

Effects of foraging mode and season on the energetics of the Marine Iguana, *Amblyrhynchus cristatus*

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Summary

1. Marine Iguanas (*Amblyrhynchus cristatus*) inhabiting the rocky shores of the Galápagos Islands apply two foraging strategies, intertidal and subtidal foraging, in a seasonal climate. Effects of both foraging strategy and seasonality on the daily energy expenditure (DEE) were measured using doubly labelled water.

2. Difference in foraging mode did not result in significant differences in DEE.

3. On Santa Fé the DEE in the warm season was significantly higher than in the cool season ($67.8 \pm 21.8 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$ vs $38.0 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$). This difference can be explained by body temperature. A model estimate of the body temperature was used to predict monthly DEE figures, giving a year round budget. On average a 1-kg iguana would need only 47 kJ day^{-1} , or 17 mJ year^{-1} . This is lower than previous estimates in which body temperatures were not taken into account.

4. The water flux of the Marine Iguana increases with increasing foraging time. The linear rise per minute foraging is roughly two times as high for subtidally foraging animals as for intertidal foragers.

Key-words: Daily energy expenditure, doubly labelled water, Galápagos, temperature, water flux

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Introduction

The Marine Iguana (*Amblyrhynchus cristatus*) is endemic to the Galápagos Islands, inhabiting the rocky shores in dense populations. It lives on a herbivorous diet throughout life, feeding on macrophytic algae along the rocky shores of the islands (Bartholomew, Bennet & Dawson 1976; Trillmich & Trillmich 1986; Wikelski, Gall & Trillmich 1993). Two foraging strategies are distinguished, intertidal and subtidal foraging. In intertidal foraging the animals exploit algae which are exposed during low tide in the intertidal zone. During subtidal foraging the iguanas swim out on the sea and make several dives, to feed under water on submerged algae beds (Trillmich & Trillmich 1986).

In earlier studies, measurements of oxygen consumption of the Marine Iguana during swimming (Vleck, Gleeson & Bartholomew 1981) and walking (Gleeson 1979) were carried out. Gleeson (1979) combined the information on locomotory costs and concluded that the swimming mode of foraging only

amounts to 8% of the daily energy budget. These costs are much lower than the 30% of the daily energy budget needed for foraging on land as calculated hypothetically by Gleeson. Subsequently, energy expenditure measurements on free-living marine iguanas using the doubly labelled water (DLW) technique showed that the costs of foraging, in agreement with Gleeson (1979), account for only 8% of the total daily energy expenditure (Nagy & Shoemaker 1984). In the study of Nagy & Shoemaker (1984), however, no attention was given to foraging mode. Thus the earlier suggestions of Gleeson (1979) could not be confirmed in detail.

Apart from the foraging mode the seasonal environment of the Galápagos Islands (Colinvaux 1984) could have large energetical repercussions for the marine iguana. In a number of studies in more temperate regions seasonality was clearly reflected in the energy expenditures of the reptiles studied (Rismiller & Heldmaier 1991; Nagy & Shoemaker 1975). Also in tropical regions distinct seasonal patterns in energetics have been observed. The Frillneck Lizard *Chlamydosaurus kingii*, in northern Australia, has a four-fold difference in the field metabolic rate between seasons (Christian & Green 1994; Christian,

Griffiths & Bedford 1996). The varanid lizards *Varanus gouldii* and *V. panoptes* both have a three times higher energy expenditure between seasons (Christian *et al.* 1995). So a seasonal environment can have a clear effect on the energy expenditure. However, van Marken Lichtenbelt *et al.* (1993) did not find a season related energy expenditure variation in the Green Iguana *Iguana iguana* on the tropical island of Curaçao.

