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# Effect of tidal cycle and food intake on the baseline plasma corticosterone rhythm in intertidally foraging marine iguanas

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## Abstract

In most species, plasma levels of baseline glucocorticoids such as corticosterone (B) have a circadian rhythm. This rhythm can be entrained by both photoperiod and food intake and is related to aspects of energy intake and metabolism. Marine iguanas (*Amblyrhynchus cristatus*) offer a unique opportunity to better understand the relative importance of the light:dark cycle versus food intake in influencing the rhythm in baseline B in a natural system. Compared to other species, food intake is not as strictly determined by the phase of the light:dark cycle. Animals feed in the intertidal zone so feeding activity is heavily influenced by the tidal cycle. We measured baseline plasma B levels in free-living iguanas over several 24-h periods that varied in the timing of low tide/foraging activity. We found that baseline B levels were higher during the day relative to night. However, when low tide occurred during the day, baseline B levels dropped coincident with the timing of low tide. Whether the baseline B rhythm (including the drop during foraging) is an endogenous rhythm with a circatidal component, or is simply a result of feeding and associated physiological changes needs to be tested. Together, these data suggest that the baseline B rhythm in marine iguanas is influenced by the tidal cycle/food intake as well as the light:dark cycle.

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## 1. Introduction

In most vertebrate species, plasma levels of baseline glucocorticoids such as corticosterone (B) and cortisol fluctuate dramatically over a 24-h period (e.g., Breuner et al., 1999; Dauphin-Villemant and Xavier, 1987; Krieger, 1974; Krieger, 1979; Romero and Remage-Healey, 2000; Summers and Norman, 1988). In many cases, this rhythm has been shown to be circadian, meaning that in the absence of certain external cues, the rhythm persists and has a period of approximately 24 h (Aschoff, 1979). The primary external cue (zeitgeber) that entrains the diel glucocorticoid rhythm is the

light:dark cycle (Krieger, 1979) and lesions to the suprachiasmatic nucleus abolish the diel glucocorticoid rhythm (Abe et al., 1979).

The diel glucocorticoid rhythm is also influenced by food intake and there is a bi-directional relationship between food intake and glucocorticoids (Dallman et al., 1993). In rats and humans, basal glucocorticoids peak right before or at feeding (for review, see Krieger, 1979). Both fasting and, in some cases, feeding appear to stimulate increased plasma glucocorticoids (Dallman et al., 1993) such that the peak associated with feeding in animals may be a consequence both of the preceding fast and the feeding. In turn, glucocorticoids modulate food intake and have well known effects on intermediary metabolism, including increased catabolism by muscle and adipose tissue and increased gluconeogenesis in the liver (Hadley, 2000). The effects of glucocorticoids are also modulated by insulin.

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The timing of food intake can act as a zeitgeber and can override entrainment by the light:dark cycle (Boulos and Terman, 1980; Leal and Moreira, 1997; Stephan, 1982). For example, in rats fed ad libitum, baseline levels of glucocorticoids peak at the onset of the activity period when animals first begin to eat. However, if feeding each day is experimentally restricted to a 2-h interval out of phase with the onset of activity, the baseline glucocorticoid rhythm adjusts so that the peak in baseline glucocorticoids occurs just before the time of food presentation (Krieger, 1974). The ability of food intake to act as a zeitgeber, plus the well known effects of glucocorticoids on energy metabolism, suggest that the diel rhythm in baseline glucocorticoids functions primarily in some aspect of energy intake, mobilization, and/or deposition (Dallman et al., 1993). Furthermore, shifts in food intake are often accompanied by shifts in food anticipatory activity (Hau and Gwinner, 1996; Mistlberger, 1994) and core body temperature (Fuller and Sulzman, 1982; Krieger, 1979) suggesting that the rhythm in baseline glucocorticoids could also be related to food seeking behavior and thermoregulation. For example, studies indicate that plasma glucocorticoids (i.e., B) and body temperature are positively correlated in several ectotherms (Girling and Cree, 1995; Tyrrell and Cree, 1998).

It is difficult to distinguish among different potential determinants and functions of the diel glucocorticoid rhythm because in most species, the light:dark cycle and food intake are tightly coupled temporally. Marine iguanas (*Amblyrhynchus cristatus*) provide a natural system to examine the relative roles of photoperiod versus schedule of food intake in the rhythm of baseline B (the major circulating glucocorticoid in reptiles). Unlike most terrestrial vertebrate species, food intake in marine iguanas is influenced not only by the light:dark cycle but also by the tidal cycle. The majority of marine iguanas feed solely on macrophytic algae exposed only at low tide (in the intertidal zone) and therefore foraging is heavily influenced by the rhythm of the tides (Buttner and Dawson, 1993; Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). Low tide occurs approximately every 12.4 h so low tide (and consequently foraging behavior) occurs about 50 min later each successive day.

