

Avian and Reptilian Evaporative Compartmentalization

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Evaporation of water vapor from the body of an animal is an especially interesting mode of biological heat transfer, because evaporation differs from the other modes (conduction, convection, and radiation) in fundamental ways. First, unlike the other three modes, evaporation always represents a release of heat from the body, resulting in a decrease in the temperature of the evaporating surface. On the other hand, depending on microclimatic conditions, an animal might gain or lose heat either conductively, convectively, or radiatively. Second, evaporation always results in a loss of water, on which nearly all biochemical processes depend. Such a coupling of heat-loss with resource-loss is not associated with the other modes of exchange. These fundamental differences underlie an important biological conflict of interests: the animals with the least access to water for hydrostasis (such as desert forms) are the animals with the greatest need to lose water for thermostasis. While this statement obviously applies to endothermic homeotherms, the implications for ectothermic heterotherms should not be overlooked.

Since the hydrostatic need for water retention in such animals is in diametric opposition to the thermostatic need for water evaporation, it is reasonable to expect that animals differ in the fractional compartmentalization of total evaporation into the different evaporative routes, based on any differences in energetic efficiency that might exist between those routes. An animal possesses various epithelia, several of which are exposed (whether continuously or intermittently) to ambient air. These exposed epithelia represent routes of evaporation, and historically these routes have been termed "respiratory" and "cutaneous". The former refers to buccopharyngeal evaporation, and the latter refers to all other evaporation. Most truly terrestrial vertebrates have a single orifice for reproductive, excretory, and digestive products; these are the reptiles and birds, the subjects of my dissertation. I recognize in these taxa three distinct routes of evaporation: buccopharyngeal, cutaneous, and cloacal. The studies in my dissertation include novel approaches to experimentally compartmentalizing evaporation into these three routes.

Studies of evaporation have been undertaken for many species of disparate taxa. Historically, measurements of reptilian evaporation have been considered almost exclusively in terms of the detrimental loss of body water. Studies of evaporation in birds and mammals, on the other hand, include considerations of the cost of water loss and the benefit of evaporative cooling. My dissertation includes investigations of evaporation in two reptile species and three bird species, with an emphasis on whether evaporation is thermoregulatorily important. The major findings of the experimental work include the following:

- I present the first empirical evidence that a bird is able to rapidly adjust the rate of non-buccopharyngeal evaporation (e.g., from the skin). When evaporation from the mouth and pharynx is experimentally suppressed, mourning doves respond by increasing the rate of evaporation from the rest of the body. The increase is not a

passive consequence of increase in skin temperature, and the evaporative enhancement is thermoregulatorily significant.

- The cloaca is a major source of evaporation for Gila monsters at thermally challenging temperatures. These are the first data that indicate such an evaporative mechanism exists in any reptile. Moreover, when these lizards resort to gaping the cloaca, the increase in evaporation is dramatic, indicating that they might be able to increase their time of exposure during foraging bouts.
- The cloaca is a major source of evaporation for some birds at thermally challenging temperatures. I demonstrate for the first time that a bird is able to evaporate from the cloaca at a rate that can be important for thermoregulation. Inca doves can lose up to one-fifth of their evaporating water from the cloaca, and at high ambient temperature the increase in cloacal evaporation is significant.
- Similar to mourning doves, Inca doves show an ability to adjust non-buccopharyngeal evaporation. A refinement of the experimental technique indicates that the cutaneous and cloacal components are separately adjusted. I suggest a possible thermoregulatory strategy involving a stepwise transition from buccopharyngeal evaporation to cutaneous evaporation to cloacal evaporation.
- Reliance upon cloacal evaporation is not a uniform feature of avian thermoregulation. I present a comparison of Inca doves and Eurasian quail with respect to the use of cloacal evaporation. In Eurasian quail, which are unable to tolerate high experimental temperatures, the majority of evaporation is non-buccopharyngeal. But despite the much larger ratio of cloaca to skin surface in these birds compared to Inca doves, the cloacal fraction of non-buccopharyngeal evaporation in Eurasian quail is negligible.
- Reliance upon cloacal evaporation is not a uniform feature of reptilian thermoregulation. I contrast the evaporative response in ball pythons with that in Gila monsters by showing that a negligible fraction of non-buccopharyngeal evaporation in ball pythons is cloacal, even at high ambient temperature. Ball pythons do, however, undergo a comparatively steep, temperature-dependent increase in cutaneous evaporation. In Gila monsters, cutaneous evaporation changes very little as ambient temperature increases, and cloacal evaporation is significant at high ambient temperature.

Experimental Summaries

Mourning doves

- Birds were placed in a two-compartment chamber with a latex sheet separating the head from the rest of the body.
- Buccopharyngeal and non-buccopharyngeal evaporation rates were measured separately.
- For half of the trials, water-saturated air was flowed to the head chamber; for all trials, dry air was flowed to the body chamber.
- Trials were conducted at 35°, 45°, and 50°C ambient temperature.
- Buccopharyngeal and non-buccopharyngeal evaporation increased as ambient temperature increased.
- When buccopharyngeal evaporation was suppressed by humid air, non-buccopharyngeal evaporation increased to partially compensate.

Gila monsters

- Lizards were placed in a two-compartment chamber with a latex sheet separating the head from the rest of the body.
- For half of the trials, a latex diaper was applied to block the cloaca.
- Buccopharyngeal and non-buccopharyngeal evaporation rates were separately measured, and cutaneous and cloacal evaporation rates were calculated.
- Trials were conducted at 20°, 30°, 35°, 37.5° and 40°C ambient temperature.
- Non-buccopharyngeal evaporation greatly increased above 37°C.
- Nearly all of the increase in non-buccopharyngeal evaporation was cloacal.

