4	4,263	4,308	3,186	829	41.1	Weathers and Caccamise 1975
Common poorwill (*Phalaenoptilus nuttallii*)	d	40	683	1,557	...	...	41.5	Bartholomew et al. 1962
Rock pigeon (*Columba livia*)	n	314.6	9,539	11,414	399	948	42.6	Calder and Schmidt-Nielsen 1966, 1967
Spinifex pigeon (*Geophaps plumifera*)	d	89	1,519	3,272	0	797	42.8	Withers and Williams 1990
Spinifex pigeon (*Geophaps plumifera*)	d	82.3	1,725	2,737	...	...	42.7	Dawson and Bennett 1973
Diamond dove (*Geopelia cuneata*)	d	34.4	1,160	1,306	...	...	45.4	Schleucher et al. 1991
Inca dove (*Scardafella inca*)	n	40.4	1,408	1,899	−129	259	43.6	Lasiewski and Seymour 1972; MacMillen and Trost 1967

Table A1 (*Continued*)

Species[a]	Category[b]	Body Mass (g)	M (J h^{-1})	E (J h^{-1})	$C(dT_b/dt)$ (J h^{-1})	h (J h^{-1} C^{-1})	T_b (°C)	Source
Double-banded sandgrouse (*Pterocles bicinctus*)	d	196.7	2,634	4,766	1,184	947	41.5	Hinsley 1992; Thomas and Maclean 1981
Tristram's starling (*Onychognatus tristrami*)	d	123	7,232	7,582	395	496	43.5	Dmi'el and Tel-Tzur 1985
Common starling (*Sturnus vulgaris*)	n	83	7,083	6,788	...	...	45.8	Dmi'el and Tel-Tzur 1985
Dune lark (*Certhilauda erythrochlamys*)	d	27.3	2,597	2,887	65	394	44.1	J. B. Williams, unpublished data
Horned lark (*Eremophila alpestris*)	d	26	1,551	1,907	−357	191	45	Trost 1972
Black-rumped waxbill (*Estrilda troglodytes*)	n	6.4	850	944	363	152	42	Cade et al. 1965
Zebra finch (*Taeniopygia guttata*)	d	11.5	1,501	1,394	218	221	44.5	Cade et al. 1965
White-throated munia (*Lonchura malabarica*)	d	10.9	1,137	1,009	210	103	44.2	Willoughby 1969
Cassin's finch (*Carpodacus cassinii*)	n	26.8	2,089	2,995	...	...	43	Weathers 1981; Weathers et al. 1980
House finch (*Carpodacus mexicanus*)	d	20.4	1,782	1,924	125	666	44.6	Weathers 1981
Black-throated sparrow (*Amphispiza bilineata*)	d	11.6	1,528	1,595	401	360	43.7	Weathers 1981
Variable seedeater (*Sporophila aurita*)	n	10.5	1,160	1,142	160	236	44.4	Weathers 1997
Red-winged blackbird (*Agelaius phoeniceus*)	n	46.3	3,823	4,735	471	1,728	44.2	Weathers 1981
Cardinal (*Cardinalis cardinalis*)	n	41.3	2,364	2,354	390	316	43.8	Hinds and Calder 1973
Pyrrhuloxia (*Cardinalis sinuatus*)	d	32	1,773	2,136	159	401	43.7	Hinds and Calder 1973

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.
[a] Species names according to Sibley and Monroe (1990).
[b] d = desert, n = nondesert.

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