Marine iguanas on Genovesa island, for example, have an endogenous bitidal foraging rhythm (Wikelski and Hau, 1995). Animals spend the night in bushes approximately 30 m from the shoreline. After daybreak, animals begin to move across the sand to the foraging sites located in the intertidal zone. The exact time that animals move to the shoreline depends on the timing of low tide. At the shoreline, animals bask on rocks near the foraging sites or feed in the intertidal zone, depending on the timing of low tide. At the end of the day, animals return to the bushes for the night. Actual

feeding occurs for about 2 h around low tide. They only feed during the day: as low tide advances into the evening, marine iguanas switch from afternoon foraging to morning foraging. Field enclosure experiments indicated that this bitidal foraging rhythm was endogenous and Wikelski and Hau (1995) proposed that the rhythm results from an interaction between circadian and circatidal systems.

Since the timing of feeding is heavily influenced by the tides, and food intake has been shown in other species to alter the diel rhythm of baseline glucocorticoids, we hypothesized that the tidal cycle would influence the rhythm of baseline B levels. In Expt. 1, we measured baseline B every 6 h on two different days that had opposite tidal cycles but the same photoperiod to maximize our chances of teasing apart the effects of tidal cycle and light:dark cycle. In Expt. 2, we measured baseline B on two different days, sampling more frequently than in Expt. 1 to provide a finer time resolution. Expt. 2 indicated that B levels dropped significantly at the time of low tide, which is when animals are feeding in the intertidal zone. To further confirm the results of Expt. 2 and to better understand the mechanism underlying the drop in B at low tide, in Expt. 3 we measured the ability to secrete B in response to a stressor in animals collected at the time of low tide that were either about to forage, or were actually foraging. Together, these data indicated that marine iguanas possess a diel rhythm in baseline B levels that seems to have a tidal component. The degree to which the diel rhythm is endogenous needs to be tested.

## 2. Materials and methods

Marine iguanas were studied on two different islands in the Galápagos: Genovesa (study site: Salvaje de corazón, 0°19' N; 89°57' W) and Santa Fe (study site: Miedo, 0°50' S, 90°5' W). Times for high and low tide were obtained from the tidal chart of the Ecuadorian Navy for the islands of San Cristobal at Bahia de Agua (0°54' S, 89°37' W) and Genovesa at Darwin Bay. We used tide charts from San Cristobal for Santa Fe because the latter were unavailable. All procedures were conducted in accordance with guidelines from the American Society of Ichthyologists and Herpetologists and approved by the Tufts, Princeton University, and Arizona State University Institutional Animal Care and Use Committees with permission from the Galápagos National Park Service, Ecuador.

### 2.1. Experiment 1 – Genovesa

We collected blood samples every 6 h over a 24-h period from marine iguanas on Genovesa Island on

December 8–9, 1998 and on December 15–16, 1998. We sampled on these two dates because they had opposite tide cycles yet photoperiod was the same. On December 8, low tide was at noon and midnight; on December 15, low tide was at dawn and dusk. Since December is the breeding season and territorial males often fast several days (Trillmich and Trillmich, 1984), we collected only females. Males and females were sexed by noting body size, coloration, and probing the depth of the cloacal pouch. Sample size for each time point was 7–8 females. Animals were selected at random and captured by hand or noose. Adult marine iguanas have no natural predators, do not appear to be afraid of humans, and are usually caught within 30 s of approach. Immediately upon capture, each iguana was placed head-first into an opaque cloth bag and a blood sample from the caudal vein was taken with 24-gauge needles and heparinized capillary tubes. Animals were bled as quickly as possible (almost always within 3 min from capture), weighed, measured for snout-to-vent length, and released. Also, animals were marked with paint to avoid recapture at subsequent sampling times. Blood was maintained on ice for up to 6 h. Blood was centrifuged and the plasma fraction was frozen at  $-4^{\circ}\text{C}$  until permanent storage at  $-20^{\circ}\text{C}$ . This study was done several months after the El Niño of 1997–1998 and animals had a mean Body Condition Index of  $59 \pm 0.5$  (computed as  $[\text{body mass}/\text{snout-vent length}^3] \times 10^6$ ) indicating good health (Wikelski and Trillmich, 1997). The behaviors of animals are synchronized such that animals sampled on a particular day at a particular time were exhibiting similar behaviors (e.g., resting in bushes, foraging, moving toward intertidal zone, etc.).

