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Global warming and avian occupancy of hot deserts; a physiological and behavioral perspective

Calentamiento global y ocupación de desiertos cálidos por aves; una perspectiva fisiológica y conductual

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ABSTRACT

Avian adjustments to desert environments are characterized by an integration of behavior and physiology. These responses serve to maintain homeostasis and conserve vital resources such as water. The small size of birds confers a close coupling to the thermal environment and demands rapid adjustments to environmental challenges. Physiological responses to heat stress include hyperthermia, and increased evaporative cooling as environmental temperatures approach body temperature. Behaviorally, desert birds respond to heat stress by drastically reducing activity during the hottest parts of the day and selecting cool shaded microsites. This characteristic behavioral response presents a potential problem in the face of global warming. If birds totally forgo foraging during extremely hot periods, increased evaporative water loss rates due to higher environmental temperatures could lead to significant episodes of direct mortality for birds in these regions. A simple model is presented which integrates behavior and physiology to predict survival times based on dehydration tolerance, microsite selection and environmental temperature.

Key words: global warming, hot deserts, birds, water balance, evaporative water loss, avian distribution.

RESUMEN

Los ajustes de las aves a ambientes desérticos se caracterizan por la integración de la conducta y fisiología. Estas respuestas permiten mantener la homeostasis y conservar recursos vitales como el agua. El pequeño tamaño de las aves las acopla al ambiente térmico de un modo estrecho y demanda que ellas muestren respuestas rápidas a los desafíos del ambiente. Cuando la temperatura ambiente se aproxima a la temperatura corporal, las respuestas fisiológicas al estrés térmico incluyen hipertermia, así como un aumento en el enfriamiento por evaporación pulmo-cutánea. Conductualmente las aves responden al estrés calórico con la reducción de los patrones de actividad durante la parte mas calurosa del día, y seleccionando micro-sitios sombrados y más frescos. Frente al fenómeno de calentamiento global, estas características respuestas conductuales presentan problemas potenciales. Si las aves deben forrajear durante las horas más cálidas del día, la elevada pérdida de agua evaporativa podría significar episodios directos de mortalidad en estas regiones. Se presenta un modelo simple que integra fisiología y conducta para predecir tiempos de sobrevivencia basados en tolerancia a la deshidratación, selección de micrositios y temperatura ambiente.

Palabras clave: calentamiento global, desiertos cálidos, aves, balance hídrico, pérdida de agua evaporativa, distribución de aves.

INTRODUCTION

How global warming will affect the distribution of animals in coming millennium is a question of vital importance to those interested in biodiversity. Although global trends in air temperature are well established, regional changes are hard to predict (IPCC 1995). Even more confounding are the plant and animal responses to these changes. In this essay, I survey what is currently known about the behavioral and physiological responses of desert birds to increasing environmental temperatures and heat stress during the summer. I focus on water use and conservation by birds living in hot sub-tropical deserts and how increasing short-term heat stress might affect the survival and distribution of desert birds. An examination of these responses in the context of global warming provides an

(Managed by F. Bozinovic)

opportunity to examine how increased regional temperatures might affect avian distributions.

CHARACTERISTICS OF BIRDS AND PHYSIOLOGICAL RESPONSES TO HIGH ENVIROMENTAL TEMPERATURES

Although apparently inhospitable, sub-tropical deserts have been colonized by a diversity of plants and animals. Very high air temperatures, intense solar radiation, and extreme aridity, when combined with scarce free-water resources can place significant demands on the abilities of animals to balance their water budgets in these environments. The success of birds in such regions is striking because many of the basic attributes of this group would seem to exacerbate problems of heat and aridity (Bartholomew & Cade 1963). For example, most birds are diurnal and do not use burrows for refuge, thus they must directly confront the hottest periods of the summer day (but see Williams & Tieleman 1998). Small birds also have high mass-specific metabolic rates, which result in high rates of internal heat production and frequent ventilation of respiratory surfaces (with resultant high rates of pulmonary water loss) (Dawson 1982, Wolf & Walsberg 1996a). In addition, because of their small size they have a low thermal inertia and very limited capacity for storage of vital resources such as water (Dawson 1976).

