

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.

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*)

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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 $T_a \geq 45^\circ\text{C}$. 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 photoperiod), 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 \pm 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):