Frozen plasma samples were shipped to Arizona State University where they were analyzed for plasma corticosterone using column chromatography and radioimmunoassay following the methods of Moore (1986). Samples were assayed in duplicate using an antibody from Endocrine Sciences (Calabasas, CA, antibody B21-42). All samples were assayed in a single assay and the intraassay coefficient of variation was 14%.

## 2.2. Experiment 2 – Santa Fe

We collected blood samples every 3 h in a 24-h time period from iguanas on Santa Fe Island in May 17–18, 1998 and in early June, 1999. In 1998, low tide was at 13:30 h and in 1999 low tide was at 10:30 h. We selected animals at random and captured them by hand within 30 s of approach. During the El Niño conditions of spring 1998, animals that were in poor body condition were excluded from the analysis. Poor condition was determined with a Body Condition Index and all animals with conditions less than 35 were excluded since animals worse than this have altered B responses, presumably due to starvation conditions (Romero and

Wikelski, 2001). Consequently, sample sizes for 1998 ranged from 5 to 8 animals and in 1999 ranged from 7 to 8 at each time point. Male and female B levels do not differ in marine iguanas (Romero and Wikelski, 2001), so sex was ignored.

Immediately upon capture, we placed each iguana head-first into an opaque cloth bag and took a blood sample from the caudal vein. Blood was collected into 2-ml heparinized vacutainer tubes. The initial blood sample was collected within 3 min of capture for all iguanas. All initial samples were grouped together for statistical purposes. Upon conclusion of blood sampling, iguanas were weighed, measured for their snout-to-vent length, sexed, and released. Blood samples were maintained on ice for up to 12 h and then centrifuged at approximately 400g for 6 min. A broken centrifuge on Santa Fe in 1998 required plasma to be separated from blood cells with gravity by leaving samples overnight at  $4^{\circ}\text{C}$ . Frozen plasma samples were shipped to Tufts University where corticosterone was analyzed by radioimmunoassay using a previously described method (Wingfield et al., 1992). Each sample was assayed in duplicate using an antibody from Endocrine Sciences (Calabasas, CA, antibody B21-42). Intraassay and interassay coefficients of variation were 6 and 12%, respectively.

## 2.3. Experiment 3 – Genovesa: acute stressor and foraging

Marine iguanas on Genovesa were captured on May 21, 1999 either prior to their initiation of foraging (captured from 10:30 to 12:00;  $n = 10$ ) or while they were actively foraging (captured from 12:30 to 13:30;  $n = 8$ ). Low tide was at noon. All these animals were placed in cloth bags, bled initially within 3 min of capture, and bled again after 15 and 30 min of restraint in the cloth bags. Other methods including processing of blood samples and radioimmunoassays were as described in Expt. 2. As described above, male and female B levels do not differ in marine iguanas, so sex was ignored.

## 2.4. Statistical methods

B data were log transformed to satisfy assumptions of parametric statistics. Experiments 1 and 2 were analyzed with two-way ANOVAs with time of day and date as factors. In experiment 2, we calculated a Z-correlation coefficient comparing the means at the different time points to test for correlations between the two hormone profiles. Experiment 3 was analyzed with a repeated measures ANOVA with behavior (foraging versus preforaging) and handling stress (baseline versus 30 min capture stress) as factors. Significant ANOVAs were followed by post hoc tests (Student–Newman–Keuls);  $p < .05$  was considered significant.

### 3. Results

#### 3.1. Experiment 1

In samples collected from Genovesa, baseline B levels varied significantly according to time of day ( $F[3, 69] = 4.83, p < .005$ ) and post hoc tests indicated that levels were significantly higher at noon relative to midnight (Fig. 1). The overall pattern did not vary according to the time of low tide (no interaction between time of day and sampling day ( $F[3, 69] = .314, p = .81$ )). Interestingly, baseline B levels were higher when low tide was at noon (December 8, 1998) than when low tide was at dawn/dusk (December 15, 1998) (effect of sampling day:  $F[1, 69] = 18.6, p < .001$ ).

