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# The energetic savings of sleep versus temperature in the Desert Iguana (*Dipsosaurus dorsalis*) at three ecologically relevant temperatures

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**Abstract**

One of the proposed ecological functions of sleep is to conserve energy. The majority of studies that support this theory have been done on endothermic animals whose body temperatures drop during sleep due to the reduced neurological control of thermoregulation. In the present study, we examined typical temperatures to which the Desert Iguana, *Dipsosaurus dorsalis*, is exposed to in the field and found that mean high temperatures ranged from 24–58 °C throughout the active portion of the year. We also examined the ecological savings that sleep could provide for this ectothermic iguana using a closed system respirometer. We found that laboratory-acclimated iguanas are able to save significantly more (27.6%) energy by sleeping than by being awake and that field iguanas also had significant savings of energy (69.1%) while asleep. However, iguanas could save more energy by remaining awake at cooler temperatures than by sleeping at warmer temperatures. In addition, we found no correlation for time of night with metabolic rate. Our study supports the hypothesis that one potential function of sleep is to conserve energy.


*Keywords:* Desert Iguana; *Dipsosaurus dorsalis*; Metabolism; Reptile; Sleep

## 1. Introduction

Sleep, although commonly observed in nearly all vertebrates (Campbell and Tobler, 1984; Kavanau, 1998), is a perplexing behavior in nature. During sleep, animals generally cannot reproduce, forage for food, defend territories, or be vigilant for predators (Rechtschaffen, 1998). Thus, sleep seems maladaptive. Clearly, we expect that the benefits of sleep must somehow be greater than these costs. Otherwise, it should be expected that animals requiring little or no sleep would out-compete those requiring greater periods of sleep to survive.

Many theories on why animals sleep have been proposed, yet a consensus has not been reached (Meddis, 1975, 1983; Rechtschaffen, 1998). Some of these theories postulate that sleep functions in immune system repair (Benca and Quintas, 1997; Benca and Quintas, 1997; Everson and Toth, 2000), memory and sensory consolidation (Kavanau, 1998; for a contrasting view, see Siegel, 2001), and as an antipredatory behavior (Meddis, 1975; Gauther-Clerc and Tamisier, 1994). Another popular theory is that sleep serves to conserve energy (Zepplin and Rechtschaffen, 1974; Berger and Phillips, 1995; Rechtschaffen, 1998).

Conserving energy during sleep might allow animals to utilize this energy elsewhere, such as in producing or caring for offspring, searching for mates, defending territories, accelerating growth, or evading predation. Previous studies have shown that the metabolic rates of mammals during sleep can lead to substantial energetic savings (Berger and Phillips, 1995), although Rechtschaffen (1998) suggests that these savings may be minimal. Endothermic animals, such as mammals, also experience a reduction in body temperature during sleep due to the reduced neurological control of the thermoregulatory process (Rechtschaffen, 1998). Therefore, the energetic savings sleep, as applied to mammals may be more of a function of reduced body temperature than sleep itself. The hypothesis that sleep serves an energy conservation function can be more adequately studied when applied to ectothermic animals such as reptiles, whose metabolic rates change as a function of

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temperature even during wakefulness (Bennett and Dawson, 1972). Thus, the effects of sleep and the effects of temperature can be assessed separately.

Numerous metabolic studies have been conducted on reptiles in various states of activity. These studies have examined the metabolic rates of reptiles at rest (e.g., Bennett and Dawson, 1972), under a variety of dietary conditions (e.g., Nussear et al., 1998; Overgaard et al., 2002), and during exercise (e.g., Bennett and Dawson, 1972; Hancock et al., 2001). A large number of metabolic studies have been done on the Desert Iguana, *Dipsosaurus dorsalis* (Bennett and Dawson, 1972; Hancock et al., 2001; Simandle et al., 2001). To our knowledge, there have been no studies that have addressed the metabolic rates of *D. dorsalis* or any other reptile during sleep.