The aim of the present study is two-fold. The first aim is to fill the gap in the understanding of energetic costs and gains to animals using the intertidal or subtidal foraging strategy by exploring their energetic consequences. Is subtidal foraging really energetically cheaper, as predicted, and if so, why do iguanas still forage in the intertidal? Secondly, we want to evaluate the effect of seasonality in climate on the daily energy budget of marine iguanas. Seasonal differences in food availability and the thermal environment can lead to variations in the DEE.

Materials and methods

STUDY AREA AND TIME

Fieldwork was carried out in the Galápagos Archipelago during the first half of 1994. Study sites were located on Genovesa at 'Salvaje de Corazon' (0°19'N, 89°59'W) and on Santa Fé at 'Miedo' (0°50'S, 90°02'W) (for population characteristics at these sites see Laurie 1990; Laurie & Brown 1990; Wikelski, Carrillo & Trillmich 1997). The Galápagos experiences a seasonal climate. In general, the first five to six months of the year are sunny and warmer (hot season) than the second half of the year when it is much more overcast and cooler (*Garua*) (Colinvaux 1984). In this *Garua* period sea-water temperatures are lower and the nutritional supply for algal growth is better than in the hot season (Houvenaghel 1978). Investigations were made on Genovesa during January 1994. On Santa Fé, work was done during February and June 1994. January and February fell in the hot season, while June fell in the cool *Garua* season.

DOUBLY LABELLED WATER PROCEDURE

Measurements of the daily energy expenditures using doubly labelled water (DLW) were carried out with male Marine Iguanas of similar body mass. During the periods of measurement the males were not reproductively active.

On Genovesa six intertidally foraging and six lagoon foraging male Marine Iguanas were measured. On Santa Fé six subtidal animals and five intertidal animals were caught and injected in February. In June on Santa Fé 16 animals were used for the experiments, 8 subtidal and 8 intertidal. Lagoon foragers of Genovesa fed submerged in a small lagoon with an approximate depth of 0.5 m.

With respect to their foraging mode, lagoon feeders are comparable to subtidal feeders from Santa Fé. However, the lagoon feeders swim less than the subtidals and dive to 0.5 m maximum, while subtidals forage at depths of 3–5 m. Furthermore the water temperatures in the lagoon are higher than in the open sea and the algal composition tends to be different from the subtidal areas (Wikelski *et al.* 1997).

At the end of the day, a little after sunset, the animals were caught by having their tails grasped. The body mass and snout–vent length (SVL) were measured to the nearest g and mm, respectively. The animals were marked with a painted code. A blood sample was taken from the tail vein, for the determination of the background isotopic levels. As in all blood samples taken, six subsamples were flame sealed in 25- μ l capillaries. The animals were then injected intraperitoneally with a mixture of H_2^{18}O (50 atom percentage) and $^2\text{H}_2\text{O}$ (99.9 atom percentage) weighed to the nearest mg. On Genovesa this mixture contained 0.72 g of H_2^{18}O and 0.18 g $^2\text{H}_2\text{O}$ administered per kg body mass. On Santa Fé in February the amounts injected for the subtidals were 0.56 g H_2^{18}O and 0.14 g $^2\text{H}_2\text{O}$ per kilogram body mass, and for the intertidals they were 0.4 g H_2^{18}O and 0.1 g $^2\text{H}_2\text{O}$ per kilogram body mass. In June the subtidal foraging animals were injected with 1.4 g H_2^{18}O and 0.35 g $^2\text{H}_2\text{O}$ per kilogram body mass, the foraging animals were injected with 1.0 g H_2^{18}O and 0.25 g $^2\text{H}_2\text{O}$ per kilogram body mass. Subtidally foraging animals were injected with a higher dose, because of an expected higher water flux, which dilutes the isotopes more rapidly.

After the injection the animals were left overnight in an enclosure for 8–10 h to let the isotopes equilibrate with the body water. In the morning an initial blood sample was taken and the animals were released where they were caught. Some 6–8 days after the initial blood sample, before sunrise, a final blood sample was taken and the animal was weighed again. Analyses of the blood samples were carried out according to the procedures described in Masman & Klaassen (1987), at the Centre for Isotope Research, University of Groningen, the Netherlands.