#### 3.2. Experiment 2

In samples collected from Santa Fe, baseline B levels varied across the 24-h sampling period (Fig. 2) (effect of time of day:  $F[7, 99] = 5.76, p < .001$ ). There was no effect of year on baseline B ( $F[1, 99] = .18, p = .67$ ) but there was a marginally significant interaction between time of day and year ( $F[7, 99] = 2.06, p = .055$ ). To better understand the marginally significant interaction, the two baseline B profiles were standardized according to time of low tide (Fig. 2C). The resultant profiles were significantly correlated (when standardized to low tide,  $Z = 2.22, p < .027$ , count = 8; when not standardized to low tide,  $Z = 1.73, p = .47$ , count = 8). Post hoc tests indicated that in both years, levels were higher during the day relative to the night with a significant difference in plasma B at low tide versus 3 h before low tide (Fig. 2C).

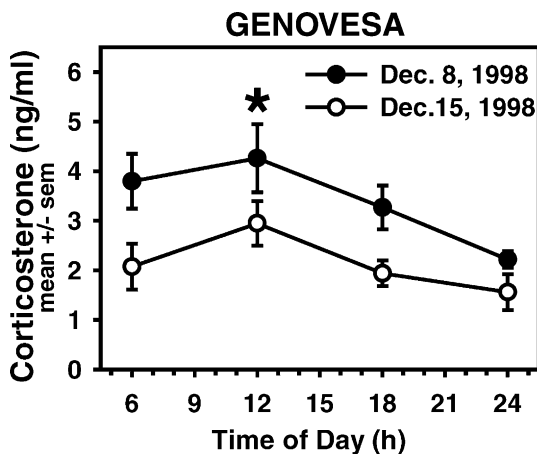


Fig. 1. Plasma levels of baseline corticosterone from Genovesa collected in 1998 (Expt. 1).  $N = 7$  to  $8$  for each time point. For both profiles, \* indicates that levels at 12h are significantly greater than 24h. Levels on December 8 are significantly higher than levels on December 15 (see text).

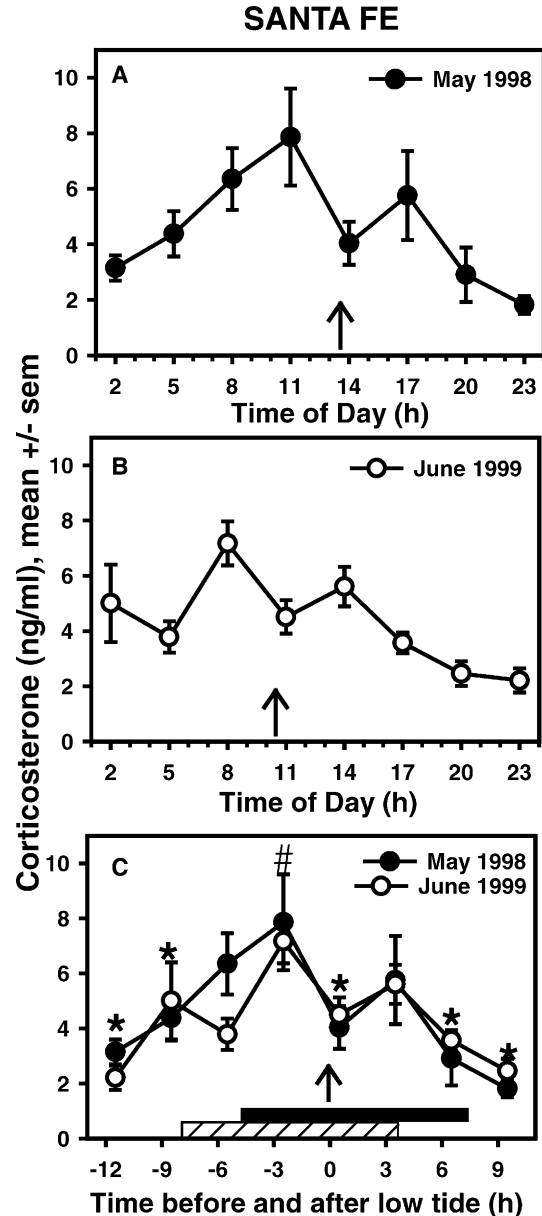


Fig. 2. Plasma levels of baseline corticosterone from Santa Fe (Expt. 2). Arrows indicate time of low tide. (A) Profile from May 1998.  $N = 5$ – $8$  for each time point. (B) Profile from June 1999.  $N = 7$ – $8$  for each time point. (C) Profiles from May 1998 and June 1999 normalized according to the timing of low tide. Bars indicate the time span from 6 to 18 h for each corticosterone profile (stippled bar, 1999; black bar, 1998). The results of some of the significant post hoc tests are indicated with symbols. For both profiles, the point indicated with # is significantly different than points indicated with \* ( $p < .05$ ).