But birds also show a number of attributes that potentially favor their residence in these environments. First, although their mass-specific rates of water and energy usage are relatively large, their overall resource requirements are modest because of their small body size. Thus, they can potentially inhabit regions where food and water resources are in short supply. Birds are also highly mobile and can travel long distances in search of resources in very short periods of time. As a consequence some species are able to take advantage of temporally or spatially localized resources over broad areas. In addition, the body temperatures of birds are on average 3 to 4°C higher than those of mammals. Birds also readily allow their body temperature to increase an additional 2 to 4°C in response to heat or water stress and exercise (Webster 1991). These higher body temperatures provide more favorable conditions for heat loss to the environment by mechanisms such as radiation, conduction or convection. Radiative, conductive and convective heat transfer mechanisms rely on temperature gradients to drive heat flow and thus help conserve precious water resources.

When the temperature of the physical environment approaches or exceeds avian body temperature, the thermal gradient for passive heat transfer (radiation, conduction and convection) is diminished or even reversed and evaporative water loss becomes an essential means of heat transfer. During these periods, both endogenous heat loads (metabolic heat) and exogenous heat loads (heat absorbed from the environment) must be lost through evaporation. Birds resident to sub-tropical deserts during the summer are routinely exposed to these conditions (Walsberg 1994). Air temperatures during the summer in the Sonoran Desert of Arizona, USA, may commonly exceed 42°C for 8 hours or more of each day and occasionally can even exceed 50°C (Fig. 1) (Azmet 1990). Increases in environmental temperatures above avian body temperature leads to dramatic increases in evaporative water loss. For example, in Verdins (*Auriparus flaviceps*), which are small (ca. 6.5 g) year-round residents of the Sonoran Desert, total evaporative water loss increases seven-fold between 38 and 48°C under resting conditions (Fig. 2) (Wolf & Walsberg 1996b). In this situation, evaporative water loss may account for 80% or more of the Verdin's total water loss and can exceed 5% of a small bird's body mass each hour (Wolf & Walsberg 1996b). Under these conditions the need to evaporate water in order to maintain body temperature below critical limits is in direct conflict with the maintenance of an adequate state of hydration (Webster 1991). The above attributes, combined with the high surface-area-to-volume-ratios of small birds means they are closely coupled to their physical environments and are must respond rapidly to

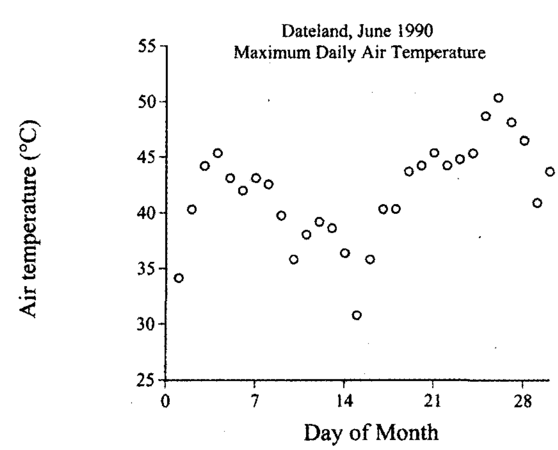

Fig. 1. Maximum daily air temperatures for June of 1990 for Dateland, AZ (Azmet 1990).

Temperaturas máximas del aire durante junio de 1990 en Dateland, AZ.

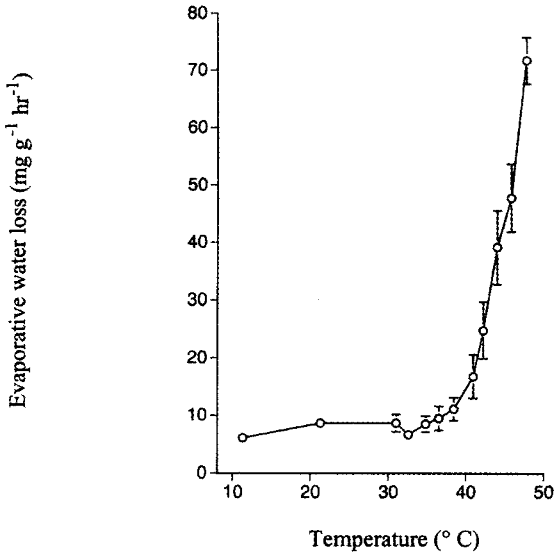

Fig. 2. Total evaporative water loss rates for Verdins resting in the dark. Means are for 12 individuals at each data point, and 95% confidence intervals are shown at each temperature. From Wolf & Walsberg (1996b).

Tasas de perdida total de agua evaporativa para verdines descansando a la sombra. Promedios corresponden a 12 individuos para cada punto, y se presentan los intervalos de confianza del 95% para cada temperatura. En Wolf & Walsberg (1996b).

changes in the thermal environment if they are to maintain homeostasis (Goudie & Piatt 1990). As a consequence, these animals may be under extreme selective pressures to optimize their use of water resources.