In the present study, we examined the metabolic rates of *D. dorsalis* during states of sleep and wakefulness at three ecologically relevant temperatures. *Dipsosaurus dorsalis* was chosen for this study because it has been shown to undergo changes in metabolic rate as a function of temperature when awake (Dawson and Bartholomew, 1958) and because a previous study on the electrophysiology of sleep in the Desert Iguana has confirmed that behavioral postures can be used to reliably distinguish the states of sleep and wakefulness (Huntley, 1987).

## 2. Methods

### 2.1. Animal subjects

Ten male Desert Iguanas (*D. dorsalis*) (ranging from 25.6 to 82.1 g, mean of 52.8 g), caught near El Mirage, San Bernardino County, CA (USA) (N34°39.27′, W117°35.78′), were maintained in captivity from May 2003 to May 2005 prior to the experiment. Iguanas were housed individually in 30 L plastic Rubbermaid containers (70L × 45W × 45H cm) with a sand substrate, basking brick, plastic PVC pipe for refugia, and a 100 W heat lamp maintained on a 14:10 light:dark cycle that kept containers between 25–45 °C. The experiment was conducted in the summer of 2005, approximately six months after the iguanas had been brought out of a three-month artificial hibernation (13–16 °C) with occasional sunlight exposure.

### 2.2. Weather and burrow temperature

For choice of temperatures used in this study, we considered temperatures typically experienced by Desert Iguanas in the wild. We obtained average highs, lows and mean temperatures for locations from which laboratory animals were collected from the El Mirage Vehicular Recreation Area (www.weather.com). Sub-surface temperatures were obtained from an artificial burrow near Gene Autry Trail in Palm Springs, California (N33°52.09′, W116°30.24′). The burrow was constructed of a 6 cm diameter PVC pipe that was buried vertically in the ground, creating a hollow tube with one opening and was located approximately one meter east of a large creosote bush to prevent burial by wind-blown sand. We affixed iButtons (Dallas Semiconductor) by Super Glue to a 2 × 40 cm wooden rod at intervals of < 1, 10, 20, and 30 cm along its length. The rod was then placed within the PVC pipe and the opening covered with a 3 mm thick piece of cardboard and a layer of sand. The iButtons used in the artificial reference burrow were set to record temperatures every 30 min from May to August, 2005.

To verify the accuracy of the artificial burrow, we compared the temperatures of this burrow to the surface body temperatures of four different Desert Iguanas (using attached iButtons) in their burrows at known depths (Revell, in prep). These iguanas were excavated on different days at approximately 0700, 0930, 1000, and 1100 h. The depths that these lizards were found at ranged from 10 cm to 38 cm. In each case, the iButtons of the four iguanas were within ±2.0 °C of iButtons at corresponding depths in the artificial burrow.

### 2.3. Metabolic chamber

We used a closed system respirometer similar to those used by Nussear et al. (1998) in their metabolic study of the Common Chuckwalla (*Sauromalus ater*), Overgaard et al. (2002) in their study of the snake, *Python molurus*, and by Simandle et al. (2001) studying the metabolism of *D. dorsalis*. The metabolic chamber was constructed of a 5 D × 42 L cm piece of translucent Tenite Butyrate pipe (US Plastic). One end was sealed with a #11 rubber stopper. The other end of the chamber was also sealed with a #11 rubber stopper which had a 1.8 cm diameter oxygen probe pushed through and sealed within the stopper. A piece of wire screen placed inside the chamber prevented the iguana from contacting the probe. A small (2.2 × 6 cm) glass vial with two holes drilled into the top was also placed inside the tube opposite the probe. This vial contained Ascarite and Drierite to remove $CO_2$ and water vapor, respectively, as used in other metabolic studies (Vleck, 1987; Simandle et al., 2001).

The entire chamber (including the vial of Ascarite/Drierite) was then placed into a 29.3 L water bath with two, 2.7 kg bricks to hold the metabolic chamber in position. A heated immersion circulator (VWR, #1112A, Westchester, PA) was used to circulate the water bath, and control temperature at 20, 30, and 40 ± 1 °C.