#### 3.3. Experiment 3

B levels were higher in preforaging animals at all time points (Fig. 3) ( $F[1, 16] = 12.23, p < .003$ ). In addition, there was an overall significant effect of 30 min of handling stress ( $F[2, 32] = 5.11, p < .02$ ). There was no significant interaction between foraging behavior and the stress response ( $F[2, 32] = 1.75, p = .19$ ). To better

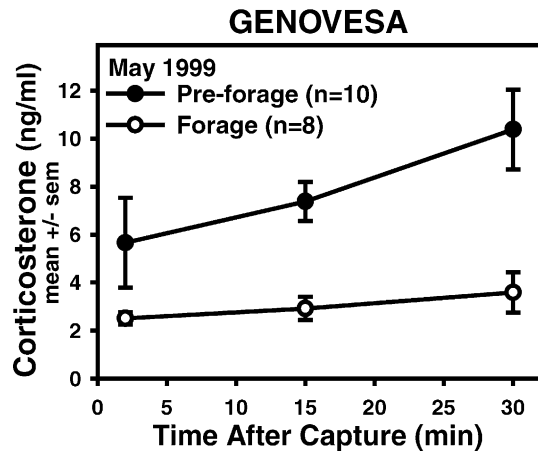


Fig. 3. Baseline and stress levels of plasma corticosterone in animals shortly before ( $n = 10$ ) and during foraging ( $n = 8$ ) on Genovesa (Expt. 3). Samples were collected from 10:30 to 13:30 h. Low tide was at noon. Capture (restraint) stress increased plasma corticosterone in animals captured before foraging but not during foraging (see text).

understand which group contributed most strongly to the overall significant stress response, we did one-way ANOVAs for each group with stress as a factor. Preforaging animals had significantly greater B levels with handling stress ( $p = .037$ ) but foraging animals did not ( $p = .21$ ).

#### 4. Discussion

Marine iguanas represent a natural system to examine the relative roles of photoperiod versus schedule of food intake in the rhythm of baseline B because unlike most vertebrate species, food intake is influenced not only by the light:dark cycle but also by the tidal cycle. Free-living marine iguanas possess a diel rhythm in basal levels of plasma B with higher levels during the day relative to the night. However, when low tide occurred during the day, basal B levels dropped coincident with the timing of low tide and the commencement of foraging. Together, these studies indicate that basal B is influenced by both the light:dark cycle and the tidal cycle. It is not clear if the drop in B at low tide is the result of an endogenous circadian rhythm or a direct effect of feeding.

Experiment 1 demonstrated that a dramatic shift in the timing of low tide, and hence, feeding activity, did not result in a dramatic shift in the overall pattern of the rhythm of baseline B. Regardless of the timing of low tide, baseline levels of B in marine iguanas were higher during the day relative to the night. This pattern was also found in the study done in Santa Fe (Expt. 2) and is similar to what has been found in captive lizards, in which the highest B levels were found during daylight hours (Callard, 1972; Dauphin-Villemant and Xavier,

1987; Girling and Cree, 1995; Summers and Norman, 1988). Therefore, the tidal cycle did not completely override the influence of the light:dark cycle on plasma B levels. However, the cycles of baseline B from Expt. 2, with finer time resolution, revealed that baseline B peaked shortly before the timing of low tide. Expt. 3 provided additional evidence that B drops as animals begin to forage at the time of low tide, and indicated that the drop is due to a suppression of B secretion.

The diel rhythm in baseline B could be the result of both endogenous and exogenous rhythms. Wikelski and Hau (1995) showed that the bitidal foraging rhythm was endogenous with both circadian and circatidal components. For example, animals temporarily housed in outdoor enclosures (deprived of cues from the intertidal zone) still showed a rhythm of bitidal foraging behavior comparable to free-ranging animals. It is possible that the diel rhythm of B has a similar regulation. The overall elevation in B during daylight hours could be a circadian rhythm and the drop in B at low tide could be circatidal with feeding acting as a circatidal zeitgeber. However, it is also possible that the drop in B at low tide is simply a metabolic response to the onset of feeding and other feeding-associated cues. Whether the diel rhythm in baseline B is endogenous can be tested with enclosures. If baseline B levels in animals in enclosures still peak before, and then drop coincident with, low tide, then cues associated with the tidal zone (such as feeding or body temperature changes) do not directly determine the B pattern.

