

THE PHYSIOLOGY OF HEAT STRESS IN DESERT BIRDS

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Introduction

Arid environments pose a unique set of challenges to living organisms. These challenges include the lack of basic resources such as food and water, as well as extremes in temperatures. Recent studies have shown that desert birds have physiological specializations that allow them to survive in arid environments.

Anatomical and physiological adaptations of birds to life in the desert

Kidney

Avian kidneys are elongated, flattened and closely fitted into the bony concavity formed by the synsacrum (Braun and Dantzler, 1972). They contain both reptilian-type and mammalian-type nephrons (Braun and Dantzler, 1972). The mammalian-type nephrons can be further differentiated into long loop and short loop mammalian-type nephrons (Braun and Dantzler, 1972). When desert birds are subjected to severe dehydration or salt loads, a rise in plasma osmolality must be prevented by secreting ions extra-renal, producing concentrated urine, or reducing the glomerular filtration rate or any combinations of these (Braun and Dantzler, 1972). Desert quails can also decrease the overall glomerular filtration rate by reducing the number of functioning reptilian-type nephrons to increase water conservation at the expense of waste excretion, whilst maintaining the functions of the mammalian-type nephrons to increase the urine-concentrating capability of the kidney (Braun and Dantzler, 1972). In contrast to many other birds, chickens, as do mammals, increase tubular absorption in the kidneys to conserve water (Stallone and Braun, 1985).

Desert mammals were found to have a larger medullary mass relative to total kidney mass compared to those adapted to a moist environment (mesic) mammals (Schmidt-Nielsen and O'Dell, 1961; Heisinger and Breitenbach, 1969). The vasa recta, loops of Henle and collecting ducts in birds are encapsulated in the medullary cone, making the division between cortex and medulla less clear in bird kidneys (Williams and Tieleman, 2001). Therefore, similar studies in birds to identify differences in kidney structure between desert and mesic birds depend on measurements of relative medullary cone length instead of relative medullary mass. One such study by Goldstein and Braun (1989) found that there was no association between relative medullary cone length and maximal ureteral urine concentration. Desert birds were also not found to have superior urine concentrating abilities to non-desert birds (Goldstein and Braun, 1989). Williams and Tieleman (2001) commented that these results might be due to the small sample size, and that two of the seven species studied were seabirds with salt glands and larger kidneys. Goldstein and Braun (1989) also suggested that smaller birds had better urine concentrating abilities regardless of habitat affinity and that there was a negative correlation between the maximal ureteral urine concentration and the length of the loop of Henle.

It has been suggested that the maximal ureteral urine concentration may correlate with the mass-

adjusted field metabolic rate of a species because a lower metabolic rate means there is less metabolic waste for the kidneys to eliminate (Williams and Tieleman, 2001). This could therefore partly explain the significance of a lower field metabolic rate in desert birds compared to non-desert birds (Williams and Tieleman, 2001).

Gastro-intestinal tract

Birds are able to move urine from the cloaca by anti-peristalsis into the rectum (Brummerman and Braun, 1995), where water is passively reabsorbed to reduce water loss via urine (Anderson and Braun, 1985).

Desert birds were found to have 15% lower water content in the lumen contents of their lower gastrointestinal tract compared to non-desert birds, suggesting that they might better reabsorb water from the gastrointestinal tract (Amanova, 1984). However, more studies are needed to evaluate this hypothesis (Williams and Tieleman, 2001).

Some birds can also control cloacal evaporation as a means of thermoregulation at high ambient temperatures. This has been demonstrated in Inca doves (*Columba inca*), whose cloacal evaporation was negligible at 30, 35 and 40°C, but increased to 21.2% of total evaporative water loss at 42°C (Hoffman et al., 2007).

Skin

The skin of birds consists of an epidermis and a well-vascularized dermal layer (Lucas and Stettenheim, 1972). The epidermis has can secrete lipid-enriched organelles, or multigranular bodies, during times of water deficit for rapid water-proofing (Menon and Menon, 2000). Birds can also increase cutaneous water loss by vasodilating the dermal capillary bed (Peltonen et al., 1998). The balance between losing enough water to decrease body temperature and maintaining sufficient hydration is the key to survival in times of heat stress (Williams and Tieleman, 2001). Analysis done comparing lipid composition of the stratum corneum of adult desert house sparrows (*Passer domesticus*) and mesic house sparrows revealed that desert sparrows had a higher amount of ceramides and cerebroside and a lower percentage of cholesterol within the stratum corneum (Munoz-Garcia and Williams, 2005). A follow-up study also revealed that desert house sparrow nestlings showed a greater degree of plasticity in cutaneous water loss and lipid composition of the stratum corneum compared to mesic nestlings, possibly due to the increased exposure to environmental stressors (Munoz-Garcia and Williams, 2008). Similar differences were found between desert and mesic larks (Haugen et al., 2003). Desert sparrows also had lower cutaneous water loss, which can possibly be attributed to modifications in chain length and polarity of the sphingolipids that determine interactions among lipid molecules within the stratum corneum (Munoz-Garcia et al., 2008).

