

Review

A Review of the Physiological Mechanisms Found in Desert Beetles, Birds, Reptiles and Mammals Permitting Survival During Water Deprivation and Salt Imbalance in the Desert Environment

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Abstract: Water availability is limited in a desert ecosystem and many organisms have adapted unique mechanisms to maintain salt and water balance during periods of dehydration and rehydration. The darkling beetle (*Stenocara gracilipes*) and the Gambel's quail (*Callipepla gambelii*) both employ metabolic changes, where the darkling beetle will oxidize fat to produce metabolic water. The Gambel's quail has a field metabolic rate 60% lower than expected for a bird with similar mass, and they also regulate their globular filtration rate to limit water loss through urine. The kangaroo rat (*Dipodomys merriami*) and the desert iguana (*Dipsosaurus dorsalis*) both rely on food as their main water intake, and the kangaroo rat has very efficient kidneys to retain water and excrete excess salts while also having a lower water economy index than other mammals of similar size, indicating that they use water more efficiently. The desert iguana will primarily excrete excess potassium obtained from their diet through their nasal fluids to maintain ion balance during a rehydration period. This review showed that a variety of mechanisms have evolved in desert organisms to maintain salt and water balance during drought and rehydration.

The desert is an arduous ecosystem due to high fluctuations in temperature, relatively low humidity, limited water sources, and limited food availability. Thus, organisms face the risk of desiccation and many species have adapted unique mechanisms to maintain salt and water balance. Some of these mechanisms include metabolic changes, changes in kidney function, and changes in excretory pathways. This review compares and contrasts four distantly related species, the darkling beetle, Gambel's quail, kangaroo rat, and desert iguana that clearly demonstrate the adaptations and mechanisms used by desert-dwelling animals.

The darkling beetle (*Stenocara gracilipes*) is an example of an insect that will seek out water and can withstand many days without rehydrating within a desert environment. They are unique compared to other desert beetle species because they do not burrow underground to escape from the heat and instead only seek shaded areas, which increases their desiccation risk^{1, 2}. Previous research found that over a 10-day dehydration period, *Stenocara gracilipes* lost, on average, 17.54% of their starting body weight, 6.2% of their starting water content, and 14.6mg of their lipid content¹. The beetles quickly regained 10.9% of their original body weight when they regained access to water (Figure 1)¹. This result showed that weight lost during the dehydration period was not due to water loss alone and the beetles will oxidize lipid stores to obtain water metabolically during periods of drought. The study also found that there was a 36% decrease in hemolymph sodium levels, and it is thought that ions like sodium are taken up into the tissues during times of drought to help maintain the osmolarity of the hemolymph and then released again when the beetle is rehydrated¹. One additional mechanism found in the beetles is the production of a cuticular wax that slows down the rate of water loss through evaporation¹. The combination of these unique adaptations allows the darkling beetle to survive dehydration.

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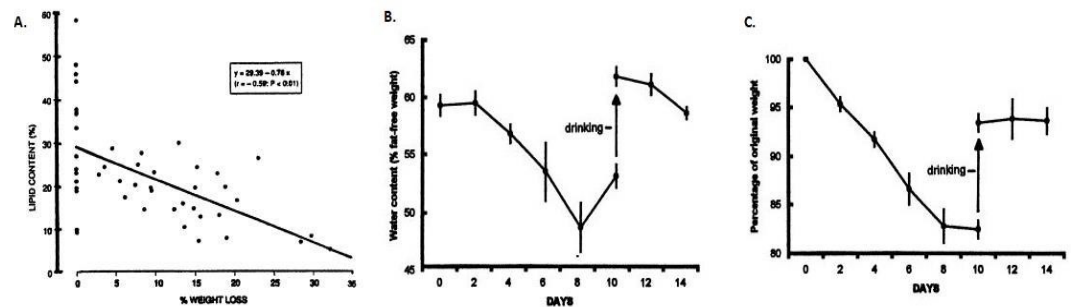


Figure 1. A) Percent lipid content decreasing with increasing percent weight loss in darkling beetles (*Stenocara gracilipes*) with a statistically significant negative correlation. B) Percent of fat-free weight loss during dehydration and regained during rehydration in darkling beetles with fat-free weight being fully regained after rehydration at day 10. C) Percent of total body weight lost in darkling beetles during dehydration and regained during rehydration. ~95% of the total body weight regained during rehydration with the ~5% deficit due to oxidization of lipids¹.

The Gambel's quail (*Callipepla gambelii*) is an example of a desert bird, and like the darkling beetle, it has acclimatized to the low water availability in deserts. Like the darkling beetle, the Gambel's quail employ metabolic changes to survive dehydration and it must also seek out water sources. The Gambel's quail survives dehydration by decreasing their field metabolic rate, which is a physiological change that conserves water by limiting waste production and lowering water loss through gas exchange^{3,4}. A research team concluded that the field metabolic rate of the Gambel's quail was 60% lower than expected for a bird of similar mass^{3,4}.