Regardless of whether the diel B rhythm is endogenous, the rhythm in baseline B could function in the bitidal foraging rhythm. Although the peak in B that precedes the timing of low tide could stimulate feeding (Dallman et al., 1993), adrenalectomy in rats does not affect food-anticipatory activity (Stephan et al., 1979), suggesting that the baseline B rhythm is a consequence and not a cause of the feeding schedule. This could be tested by elevating plasma B with noninvasive transdermal patches (Knapp and Moore, 1997) and examining changes in locomotory activity and feeding.

Alternatively, the baseline B rhythm could be related to body temperature and/or thermoregulatory behavior. Although the relationship between body temperature and B levels in reptiles have not been systematically examined, evidence in other reptiles indicate that body temperature might profoundly affect B secretion. In a species of nocturnal gecko (*Hoplodactylus maculatus*), plasma B levels and body temperatures are higher during the day than during the night, and daytime body temperatures are correlated with baseline B levels (Girling and Cree, 1995). In wild male tuataras, body temperatures are also positively correlated with baseline B levels (Tyrrell and Cree, 1998). Therefore, perhaps changes in body temperature directly affect plasma B levels. In marine iguanas, the drop in plasma B at the

time of low tide, followed by a slight increase 3 h later (Expt. 2) could be a direct consequence of body temperature changes induced by foraging behavior. While foraging, animals are subject to wave activity and cold water which causes body temperatures to drop (Bartholomew, 1966; Trillmich and Trillmich, 1986). This could also explain why preforaging animals have higher plasma B than foraging animals, and why the stress response to confinement is reduced in foraging animals (Expt. 3). In addition, two of us (L.M. Romero and M. Wikelski, in prep.) have evidence that the B responses to confinement stress is higher during the day than during the night (when body temperature is 10 °C lower relative to the day).

It is also possible that plasma B affects body temperature by modulating behavioral thermoregulation. As ectotherms, marine iguanas bask to increase body temperature (Bartholomew, 1966). Animals with a higher body temperature have a faster rate of digestion which allows them to eat more food during a foraging bout (Wikelski et al., 1993). Since ambient temperatures peak at midday (Wikelski and Wrege, 2000), basking is presumably most efficient at this time (Buttemer and Dawson, 1993). Therefore, perhaps the diel rhythm of baseline B is related to basking and/or digestion. It is well known that stress-induced B levels produce catabolic effects and inhibit digestion but non-stressful, diel fluctuations in B stimulate anabolic processes (Dallman et al., 1993; Sapolsky, 1992).

In addition to documenting a baseline B rhythm, we found a significant difference in overall plasma B levels between the two tide cycles measured one week apart on Genovesa. Overall, baseline B levels were higher when low tide was at noon (December 8), than when high tide was at noon (December 15). If baseline B levels are influenced by body temperature changes, perhaps the difference between tidal cycles is related to differences in foraging from one week to the next. Foraging is reduced when high tide is at noon: animals are not warm enough to feed at the morning low tide, and animals cannot efficiently digest (which influences how much they can ingest) when low tide is late in the afternoon (Wikelski and Trillmich, 1994). To better understand the differences in absolute levels of baseline B found in Expt. 1, we need to assess the diel B rhythm by sampling at several time points across several different tidal cycles to determine if the overall levels in baseline B fluctuate randomly or predictably.

Despite the unusual schedule of food intake in marine iguanas, the diel rhythm of B is similar in many respects to B rhythms found in more typical model organisms like mice, rats and humans: food intake is associated with changes in baseline B, and B peaks right before feeding (Krieger, 1974). This similarity in baseline B further illustrates how marine iguanas are a promising natural model for understanding the determinants and

functions of the diel B rhythm. Future experimental studies should determine whether the rhythm is endogenous. We suggest that the baseline B rhythm is related to some aspect of foraging but experimental studies are necessary to differentiate among the effects of foraging, body temperature, and thermoregulatory behavior on baseline B levels. Administration of adrenocorticotropin (ACTH) to foraging animals should elucidate whether the drop in B at low tide is due to adrenal insensitivity to ACTH to further understand the mechanism underlying changes in baseline B. Finally, study of the diel B rhythm in subtidally foraging animals that always forage at midday could further test whether food intake influences the diel B rhythm in marine iguanas.

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