Nasal passages

It has been suggested that desert animals might have more complex nasal turbinates that allow greater cooling of exhaled air, and therefore a larger reduction in respiratory evaporative water loss than non-desert animals (Schmidt-Nielsen et al., 1981). Some birds are able to reduce respiratory evaporative water loss by recovery of water from the nasal area at moderate to low ambient temperatures, but this ability becomes insignificant at high ambient temperatures eg. 45°C for Crested Larks (Tieleman et al., 1999). However, the results of that study did not support the hypothesis that desert birds had a greater ability to recover water from the nasal passages compared to non-desert birds, because Desert Larks could not reduce respiratory evaporative water loss from

the nasal passages (Tieleman et al., 1999). More studies directly comparing phylogenetically similar desert and non-desert birds are needed to confirm this finding.

Energy, Water and Thermoregulation

Desert birds constantly struggle to meet their daily energy requirements due to their high rates of metabolism (as endotherms) and relatively low food availability in the desert (Williams and Tieleman, 2001). A relatively lower metabolic rate and the consequently lower endogenous heat production in desert birds relative to non-desert birds may be beneficial because less food for energy; and less water for evaporative cooling are required (Williams and Tieleman, 2001). The lower basal metabolic, field metabolic and evaporative water loss rates described by Williams and Tieleman (2001) in desert birds relative to non-desert birds may therefore provide part of the mechanism by which desert birds cope with extreme temperatures.

Behavioural adaptations

Opportunistic feeding and omnivory appear to be the best dietary strategy to survive in the desert (Williams and Tieleman, 2001). During heat waves, microsite selection becomes an important strategy for survival. Hiding in shaded areas will minimize evaporative water loss, and if these shaded areas are large enough to allow foraging, then the birds' energy requirements can be fulfilled as well (Williams and Tieleman, 2001). However, if the body temperature needs to be kept low by seeking deep shade and pressing the body against cooler substrates then the ability to forage is limited (Williams and Tieleman, 2001). Desert birds will therefore have to take necessary risks to maintain the balance of water, energy and thermo-regulation.

The neuroendocrine system

Corticosterone has an important role in the ability to cope with stressors in birds, and heat stress is no exception. With its ability to trigger specific physiological and behavioral responses that are crucial in maintaining the balance between energy, water and thermo-regulation, corticosterone might be one of the most important determinants of a bird's ability to survive in times of heat stress.

Thyroid hormones may play a role in the development of physiological adaptations such as basal metabolic rate and thermoregulation in juvenile desert birds (McNabb and Fox, 2003) but have less adaptive plasticity in adult birds and are therefore less important than corticosterone in the physiology of heat stress in adult desert birds.

Heat shock proteins

Heat shock proteins (hsps) are a group of proteins synthesized by almost all organisms when exposed to heat or other stressors (Lindquist and Craig, 1988). They are named according to their relative molecular masses (Lindquist and Craig, 1988), eg. hsp70 and hsp90 have relative molecular masses of 70000 and 90000 kilodaltons respectively.

Heat shock proteins act as molecular chaperones, interacting with other proteins to minimize the probability that other proteins will interact inappropriately with one another (Feder and Hofmann, 1999). The rapid and intense nature of the induction of heat shock proteins indicates that it is an

emergency response (Lindquist and Craig, 1988).

The differences in heat shock protein responses to high temperatures in desert birds may hold the key to their ability to survive in these harsh conditions.

Conclusion

The implications of heat stress in avian species are important in the face of increasing global temperatures related to climate change. A better understanding of the physiology of heat stress and identification of the sensitivity of different bird species to increasing global temperatures will help wildlife managers to direct conservation efforts better by providing risk assessments for species and regions. This presentation will also demonstrate the links between climate change, as a result of human activities, and the survivability of desert birds, exemplifying the principles of the 'One Health' initiative.

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