Inca doves

- Birds were placed in a two-compartment chamber with a latex sheet separating the head from the rest of the body.
- For half of the trials, water-saturated air was flowed to the head chamber; for all trials, dry air was flowed to the body chamber.
- For half of the trials, the cloaca was sealed with cyanoacrylate.
- Buccopharyngeal and non-buccopharyngeal evaporation rates were separately measured, and cutaneous and cloacal evaporation rates were calculated.
- Trials were conducted at 30°, 35°, 40°, and 42°C ambient temperature.
- When buccopharyngeal evaporation was suppressed by humid air at 35° and 40°C, non-buccopharyngeal evaporation increased to partially compensate.
- When buccopharyngeal evaporation was suppressed by humid air at 42°C, non-buccopharyngeal evaporation no longer increased, and cloacal evaporation increased to partially compensate.

Eurasian quail

- Birds were placed in a non-compartmentalized chamber and fitted with a negative-pressure mask.
- For half of the trials, the cloaca was sealed with cyanoacrylate.
- Buccopharyngeal and non-buccopharyngeal evaporation rates were separately measured, and cutaneous and cloacal evaporation rates were calculated.

- Buccopharyngeal and non-buccopharyngeal evaporation increased as ambient temperature increased.
- Cloacal evaporation was a negligible fraction of non-buccopharyngeal evaporation.

Ball pythons

- Snakes were placed in a non-compartmentalized chamber and fitted with a negative-pressure mask.
- For half of the trials, the cloaca was sealed with cyanoacrylate.
- Buccopharyngeal and non-buccopharyngeal evaporation rates were separately measured, and cutaneous and cloacal evaporation rates were calculated.
- Trials were conducted at 30°, 35°, 40°, and 42°C ambient temperature.
- Buccopharyngeal and non-buccopharyngeal evaporation increased as ambient temperature increased.
- Cloacal evaporation was a negligible fraction of non-buccopharyngeal evaporation.

	Birds	Reptiles
Desert species	<p>Mourning doves and Inca doves tolerate high ambient temperatures. Both species are able to rapidly increase cutaneous evaporation when buccopharyngeal evaporation is suppressed. Inca doves exhibit a significant increase in cloacal evaporation at 42°C, when cutaneous evaporation is no longer significantly increasing.</p>	<p>Gila monsters tolerate high ambient temperatures for at least brief periods. When ambient temperature exceeds about 37°C, cloacal evaporation undergoes a dramatic increase. The increase in cloacal evaporation is sufficient to depress body temperature. The depression of body temperature might allow for extended period of foraging during the hottest parts of the day.</p>
Non-desert species	<p>Eurasian quail are not able to tolerate high ambient temperatures. Despite their intolerance of high temperatures, and despite the relatively large size of their cloacae, Eurasian quail do not employ cloacal evaporation. Eurasian quail start panting at a much lower ambient temperature than mourning doves or Inca doves.</p>	<p>Ball pythons tolerate high ambient temperatures for at least brief periods. Both buccopharyngeal and non-buccopharyngeal evaporation increase with increasing temperature, but cloacal evaporation is a negligible fraction of that non-buccopharyngeal evaporation.</p>

Columbiforms have long been thought to possess an extraordinary capacity for cutaneous evaporation. My results modify this assertion by showing that mourning doves and Inca doves are able to quickly change the rate of non-buccopharyngeal evaporation if buccopharyngeal evaporation is insufficient for thermostasis. Moreover, at least in Inca doves, cloacal evaporation can be a significant fraction of non-buccopharyngeal evaporation. My data imply a stepwise reliance on the three evaporative routes as ambient temperature increases. At moderate temperatures, a minimal rate of non-buccopharyngeal evaporation might be employed, with buccopharyngeal evaporation modulated to meet the remainder of the thermostatic demand. As temperature increases and buccopharyngeal evaporation is thermostatically insufficient (or perhaps inefficient), cutaneous evaporation is increased. At still higher temperatures, after cutaneous evaporation and buccopharyngeal evaporation are perhaps maximized, cloacal evaporation increases, affording that final bit of latitude with respect to temperature tolerance.

Cloacal evaporation seems to assume a similar role in Gila monsters, representing a last resort for maintaining body temperature below lethal temperatures. At moderate ambient temperatures (and therefore moderate body temperatures), Gila monsters exhibit very little cloacal evaporation, instead allowing body temperature to increase to prolong exposure to the microclimate (e.g., for foraging). When body temperature approaches the lethal limit, the Gila monster is perhaps able to suppress body temperature via cloacal evaporation and prolong exposure even further. Anecdotal field observations of Gila monsters with everted cloacae bolster this assertion.

Further evidence that cloacal evaporation is a controlled process is found in the fact that not all animals with cloacae exhibit cloacal evaporation. The Eurasian quail has a ratio of cloacal area to skin area that is roughly 2.5 times as large as that for an Inca dove. Yet Eurasian quail do not exhibit cloacal evaporation, even though they become thermally distressed at a much lower experimental temperature than either mourning doves or Inca doves.

Similarly, the rate of cloacal evaporation in ball pythons is negligible at all tested temperatures up to 42°C, despite having cloacae that are anatomically similar to those in Gila monsters. This is not a surprising finding, because ball pythons are unlikely to require cloacal evaporative cooling in nature. But the effective absence of cloacal evaporation in ball pythons, together with the suppression of cloacal evaporation below a threshold temperature in Gila monsters, suggests an adaptive role for this previously undescribed thermoregulatory mechanism.