### 2.4. Oxygen consumption

Oxygen consumption rates were measured using a TPS 90D dissolved oxygen meter (TPS, Queensland, AU) for each iguana at 20, 30, and 40 °C during both quiescence and sleep. Sleep was confirmed visually based on sleep-specific body postures (head and body in contact with the substrate, arms generally folded back along the body, palmar surfaces dorsal) and eye state (both eyes closed for extended periods of time) which has been shown to correlate with electrophysiological sleep in *D. dorsalis* (Huntley, 1987). Measurements were taken on ten laboratory iguanas ($N = 10$) in each condition. Each iguana was randomly assigned to a treatment order. At least 24 h was given between different treatments for each lizard. Food was withheld from each lizard for 24 h prior to data collection. Metabolic rates were determined for iguanas during their normal wake cycles between (0900–400 h) and their normal sleep cycles

(1800–0500), as determined in a laboratory study in which lizards were kept on a 14:10 light:dark cycle (Revell, in prep). These cycles also correspond to a previous sleep study done on Desert Iguanas kept under similar light conditions (Huntley, 1987). To account for the confounding variable of endogenous circadian rhythms, we measured metabolic rates for nine of the iguanas while awake during their normal sleep cycles. In all cases, the data logger on the metabolic equipment recorded percent saturation of oxygen every 1 min while iguanas were awake and every 5 min while asleep. This difference occurred because iguanas frequently moved while awake, yet were often motionless for long periods of time (over 2 h) while asleep. Data were recorded for 2 h for each iguana tested.

In addition to laboratory animals, we also tested metabolic rates of animals from the field. Five field animals (ranging from 55.2 to 74.5 g, mean of 65.8 g) were captured from a separate site in Palm Springs, CA (USA) and metabolic rates were measured the same evening (asleep) and the next morning (awake). These iguanas were released the following day at the same locations where captured. Field animals were only tested at the 30 °C temperature so that they could be immediately released, and to minimize interruptions in social behavior at the field site (Muth, pers. comm). Field animals were not fasted in this study.

### 2.5. Procedures

At the start of each day, the dissolved oxygen meter was calibrated at room temperature. Next, the metabolic chamber was assembled (containing the vial of Ascarite and Drierite) and submerged in the water bath. When the oxygen reading stabilized, the instrument was recalibrated with both the chamber and $O_2$ probe at the experimental temperature. The chamber was then removed from the water bath, the solid rubber stopper removed and the iguana placed into the apparatus. The glass vial containing the Ascarite and Drierite was placed in the tube behind the iguana. The solid rubber stopper was replaced and the whole apparatus containing the iguana, was placed back into the water bath. Iguanas were allowed to acclimate to conditions within the chamber for 30 min (Simandle et al., 2001), after which readings were taken every 1 min (during quiescence) or 5 min (during sleep). Iguanas were checked approximately every 2 min while awake and once every 5 min while asleep to verify that the animal had not moved or changed posture.

### 2.6. Initial oxygen calculations

We used the ideal gas law to estimate the initial volume (ml) of oxygen available in the tube, assuming that the amount of oxygen in the tube at standard temperature and pressure (STP) was equal to 210 ml/L. We measured the amount of water displaced by the interior of the tube to calculate an initial volume (including the Ascarite/Drierite container and rubber stoppers), and estimated the amount of air displaced by the iguana using an assumed density of 0.98 g/ml (De Vera and Hayes, 1995). Finally, we adjusted for experimental pressure and temperature to calculate an initial volume of gas ($V_g$) in the tube at the start of the experiment with 100% saturation. This resulted in the equation:

$$V_g = \left((P_e)(V_e) \cdot T_e^{-1}\right)\left(K \cdot P_s^{-1}\right)$$

where $P_e$ is the experimental pressure (744.18 Torr), $V_e$ is the volume of air in the tube at experimental conditions after the air displaced by the iguana is subtracted, $T_e$ is the experimental temperature in degrees Kelvin, $K$ and $P_s$ are the standard temperature (Kelvin) and standard pressure (torr), respectively. Multiplying $V_g$ by 210 ml of $O_2$ per L of air resulted in the initial volume of oxygen in the tube at the start of the experiment. We then multiplied this volume of oxygen by the amount of oxygen consumed (difference in percent saturation between start and end) which resulted in the volume of oxygen consumed during the experiment in ml.