For the calculations of the CO_2 production it was assumed that the oxygen and deuterium pool are equal in volume. Calculations were done following equation 34 of Lifson & McClintock (1966). The oxygen dilution space was taken as the total body water figure. Corrections for fractionation, $f_1 = 0.93$, $f_2 = 0.99$ and $f_3 = 1.04$ as in Lifson & McClintock (1966), were included in the calculation. Conversion of ml CO_2 to kJ was done by applying the factor 21.7 J ml^{-1} CO_2 . Evaporation loss of water in free-living Marine Iguanas was assumed to account for 40% of the water efflux (Shoemaker & Nagy 1984). The data are presented as $\text{kJ kg}^{-1} \text{day}^{-1}$. In comparisons between animals $\text{kJ kg}^{-0.8} \text{day}^{-1}$ is used according to the relationship between energy expenditure and body

mass in Nagy (1982). The water flux data presented in the results are the effluxes calculated from the $^2\text{H}_2$ dilution in the body water, the original water content of the animal determined by ^{18}O dilution and changes in body mass (Nagy & Costa 1980).

BEHAVIOURAL OBSERVATIONS

During the DLW measurement period, activities of the injected animals were recorded. Observers positioned on high coastal rock formations could easily overview the basking and foraging areas of the Marine Iguanas, using binoculars. In January and February total feeding times were noted, while during the June experiments basking, walking, swimming and feeding were recorded separately. Distances walked were measured by counting steps (conversion to metres, three steps of the same leg = 1 m, based on separate subsamples) and by plotting the distance covered on a detailed map of the area. Foraging animals were observed continuously. Swimming and diving times in the subtidal foragers and grazing times in the intertidal foragers were recorded to the nearest minute.

Results

ENERGY EXPENDITURES

The lagoon foragers on Genovesa in the warm season had a mean daily energy expenditure (DEE) of $35.8 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$ (Table 1). The intertidal foraging animals on Genovesa had a slightly lower DEE $27.3 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$, though this is not significantly lower than the DEE of the lagoon feeders (Mann–Whitney U -test, $U = 8$, $n_1 = 3$, $n_2 = 5$, $P > 0.05$).

In February 1994, also during the warm season, energy measurements were carried out on Santa Fé. Here the mean DEE of six subtidally foraging Marine Iguanas was found to be $64.5 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$. In the

same period the DEE of three intertidally foraging animals was $74.4 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$, a value not significantly different from that of the subtidal foragers (Mann–Whitney U -test, $U = 10$, $n_1 = 3$, $n_2 = 6$, $P > 0.05$).

During the cool season in June 1994, the DEE was determined for 14 Marine Iguanas. Of seven subtidal foraging marine iguanas the mean DEE was $39.5 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$. The seven intertidal animals had a comparable outcome of the mean DEE, $36.4 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$. These values are not significantly different (Mann–Whitney U -test, $U = 30$, $n_1 = 7$, $n_2 = 7$, $P > 0.05$).

Since no statistical differences between the DEEs of the separate foraging strategies were found, the data from the different foraging modes were pooled. With this information a comparison between the islands Genovesa and Santa Fé during the warm season was made. On Genovesa the mean DEE regardless of the foraging strategy was $32.6 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$. In February on Santa Fé in the same warm season the mean DEE of all the measured animals was $67.8 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$. The energy expenditure on Santa Fé was significantly higher than the energy expenditure on Genovesa (Mann–Whitney U -test, $U = 65$, $n_1 = 8$, $n_2 = 9$, $P < 0.01$ two-tailed).