The Gambel's quail also highly regulate water loss through their kidneys by altering their glomerular filtration rate (GFR). Studies in Gambel's quail while they were anesthetized originally concluded that quail lowered their GFR by up to 80% to retain water during times of drought³. However, anesthesia can have either increasing or decreasing effects on urine production by the kidney which could have influenced this conclusion^{3,5}. A research team aimed to test if GFR is lowered in unanesthetized *Callipepla gambelii* when deprived of water to determine if low GFR was one of the main mechanisms that allowed them to survive dehydration in the desert. The researchers found that the GFR of water deprived Gambel's quail decreased to 56.5% of normal GFR when hydrated, which were similar results to previous studies that did use anesthesia (Table 1)³. However, this decrease was not significantly different than decreases in GFR observed in non-desert dwelling bird species when deprived of water (Table 1)³. The decreased GFR was due to the constricting of vessels supplying blood to the reptilian-type nephrons caused by the hormone arginine vasotocin (AVT), stopping them from filtering while the mammalian-type nephrons continued to filter^{3,6}. Further study is needed to determine why the hormone AVT does not affect the mammalian-type nephron and thus further reduce GFR during water deprivation³.

The adaptation of Gambel's quail are similar to the kangaroo rat (*Dipodomys merriami*) that have very efficient kidneys that can highly concentrate urine and produce very dry feces to retain water⁷. However, in contrast to the darkling beetle and the Gambel's quail, the kangaroo rat can survive purely off the water found in its food. A study examining the water requirements of desert kangaroo rats found that the water intake requirement was 41% less than expected for a mammal of similar mass and 25% less than other desert mammals^{7,8}. They also found that their ratio of water intake rate to field metabolism rate, known as the water economy index (WEI), was lower than expected with an average of 0.071 mL/kJ over a 15-month observation period, the lowest being 0.045 mL/kJ when eating seeds alone⁷. A low WEI indicates that less water is required by the kangaroo rat for survival, which is similar to the Gambel's quail. In contrast to the Gambel's quail, the kangaroo rat also has a countercurrent heat exchanger in their nose that captures water from humid air to reduce evaporative water loss when thermoregulating and respiring⁷.

Table 1. The change in GFR between normally hydrated (NH) and water deprived (WD) birds in domestic and wild species³.

Species	Time without H ₂ O (d)	GFR (mL/h)		Percentage of Control GFR ^a	Source
		NH	WD		
<i>Gallus gallus</i>	2	238	115.2	48	Korr 1939
<i>G. gallus</i>	1.5	262.8	196.7	72.6	Skadhauge and Schmidt-Nielsen 1967
<i>Melopsittacus undulatus</i>	3–32	7.7	7.7	...	Krag and Skadhauge 1972
<i>Dromaius novaebollanidae</i>	7	1,404.2	881.5	37.2	Dawson, Herd, and Skadhauge 1985
<i>Coturnix pectoralis</i>	21–120	50.1	29.1	41.9	Roberts et al. 1985
<i>Coturnix chinensis</i>	6–18	32.6	16.4	50.0	Roberts et al. 1985
<i>Sturnus vulgaris</i>	1.0	11.4	4.2	63.2	Roberts and Dantzer 1989
<i>Passer domesticus</i>	1.25	7.66	3.54	53.8	Goldstein and Braun 1988
<i>Callipepla gambeli</i>	4–5	17.7	7.7	56.5	This study

^a Calculated as [(GFR of control – GFR of WD)/GFR of control] × 100.

A study also found that the kangaroo rat can maintain water balance, based on metabolic water produce by their diet and the water absorbed in their food, when the humidity is above 2.2 mg H₂O/L air⁹. This finding is significantly lower compared to non-deserts rodents like white rats and hamsters, which required the humidity to be above 21 mg H₂O/L air to maintain water balance without consuming water⁹. It was also previously thought that the kangaroo rat could not tolerate high temperatures, would hide in cool and humid burrows during the day, and almost solely relied on a seed diet to obtain water. However, another study showed that they would remain in shallow burrows that could become hot and dry during the day, showing that they are resilient in high temperatures¹⁰. They also found that kangaroo rats would instead seek out insects and vegetation for food when under water-stress to maintain water balance during hot summer days¹⁰. These physiological and behavioral adaptations allow them to survive on seeds alone for most of the year and on vegetation and insects for part of the year with no free-standing water consumption.