### 2.7. Metabolic calculations

Metabolic rates were calculated from the volume of oxygen consumed by dividing by the mass of the iguana and the time of the experiment. We considered the initial volume of water and $CO_2$ to be negligible due to the presence of Drierite and Ascarite (De Vera and Hayes, 1995).

In addition to calculating individual metabolic rates, we also used a Pearson correlation to compare the metabolic rates of each iguana during sleep as a function of time of night. This was done by compiling data from all lizards from all nighttime hours. These rates were not computed for iguanas that were awake because of the short treatment time used for that state.

Furthermore, to test whether metabolic differences were more related to endogenous rhythms or behavioral state (asleep vs. awake), we examined the metabolic rates of iguanas kept awake during their normal sleep times. This was accomplished by placing the iguana in the metabolic tube and keeping the lights on. If iguanas began to sleep, we gently rotated the tube so that they stayed awake. Iguanas rarely moved during this treatment.

### 2.8. Data analysis

Data were log-transformed and found to meet the assumptions for parametric statistics. One iguana was removed from the analysis because it continually moved while awake, which resulted in abnormally high oxygen consumption readings at 30 and 40 °C.

Metabolic rates calculated for each laboratory iguana were analyzed by a $2 \times 3$ repeated measures ANOVA, treating both state (asleep vs. awake) and temperature (20, 30, and 40 °C) as within-subjects factors. Related samples $t$-tests were used to compare the metabolic rates of iguanas sleeping vs. awake at each of the experimental temperatures. We also used related samples $t$-tests to analyze the metabolism of iguanas asleep at 20 °C vs. those awake at 40 °C. Likewise, we analyzed metabolism for iguanas awake at 20 °C vs. those asleep at 40 °C. We also computed metabolic rates as a function of time

(5 min intervals) by pooling all iguanas for each temperature and subjected these data to a Pearson correlation. We compared the metabolic rates at 30 °C for iguanas that were awake during the night portion of the sleep cycle to those awake and asleep during their normal cycles by using a one-way repeated measures ANOVA treating state (awake at night, awake normal, asleep normal) as a within subjects factor.

Data for field iguanas were compared to those of laboratory-acclimated animals by a 2×2 ANOVA treating state (asleep vs. awake) as a within-subjects factor, and location (laboratory vs. field) as a between-subjects factor. An individual, related samples *t*-test was also computed comparing iguanas that were awake to those asleep from the field.

All analyses were run using SPSS 11.5 with $\alpha=0.05$. We confirmed that assumptions of parametric tests were met before conducting statistical tests. For significant ANOVA results, post-hoc multiple comparisons (Bonferroni) were used to examine differences between specific days. Effect sizes (adjusted partial $\eta^2$ values) are reported for significant ANOVA effects to indicate the approximate amount of variance explained by the independent variables. When multiple independent variables were considered, effect sizes provided by SPSS were adjusted by dividing each partial $\eta^2$ by the sum of all partial $\eta^2$ values for effects tested.

## 3. Results

Weather and burrow temperature data revealed that *D. dorsalis* are typically exposed to mean high temperatures from 24.6 to over 40 °C during their normal activity and sleeping cycles (Fig. 1). These results suggest that Desert Iguanas in the field are regularly exposed to the temperatures we used as treatments.

Metabolic rates of iguanas asleep and awake changed significantly as a function of temperature in laboratory animals (Fig. 2). There was a significant affect of sleep state ($F_{1,8}=10.75$, $P=0.011$, adjusted partial $\eta^2=0.25$) and temperature ($F_{2,16}=30.16$, $P<0.001$, adjusted partial $\eta^2=0.35$) on metabolic rate. We found that the overall mean metabolic rate of