BEHAVIORAL RESPONSES OF BIRDS TO HIGH ENVIRONMENTAL TEMPERATURES

The behavior of birds exposed to increasingly hot environmental temperatures during a summer day reflects the need to minimize rates of evaporative water loss. Thus, an important correlate of desert residency is the suppression of activity during the hottest periods of the day. This occurs in most animals that have been studied, including birds (Austin 1976, 1978, Calder 1968, Dawson 1954, 1976, Grue et al. 1981, Moldenhauer & Wiens 1970, Ricklefs & Hainsworth 1968). Vital activities such as foraging, reproductive behavior, and territorial maintenance may all be suppressed. For example, Cactus Wrens (*Campylorhynchus brunneicapillus*) significantly reduce visits to their nest, favor shaded areas, and reduce overall activity at air temperatures above 35°C (Ricklefs & Hainsworth 1968). Greater Roadrunners (*Geococcyx californianus*) reduce activity by almost 50% during the hottest periods of the day in June and July (Calder 1968). Verdins also strongly reduce activity as environmental temperatures increase; below 35°C about 75% of each hour is occupied by foraging, as temperatures increase to 45 °C, however, foraging activity declines to only 25% of each hour (Austin 1976, 1978).

This universal reduction in activity by desert birds is also importantly accompanied by a very pronounced retreat from sunlit to shaded sites (Austin 1976). Movement from sunlit to shaded microsites confers a very significant reduction in environmental heat load. For small birds, such as the Verdin, this reduced heat load is thermally equivalent to a 12°C decrease in air temperature at low wind speeds (ca. 0.4 ms^{-1}, Wolf & Walsberg 1996b). Birds living in these environments also appear to actively select very specific microsites or thermal refuges. These refuges appear to minimize heat loads and rates of evaporative water loss experienced by their occupants. This behavior has been observed in a number of settings and species. In the Namib Desert of Namibia, Willoughby (1971) observed Karroo Larks (*Certhilauda albescens*) and Stark's Larks (*Eremalauda starki*) routinely resting in the shade provided by large grass clumps and rocks during the hottest periods of the day. Williams et al. (1999) observed four species of larks using the burrows of Egyptian spiny-tailed lizards (*Uromastyx aegypticus*) as thermal refuges during the summer in the Arabian Desert. During periods of burrow use by Hoopee Larks (*Alaemon alaudipes*) air temperatures averaged 44.1 °C outside the lizard burrow and 41.5 °C within the burrow. Occupancy of these thermal refuges was estimated to reduce water loss during the day by 65 to 81%. Similarly, in the Sonoran Desert of Arizona during the summer, Wolf et al. (1996) observed Verdins and Black-tailed Gnatcatchers (*Polioptila melanura*) sitting in deeply shaded microsites (against the trunk or in knotholes of large paloverde trees, *Cercidium floridum*) during the hottest part of the day. The Verdin's occupancy of these thermal refuges, which were about 3°C cooler than shade air temperature, was estimated to reduce evaporative water loss rates by 50 to 66% when compared to occupancy of a shaded site at the average shade air temperature.

Taken together, these behaviors suggest that desert birds in general accrue smaller water deficits by suspending activity and seeking thermal refuges during the hottest periods of the day rather then by continuing to forage. Continued foraging activity could increase water loss rates in two ways. First, increased activity is accompanied by increases in metabolic heat production and thus a greater need to evaporate water to maintain body temperature. Secondly, as described above, the thermal environments occupied during foraging are likely to be hotter than the thermal refuges used when activities are suspended. This suppression of activity during the hottest periods of the day also suggests that these birds are "betting" that they won't exceed critical osmoregulatory limits due to continued water loss during that period of inactivity.

SHORT-TERM DEHYDRATION TOLERANCE

How can we evaluate the physiological consequences of these behaviors and their affects on the Verdin's water balance and potential survival? As we know there is this large and constant demand to evaporate water to stay cool, but birds must also regulate body fluid concentrations within acceptable limits or perish. For birds living in sub-tropical deserts during the summer their continued survival is mediated by several factors which include: environmental temperature and water loss rate (determined by microsite selection), the animal's short-term limits of dehydration tolerance, and the duration of inactivity period. So how much water loss can a small bird sustain in a single day when exposed to a hot environment? Unfortunately, most studies examining dehydration tolerance, where water is withheld, have been preformed in the absence of any type of thermal stress and examined only changes in body mass over periods of days to weeks (Bartholomew & MacMillen 1960, 1961). Mass loss over these periods typically includes water and tissue losses and thus doesn't accurately reflect limits of dehydration tolerance (MacMillen 1962). Wolf & Walsberg (1996b), however, found that Verdins could lose approximately 11% of their total mass in water (0.75 ml) before losing the ability to move effectively.