A seasonal comparison of the combined intertidal and subtidal foragers of February and the combined foragers of June shows that the mean DEE of all the measured animals on Santa Fé in June, the cool season, is $38.0 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$. The mean DEE on Santa Fé in the warm season was $67.8 \text{ kJ kg}^{-0.8} \text{ day}^{-1}$, a much higher value. The difference between the two seasons on Santa Fé is statistically significant (Mann–Whitney U -test, $U = 110$, $n_1 = 9$, $n_2 = 14$, $P < 0.01$ two-tailed).

ACTIVITIES

The average time per day spent on foraging activities by the intertidal and lagoon feeders on Genovesa did not show any significant differences (Mann–Whitney U -test, $U = 22$, $n_1 = 6$, $n_2 = 6$, $P > 0.05$ two-tailed). On Santa Fé both in February and in June the subtidals use significantly more time for foraging activities than the intertidal foragers (Mann–Whitney U -test, $U = 0$, $n_1 = 5$, $n_2 = 5$, $P = 0.01$ two-tailed and $U = 55.5$, $n_1 = 8$, $n_2 = 8$, $P = 0.01$ two-tailed) (Table 2).

The intertidal feeders on Genovesa (January) forage significantly longer than the intertidal feeders on Santa Fé. This holds for both February (Mann–Whitney U -test, $U = 28$, $n_1 = 5$, $n_2 = 6$, $P = 0.02$) and June (Mann–Whitney U -test, $U = 42.5$, $n_1 = 6$, $n_2 = 8$, $P = 0.02$ two-tailed). Foraging time of lagoon feeders on Genovesa and subtidal foragers on Santa Fé in February was not significantly different (Mann–Whitney U -test, $U = 19$, $n_1 = 5$, $n_2 = 6$, $P > 0.05$ two-tailed). However, compared with Santa Fé in June, the lagoon feeders spend more time forag-

Table 1. The mean daily energy expenditures as measured by the DLW method, of the Marine Iguanas on Genovesa and Santa Fé categorized per island and foraging strategy. Significant differences as given by the Mann–Whitney U -test (further statistics are mentioned in the text)

Island	Month	Foraging	Mean daily energy expenditure				
			$\text{kJ kg}^{-1} \text{ day}^{-1}$	SD	$\text{kJ kg}^{-0.8} \text{ day}^{-1}$	SD	n
Genovesa	January	Lagoon	37.5	22.3	35.8	21.7	5
		Intertidal	30.2	4.7	27.3	4.6	3
			34.8	17.5	32.6 ^a	17.2	8
Santa Fé	February	Subtidal	55.8	11.8	64.5	13.5	6
		Intertidal	64.3	29.9	74.4	36.7	3
			58.6	18.1	67.8 ^{ab}	21.8	9
Santa Fé	June	Subtidal	34.0	14.4	39.5	16.7	7
		Intertidal	31.0	15.2	36.4	18.0	7
			32.5	14.3	38.0 ^b	16.8	14

^aSignificant difference ($P < 0.02$) between Genovesa January and Santa Fé February.

^bSignificant difference ($P < 0.02$) between Santa Fé February and Santa Fé June.

ing than the subtidals (Mann–Whitney U -test, $n_1 = 6$, $n_2 = 8$, $U = 42$, $P = 0.02$ two-tailed).

A comparison of the intertidal foraging times in February and June on Santa Fé does not reveal any significant differences (Mann–Whitney U -test, $U = 29$, $n_1 = 5$, $n_2 = 8$, $P > 0.05$ two-tailed). The subtidal foragers, however, use significantly more time for foraging in February during the warm season than in June during the cool season (Mann–Whitney U -test, $U = 36$, $n_1 = 5$, $n_2 = 8$, $P = 0.02$ two-tailed).

Activity level differences do not contribute significantly to the explanation of the variation in DEE as is shown by the Spearman rank correlation $r_s = 0.08$, $n = 38$, $P > 0.05$ two-tailed.