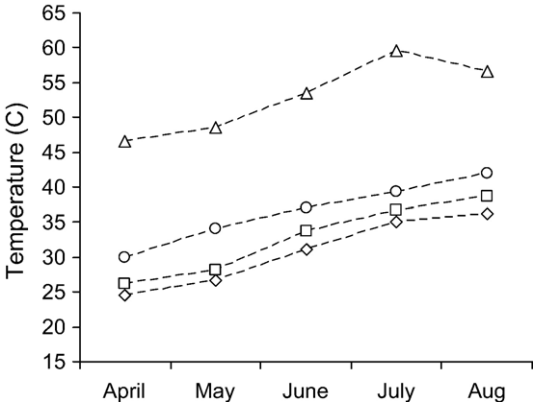


Fig. 1. Temperature data obtained from an artificial burrow in Palm Springs, CA. Symbols represent mean highs for <1 cm (△), 10 cm (○), 20 cm (□), and 30 cm (◇) below the surface.

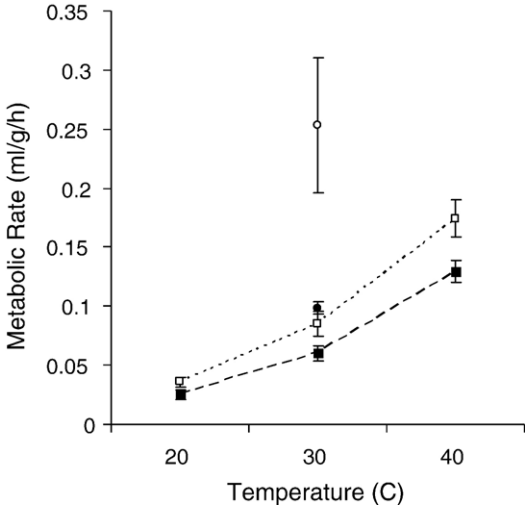


Fig. 2. Mean (±1 SE) metabolic rates for lab-maintained and field-captured *D. dorsalis* at three temperature while asleep and awake. $N=10$ for laboratory iguanas and $N=5$ for field iguanas. Boxes represent laboratory animals asleep (■) and laboratory animals awake (□). Circles represent field animals asleep (●) and field animals awake (○).

laboratory sleeping iguanas was 27.6% less than iguanas which remained awake (Table 1). Individual related samples *t*-tests revealed a difference between state at 40 °C, with those asleep having significantly lower metabolic rates than those awake ($t_8=10.42$, $P<0.001$). Field animals showed a larger difference (69.1%) between rates, with those asleep having significantly lower metabolic rates than those that remained awake (Table 1). However, we feel these results are not as reliable as tests done on laboratory-acclimated individuals because we are unaware of the conditions of exposure prior to testing. Mean metabolic rates for iguana state at the different temperatures tested are provided in Table 1. The total amount of oxygen consumed ranged from 0.4% to 12.2%. Oxygen saturation remained greater than 87.8% at all times and thus, hypoxia was unlikely to be a factor affecting metabolic rate in any treatment.

We found significantly lower metabolic rates for iguanas that were asleep at 20 °C than for iguanas that were awake and tested at 40 °C ($t_8=10.36$, $P<0.001$). Likewise, iguanas that were awake and tested at 20 °C had significantly lower metabolic rates than animals asleep at 40 °C ($t_8=5.5$, $P=0.001$) (Fig. 2).

Table 1
Mean (±1 SE) metabolic rates expressed in ml of $O_2 \cdot g^{-1} \cdot h^{-1}$ consumed for desert iguanas that were asleep and awake at three temperatures

| Temp. | Laboratory iguanas | | | Field iguanas | | |
|---|---|---|---|---|---|---|
| (°C) | Sleep | Awake | Sig. | Sleep | Awake | Sig. |
| 20 | 0.025±0.004 | 0.036±.004 | NS | | | |
| 30 | 0.060±0.006 | 0.085±.010 | NS | 0.103±0.008 | 0.149±0.067 | $P<0.001$ |
| 40 | 0.129±0.009 | 0.174±.016 | $P<0.001$ | | | |
| Mean | 0.071 | 0.098 | | | | |

$N=9$ laboratory-maintained iguanas, and $N=5$ for field-captured iguanas. Sig. = Significance.