INTEGRATION OF BEHAVIOR AND PHYSIOLOGY AND THE POTENTIAL EFFECTS OF GLOBAL WARMING

We can produce a simple model that examines the physiological consequences of behavioral decisions (microsite selection) in the absence of continued water intake (i. e. suppressed foraging) by integrating these dehydration tolerance data with microsite selection and evaporative water loss rate data (Fig. 3). So how does microsite selection affect survival times in birds that are not foraging? First, from Figure 3 it is apparent that even at moderate air temperatures retreating from sunlit to shaded microsites greatly increases survival times and increases the predicted time to death. For example, the predicted time to death for birds continuously exposed to the sun at an air temperature of 44°C is about 20 minutes; birds resting in the shade at the same air temperature are expected to survive more than seven times longer. We see that survival times are very low for birds at all temperatures if they are continuously exposed to

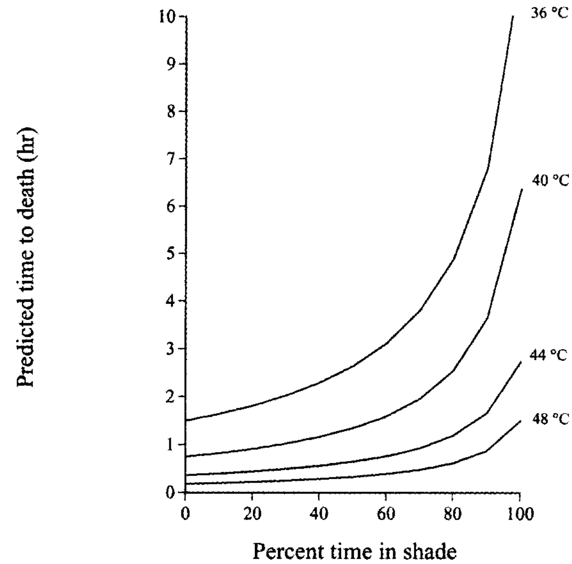

Fig. 3. Predicted time to death for Verdins as a function of microsite selection (% time in shade vs. % time in full sun) for several air temperatures (36, 40, 44, 48°C). This model assumes all activity is suspended. Each curve was produced by taking the Verdin's total evaporative water loss rate at the prevailing environmental temperature and calculating the time required for the bird to lose 0.75 ml of body mass. No excretory losses were assumed. Time to death is calculated assuming that resting in the sun raises environmental temperature by 12 °C and that Verdins can lose 0.75 ml of body water before they are ecologically dead. Values for all parameters are taken from Wolf & Walsberg (1996b).

Tiempo estimado de muerte para verdines en función de la selección de micrositios (% de tiempo a la sombra versus % de tiempo a pleno sol). Cada curva fue estimada considerando la tasa de perdida total de agua evaporativa a la temperatura ambiental predominante, y calculando el tiempo requerido para perder 0,75 ml de peso corporal por el ave. No se consideran perdidas excretorias. El tiempo de muerte se calculó asumiendo que el reposo al sol incrementa la temperatura ambiental en 12°C y que los verdines pueden perder hasta 0,75 ml de agua corporal antes de estar ecológicamente muertos. los valores utilizados en esta estimación provienen de Wolf & Walsberg (1996b).

the sun and even limited exposure to the sun severely reduces survival times. Clearly high air temperatures also have a pronounced negative affect on survival times. Birds resting in the shade at an air temperature of 40°C are expected to survive about four times longer than birds in shaded areas at 48°C. These observations indicate that even in the shade, microsite selection should be a precise process that minimizes water loss rates.

Figure 3 also suggests how global warming might affect desert bird populations. The current consensus models supported by the Intergovernmental Panel on Climate Change (1995) predict an increase in global temperatures of about 2.2°C (range 0.9 to 4.5) by the year 2100. In addition, these general circulation models also predict about 25% increase in the frequency of extremely hot temperature events. Because evaporative water loss rates in small birds increase exponentially at high air temperatures, even a modest increase of 1 - 2°C has a tremendous impact on water loss rates. In the coming decades, shade air temperatures may occasionally peak at 52 or 53°C during the day, versus 50°C as they do now; increased water loss rates in small birds associated with these higher air temperatures could lead to greatly decreased survival times during inactive periods. These conditions could potentially cause significant episodes of direct mortality in desert bird communities as has been seen in the interior deserts of Australia during the last century (Serventy 1971). Increases in maximum shade air temperatures when combined with the predicted increase in the frequency of extreme high temperature events might even alter the makeup of desert bird communities.