WATER FLUXES AND BODY WATER

Water fluxes of all labelled Marine Iguanas were

Table 2. Mean time spent on foraging activities per day. Values are given for the foraging strategies per island, which are compared within an island using the Mann–Whitney U -test. For significant differences the P -values are given

Island	Month	Foraging	Foraging time		
			min day ⁻¹	SD	n
Genovesa	January	Lagoon	40.6	21.5	6
		Intertidal	55.7	33.4	6
Santa Fé	February	Subtidal	57.5 ^a	30.8	5
		Intertidal	8.3 ^a	4.1	5
Santa Fé	June	Subtidal	18.9 ^b	7.6	8
		Intertidal	10.6 ^b	1.5	8

^aSignificant difference on Santa Fé in February ($P < 0.05$).

^bSignificant difference on Santa Fé in June ($P = 0.05$).

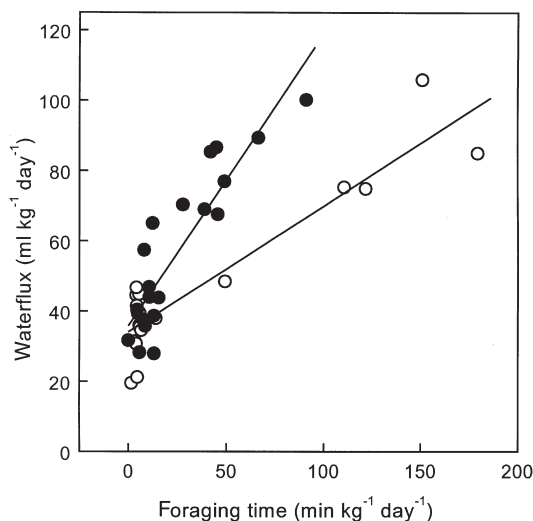


Fig. 1. The relation between the time spent on foraging activities (min kg⁻¹ day⁻¹) and the water flux in ml kg⁻¹ day⁻¹. Unfilled circles indicate intertidal foragers, filled circles combined subtidal and lagoon foragers. Least squares regressions are calculated separately for both strategies. The slope of the subtidal lagoon line is significant larger than the slope of the intertidal line ($F = 17$, $P < 0.001$).

related to the mean foraging times per day as is shown in Fig. 1, including all intertidal, subtidal and lagoon feeders. Water flux per day expressed as ml water out per kg body mass increases with the time spent on foraging (min kg⁻¹ day⁻¹). The relationship for the intertidal foragers is described by: water flux (ml kg⁻¹ day⁻¹) = 0.36 x foraging (min kg⁻¹ day⁻¹) + 34.0, $R^2 = 0.84$, $F = 98$, $n = 19$, $P < 0.001$. The combined subtidal and lagoon foragers have a linear relationship of: water flux (ml kg⁻¹ day⁻¹) = 0.83 x foraging (min kg⁻¹ day⁻¹) + 35.8, $R^2 = 0.78$, $F = 70$, $n = 20$, $P < 0.001$. The intercepts for both the relationships are statistically indistinguishable ($F = 0.2$, $P > 0.05$) but the slopes of the lines are significantly different ($F = 22$, $P < 0.001$). The slope of the subtidal and lagoon foragers is more than twice as steep, indicating higher water fluxes compared with the intertidal foragers at the same foraging time.

Mean body water as percentage of the body mass differed significantly between lagoon foragers and intertidal foragers on Genovesa in January. Lagoon foragers had a higher body water percentage than the intertidal foragers (Table 3). On Santa Fé both in February and in June the body water percentages of the two foraging strategies were not statistically different (Table 3). There is a difference in the body water percentages when comparing the means of February and June regardless of the foraging strategies applied. The iguanas have a significantly lower body water content in June than in February (Table 3).