Like the kangaroo rat, the desert iguana (*Dipsosaurus dorsalis*) receives all its water from food. However, this provides a challenge because the vegetation that they eat tends to have a higher potassium to sodium ratio compared to their normal salt levels and thus they must manage these ion fluctuations so that they can continue to use food as their primary water source^{11,12}. A research team aimed to study what pathways were employed in *Dipsosaurus dorsalis* to manage ion concentrations when rehydrating after 7-10 days with no food¹¹. When the iguanas are rehydrating, they excrete excess potassium mainly through their nasal fluids followed by their feces, but then the majority of potassium excretion switches to the urine pathway once fully rehydrated and nasal fluid becomes a minor role in potassium excretion (Figure 2)¹¹. Once the iguana is fully hydrated, potassium excretion greatly increases overall since the potassium levels have returned to normal and the water content of the urine increases due to reaching excess levels (Figure 2)¹¹. This shows that both the kangaroo rat and the desert iguana use mechanisms in their nasal passages for osmoregulation, but kangaroo rats use a countercurrent heat exchanger to save water and the desert iguana uses nasal fluids to manage salt imbalances.

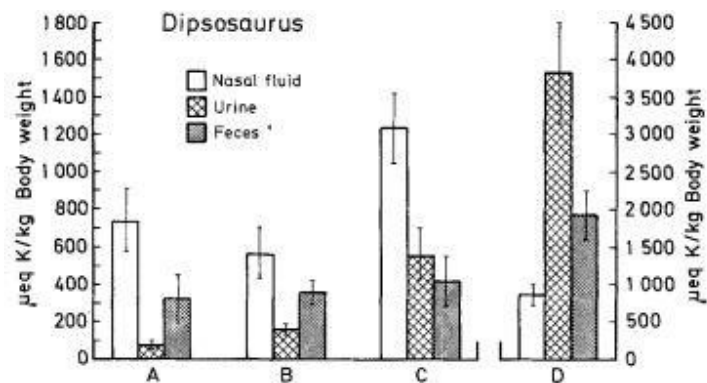


Figure 2. The amount of potassium excreted per kilogram of body weight from desert iguanas (*Dipsosaurus dorsalis*) within a 72-hour period. Group A was the most dehydrated and only had access to lettuce for two days. Group B had access to lettuce for 5 days and group C had access for 12 days. Group D iguanas were fully hydrated and had access to lettuce for 50 days¹¹.

Animals living in the desert have adapted many mechanisms to survive low water availability and acclimatize to salt and water imbalances (Table 2). The main water intake of kangaroo rats and desert iguanas are from their food, which contrasts the darkling beetle and Gambel’s quail because they both must consume water in addition to their food. The kangaroo rat and Gambel’s quail have reduced metabolic rates during dehydration to limit water loss but the kangaroo rat has a nasal countercurrent heat exchanger in addition to these adaptations. In contrast, the darkling beetle oxidizes lipids to produce metabolic water and forms cuticular wax blooms to minimize water loss and the desert iguana excretes excess potassium obtained through their diet primarily through their nasal fluid during rehydration. These combinations of similar and unique mechanisms allow these species to acclimatize during dehydration and salt imbalance for much longer than non-desert species. These adaptations are crucial for survival in desert environments where water is a scarce resource, and the relative humidity is often very low. These unique adaptations show the impressive lengths life can reach in order to survive in such an arid environment.

Table 2. Summary of osmoregulatory imbalances, physiological changes, and mechanisms.

Species	Imbalance	Length of treatment	Physiological changes	Mechanisms	Source
Darkling Beetle (<i>Stenocara gracilipes</i>)	Water Deprivation	7-10 Days	17.54% reduction in body weight, % lipid content decreased as % weight loss increased	Cuticular wax blooms, lipid oxidation for metabolic water, sodium uptake to maintain hemolymph osmolarity	Naidu 2001
Desert Iguana (<i>Dipsosaurus dorsalis</i>)	Water Deprivation followed by Excess Potassium in a lettuce diet	Water Deprivation: 10 days Fed for: A: 2 Days, B: 5 Days, C: 12 Days, D (Hydrated): 50 days	Dehydrated: primary K excretion through nasal fluids (Groups A,B,C mean nasal fluid excretion = ~725-1250 µEq K/kg) Hydrated: primary excretion through urine (Group D mean urine excretion = ~3800 µEq K/kg)	Excretion of potassium through nasal fluid, feces, and urine	Templeton et al. 1972
Kangaroo Rat (<i>Dipodomys merriami</i>)	Water Deprivation, water solely obtained through food	April - December: Seed Diet January - March: Vegetation Diet	Water intake requirement 41% lower than non-desert mammals and 25% lower than other desert mammals	Efficient kidneys highly concentrate urine, very dry feces, nasal countercurrent heat exchanger, change diet to vegetation and insects when under water-stress	Nagy et al. 1994 and Tracy and Walsberg 2002
Gambel's Quail (<i>Callipepla gambelii</i>)	Water Deprivation	4-5 Days	Glomerular filtration rate decreased to 56% of normal rate	Lower GFR by constricting blood vessels to reptilian type nephrons, lower field metabolic rate	Williams et al. 1991

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