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LITERATURE CITED

AUSTIN GT (1976) Behavioral adaptations of the Verdin to the desert. Auk 93: 245-262.

AUSTIN GT (1978) Daily time budget of the postnesting Verdin. Auk 95: 247-251.

AZMET (1990) (Arizona meteorological online archive and database) http://ag.arizona.edu/azmet.

BARTHOLOMEW GA & TJ CADE (1963) The water economy of land birds. Auk 80: 504-539.

BARTHOLOMEW GA & RE MACMILLEN (1960) The water requirements of mourning doves and their use of sea water and NaCl solutions. Physiological Zoology 33: 171-178.

BARTHOLOMEW GA & RE MACMILLEN (1961) Water economy of the California quail and its use of sea water. Auk 78: 505-514.

CALDER WA (1968) The diurnal activity of the Roadrunner, *Geococcyx californianus*. Condor 70: 84-85.

DAWSON W R (1954) Temperature Regulation and water requirements of the brown and abert towhees, *Pipilo fuscus* and *Pipilo aberti*. University of California Publications in Zoology 59: 81-124.

DAWSON WR (1976) Physiological and behavioral adjustments of birds to heat and aridity. In: Proceedings of the 16th international ornithological congress Australian Academy of Science, 455-467 Canberra City, A.C.T.

DAWSON WR (1982) Evaporative losses of water by birds. Comparative Biochemistry and Physiology 71A: 495.

JT HOUGHTON, LG MEIRA FILHO, BA CALLENDER, N HARRIS, A KATTENBERG & K MASKELL (eds) (1995) The Science of Climate Change: Contribution of Working Group I to the Second Assessment of the Intergovernmental Panel on Climate Change, Cambridge University Press, UK. 572 pp.

GOUDIE R I & JF PIATT (1990) Body size and foraging behavior in birds. Proceedings of the 20th Ornithological Congress: 811-816, New Zealand Ornithological Trust Board Wellington.

GRUE CE, RP BALDA & CD JOHNSON (1981) Diurnal activity patterns and population estimates of breeding birds within a disturbed and undisturbed desert-scrub community. Studies in Avian Biology 6: 287-291.

MACMILLEN RE (1962) The minimum water requirements of Mourning Doves. The Condor 64: 165-166.

MOLDENHAUER RR & JA WIENS (1970) The water economy of the Sage Sparrow, *Amphispiza belli nevadensis*. The Condor 72: 265-275.

RICKLEFS RE & F R HAINSWORTH (1968) Temperature dependent behavior of the cactus wren. Ecology 49: 227-233.

SERVENTY DL (1971) Biology of Desert Birds. In: Farner DS & JR King (eds) Avian Biology: 287-339. Academic Press, New York.

WALSBERG GE (1985) Physiological consequences of microhabitat selection in birds. In: ML Cody (ed) Habitat Selection in Birds: 389-413. Academic Press, New York.

WALSBERG GE (1990) Communal roosting in a very small bird: consequences for the thermal and respiratory gas environments. The Condor 92: 795-798.

WALSBERG GE (1993) Thermal consequences of diurnal microhabitat selection in a small bird. Ornis Scandinavica 24: 174 - 182.

WEBSTER MD (1991) Behavioral and physiological adaptations of birds to hot desert climates, In: Proceedings of the 20th international ornithological congress: 1765-1776. Christchurch, New Zealand.

WILLIAMS JB (1999) Heat production and evaporative water loss of dune larks from the Namib Desert. The Condor 101: 432-438.

WILLIAMS JB, IB TIELMAN & DM SHOBRAK (1999) Lizard burrows provide thermal refugia for larks in the Arabian Desert. The Condor 101: 714-717.

WILLOUGHBY EJ (1971) Biology of larks (Aves: Alaudidae) in the Central Namib Desert. Zoologica Africana 6: 133-176.

WOLF BO & GE WALSBERG (1996a) Partitioning respiratory and cutaneous evaporative water loss during heat stress in a small bird. The Journal of Experimental Biology 199: 451-457.

WOLF BO & GE WALSBERG (1996b) Thermal effects of wind and radiation on a small bird and implications for microsite selection. Ecology 77: 2228-2236.

WOLF BO, KM WOODEN & GE WALSBERG (1996) The use of thermal refugia by two small desert birds. The Condor 98: 424-428.