Discussion

In this study the possible energetical consequences of the mode of foraging, reflected in the DEE of the Marine Iguana, were investigated. In three independent experiments (Genovesa during January, Santa Fé during February and June) no significant differences in DEEs between the two foraging modes were found. An explanation for these results is that the differences in energy expenditure between the foraging modes is low compared with the total DEE. This can be shown by detailed observations of the activities of the iguanas in June in combination with relationships on energy expenditure and swimming or walking from Marine Iguanas from the literature (Gleeson 1979; Vleck *et al.* 1981). The results of calculations on the energy spent on foraging activities expressed as percentage of the total DEE, listed in Table 4, show firstly no significant differences between foraging mode (Mann–Whitney U -test $U = 26.5$, $n_1 = 7$, $n_2 = 7$, $P = 0.8$). Secondly, daily costs of locomotion are only a very small part of the total daily energy expenditure. On average only 3.5% of the daily energy expenditure was due to locomotory activities. This value does not obey the general trend observed by Christian, Baudinette & Pamula (1997) that the amount of energy spent on locomotory activities by lizards is a significant portion of the energy budget (about 20%),

although values smaller than 5% during inactive periods, are given in their data set.

Subtidal foragers travel twice the distance intertidals do, using approximately the same amount of energy. This is also reflected in the time spent on foraging. Subtidals forage significantly longer than intertidals per day. This has some ecological implications. The fact that the conditions, expressed as percentage body water, are not different between intertidal and subtidal foragers indicates that energy intake is not larger in subtidals. However, in an earlier study it was

shown that subtidal foragers have a higher rate of intake than intertidal foragers (Wikelski *et al.* 1993), but this possibly can be attributed to temporal differences in algae stock. It can be concluded that subtidals can exploit a larger area than the intertidal animals at the same cost, or can forage longer for the same cost, or can sustain activity on a lower-quality food source than intertidals. It should be noted that intertidal foraging is more efficient in time: whereas subtidals swim 30–50% of the time, intertidal foragers can feed almost continuously.

There is a large and significant difference between the daily energy expenditures in the warm season (February) and the cool season (June) on Santa Fé. The much lower energy expenditure in June can be attributed to a lower mean body temperature during the cool season. A body temperature difference of 5.4 °C between June and February using a Q_{10} of 2.9 (Bennet, Dawson & Bartholomew 1975), or of 5.9 °C lower with a Q_{10} of 2.67 (Nagy & Shoemaker 1984), would explain the decrease of the expenditure from 68 to 38 kJ kg^{-0.8} day⁻¹. A similar difference in body temperature was found in the Galápagos Land Iguana (*Conolophus pallidus*) on Santa Fé. Body temperatures during daytime were up to 4.5 °C lower during the cool season than during the warm season in the Land Iguana (Christian, Tracy & Porter 1983).

With meteorological data of 1994 collected at the Darwin Research Station on Santa Cruz an attempt was made for a rough prediction of the body temperatures of

Table 3. The mean body water as the percentage of body mass. The foraging strategies per island are tested for differences and the season means for Santa Fé are compared with the Mann Whitney *U*-test

Island	Month	Foraging	Mean percentage body water		
			% (w/w)	SD	<i>n</i>
Genovesa	January	Lagoon	83.0 ^a	0.8	5
		Intertidal	79.4 ^a	1.8	6
Santa Fé	February	Subtidal	80.9	1.6	6
		Intertidal	78.0	1.9	5
		Combined	79.6 ^b	2.2	11
Santa Fé	June	Subtidal	75.5	2.4	8
		Intertidal	75.2	2.5	8
		Combined	75.3 ^b	2.4	16

^aLagoon and intertidal differ significantly ($P = 0.002$).

^bTotal of Santa Fé in February differs significantly from total Santa Fé in June ($P < 0.02$).