Pearson correlation coefficients for sleeping iguanas at 20 °C ($r=-0.15$; $P=0.058$), 30 °C ($r=-0.07$; $P=0.335$), and 40 °C ($r=0.03$; $P=0.696$) demonstrated that metabolic rate and time of day were unrelated.

To test if metabolic rates were primarily the result of endogenous rhythm, we compared iguanas that were kept awake at night to those asleep and awake under normal conditions previously described. There was a significant difference in metabolic rates between sleeping iguanas and those kept awake at night ($F_{2,16}=9.38$, $P=0.002$, adj partial $\eta^2=0.54$). In contrast, a-posteriori Bonferroni tests, demonstrated that metabolic rates for iguanas kept awake at night did not differ significantly from iguanas awake during the day.

There was a significant difference of the main effect of field vs. laboratory iguanas on metabolic rate at 30 °C ($F_{1,12}=22.38$, $P<0.001$, adjusted partial $\eta^2=0.65$) and for the main effect of sleep state in field and laboratory animals ($F_{1,12}=18.18$, $P=0.001$, adjusted partial $\eta^2=0.60$; Fig. 2). Mean (±SE) metabolic rates for laboratory iguanas (0.073± 0.007 g/ml/h) were less than half of those of field iguanas (0.175±0.040 g/ml/h).

## 4. Discussion

In the current study we found that the Desert Iguana can conserve approximately 27.6% more energy by sleeping than by being awake. Differences between state in field animals is as much as 69.1%. However, we recognize that the previous conditions (i.e. temperature exposure and food consumption) of field animals were unknown and therefore, metabolic comparisons between the groups may not be appropriate. In any case, our results are consistent with the hypothesis that one of the main functions of sleep may be to conserve energy.

The energetic savings that we report in this study cannot be attributed to endogenous rhythmic differences. In comparing laboratory-acclimated iguanas that were kept awake at night to those that were asleep at night, we found a significant difference in metabolic rates with the former group having much higher rates. Iguanas that were kept awake, however, might have higher metabolic rates due to the methodology of keeping them alert; rotating the tube in this experiment might frighten the iguanas and drive metabolic rates upward. This method, however, is generally accepted as the most favorable in comparison to other methods, such as electric shock (Rechtschaffen and Bergman, 2002; Sauer et al., 2004). Testing metabolic rates without this or similar method, however, is difficult since the iguanas quickly fall asleep during these hours (T.R. pers. obs.).

Although in this study sleep does appear to provide a conservation of energy, the question remains whether an energetic savings of almost 28% is of sufficient benefit to explain the function of sleep. Two separate laboratory studies have shown that Desert Iguanas sleep between 12 h/day (Huntley, 1987) and 14 h/day (Revell, in prep) depending on day length at approximately 30 °C. Based on our metabolic readings, Desert Iguanas can save 14.2% more energy in a day by sleeping for 12 h than by remaining awake all 24 h. These savings increase to 17.2% for iguanas that sleep for 14 h/day at 30 °C.

Our results also suggest that there is a larger metabolic savings associated with temperature than with behavioral state. Although a sleeping iguana may conserve more energy than one that is awake, iguanas that remain awake can move to cooler temperatures with the changing environment whereas sleeping lizards cannot. This could reduce metabolism via behavioral thermoregulation. Based on reference burrow temperatures taken from the Palm Springs study site, this would be possible since there are wide ranges of temperatures available that vary by depth and time of day. In a laboratory setting, Desert Iguanas have been shown to select sleep sites with a mean temperature of 36 °C, in cages where temperatures typically ranged from 23 to 57 °C (Revell, in prep). Thus, saving energy by sleeping may not be as significant as staying awake and being able to move to cooler temperatures. For *D. dorsalis*, it may be even more beneficial to sleep in a cooler, stable environment. The metabolic savings at different temperatures greatly exceeds that of being asleep. Sleeping, however, might conserve energy that can later be spent on foraging for food, defending territories, or increasing reproductive efforts.

In conclusion, the data presented in this study support the hypothesis that sleep does conserve energy in *D. dorsalis*. However, more energy may actually be conserved by the behavioral response of seeking cooler, more constant ambient temperatures than by sleeping in conditions of variable temperatures.

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