Table 4. The costs of locomotion for the animals in June on Santa Fé are calculated and given as the percentage of the measured DEE values. Grazing costs only constitute walking costs during grazing. The relationship for walking is, cost of transport = 3.77 M^{-0.25} (ml O₂ g⁻¹ km⁻¹) (Gleeson 1979), Vleck *et al.* (1981) give the following relationship for swimming, cost swimming = 0.31 M^{-0.56} (ml O₂ kg⁻¹ m⁻¹). RQ = 0.93 (Nagy & Shoemaker 1984). The distances covered per activity are given in metres (m). All figures are per day

Strategy	kg							Totals			
		Walking		Swimming		Grazing		Locomotion		Animal	
		m	kJ	m	kJ	m	kJ	m	kJ	kJ	%
Intertidal	2.3	67	2.0	7	0.1	20	0.6	95	2.6	93	3
	2.0	48	1.3	0	0.0	20	0.5	67	1.8	48	4
	2.7	57	1.9	0	0.0	18	0.6	75	2.5		
	2.3	37	1.1	0	0.0	17	0.5	54	1.6	43	4
	2.4	56	1.7	29	0.3	11	0.3	96	2.3	57	4
	2.0	44	1.2	33	0.3	16	0.4	93	1.9	27	7
	1.9	37	1.0	29	0.3	15	0.4	82	1.6	83	2
	2.3	34	1.0	49	0.5	14	0.4	97	1.9	133	1
Subtidal	2.0	34	0.9	42	0.4	6	0.2	82	1.4	43	3
	2.0	35	0.9	131	1.3	3	0.1	169	2.3		
	1.8	27	0.7	133	1.3	7	0.2	167	2.1	96	2
	2.2	67	1.9	89	0.9	12	0.3	167	3.1	91	3
	2.2	35	1.0	140	1.4	0	0.0	175	2.4	51	5
	2.2	40	1.1	236	2.4	10	0.3	285	3.8	55	7
	2.4	31	0.9	182	2.0	0	0.0	213	2.9	127	2
	2.1	31	0.8	151	1.5	0	0.0	182	2.3	45	5

the Marine Iguanas. The night body temperature is assumed to be the same as the night air temperature (defined as the mean of the air temperature at 1800 h (t_{18}) and at 0600 h (t_6) the next morning). The body temperature during daytime is assumed to be the preferred body temperature of 35 °C (White 1973) when there was sun (number of sun hours (s)). For the remaining part of the day the air temperature at midday (1200 h (t_{12})) was taken as the body temperature. These assumptions amount to the following equation for the body temperature T_B .

$$T_B = \frac{12 \times \frac{(t_6 + t_{18})}{2} + s \times 35 + (12 - s) \times t_{12}}{24}. \quad \text{eqn 1}$$

With this equation estimates were obtained for the mean body temperatures throughout the year. According to the equation there is a mean body temperature difference of 4.7 °C between February and June. This temperature decline explains 75% of the lower energy expenditure of the Marine Iguanas in June, using a Q_{10} of 2.67 (Nagy & Shoemaker 1984). The year round calculated body temperatures (using monthly mean meteorological data) were next used to predict an annual energy budget. With the relationship between body mass and oxygen consumption of a resting Marine Iguana having a body temperature of 25 °C, as given by Bartholomew & Vleck (1979), and the Q_{10} of 2.67 (Nagy & Shoemaker 1984), the monthly resting metabolic rates could be calculated. Following Nagy & Shoemaker (1984) the DEE of a marine iguana is 1.7 times resting metabolic rate (RMR) so the estimates had to be multiplied with 1.7 to obtain the DEE.

This information is plotted in Fig. 2, and shows that the monthly DEE values actually measured by the DLW measurements in February and June resemble the DEE values calculated via the Bartholomew & Vleck relationship, very closely (both estimates fall within the standard error of the mean). On average an iguana of 1 kg expends 47 kJ day⁻¹ on a yearly basis, calculated via the Bartholomew & Vleck equation. From Nagy & Shoemaker (1984) it can be concluded that a 1-kg iguana has an energy expenditure of 70 kJ day⁻¹ on a yearly basis. This value is higher than our DLW finding, but in this estimate no temperature constraints are included, as we infer to occur during the cool season.

The clearly lower energy expenditures on Genovesa in January, compared with the energy expenditures on Santa Fé, cannot be explained by differences in activity levels. Again, body temperature could cause a part of the difference. Body temperature measurements in 1993 revealed that daily mean body temperatures were 2.3 °C lower on Genovesa than on Santa Fé (M. Wikelski, unpublished data).

Water fluxes per day increase with increasing foraging time per day. However there is a clear difference in the slopes between the animals foraging under

water and the animals foraging in the intertidal. Water fluxes of the subtidals and lagoon foragers are the same without foraging. When foraging, however, water fluxes of the subtidal and lagoon foragers increase more than two times as much with increasing foraging time than the water fluxes of the intertidal foragers. This relationship between water flux and foraging time suggests that during feeding water accompanying the algae is ingested; for iguanas foraging submerged this will presumably be more than for the intertidal foragers above the water surface. Shoemaker & Nagy (1984) arise at the same conclusion in a study on the osmoregulation in the Marine Iguana. The higher water fluxes in the subtidal and lagoon foragers could provoke extra costs incurred by extra excretion of salt via the nasal salt gland (Schmidt-Nielsen & Fänge 1958) in order to remain in salt balance.

An estimate of the body condition is the percentage of body water. Here we do find a significant difference between the seasons: in February animals are found to have a percentage of body water 5% higher (80%) than in June (75%). When assuming that the hydration of the fat-free mass is constant, the percentage of body fat must have increased by 5–6% from February to June. For a 1-kg iguana that means a deposit of 66 g fat. Body lipid stored without concomitant storage of water gives a maximal change of energy content of 39 kJ g⁻¹ (Blaxter 1989). With an efficiency of 80% at synthesis (Blaxter 1989) this means an extra net energy intake of 32 kJ day⁻¹ over a 100-day period. This implies an extra net energy intake of 40–65%, above the amount required for the DEE, depending on

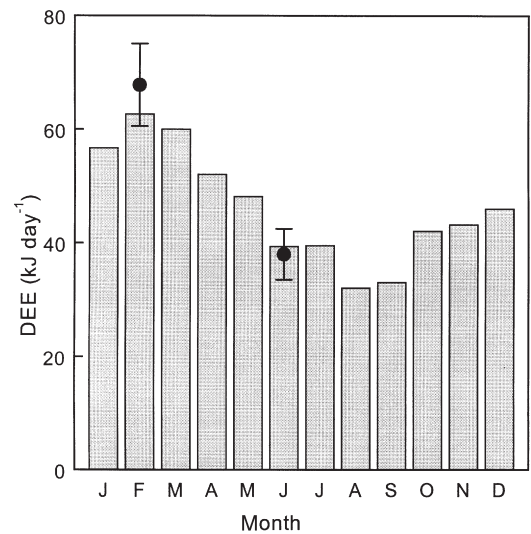


Fig. 2. The DEE (kJ day⁻¹) of a 1-kg Marine Iguana on Santa Fé during 1994. The values were calculated via the equation for RMR at 25 °C given by Bartholomew & Vleck (1979) using a Q_{10} of 2.67 and a DEE of 1.7 × RMR (Nagy & Shoemaker 1984), with body temperatures predicted by the equation given in the text. The overall mean DEEs (kJ day⁻¹) on Santa Fé in February and June are given for a 1-kg Marine Iguana, with standard errors.

the season. However, more accurate measurements on body condition and food intake are needed to confirm these findings.

February is the time after the mating season, when the males are still recuperating from a period with little foraging activity and with a low algal production. In June the nutritional status of the sea water is conducive to a high algal production and the iguanas can devote all their time to foraging. This then can result in a better body condition with a higher body fat percentage and lower total body water content than in February. This trend is in accordance with the findings of Trillmich (1983), that the body mass of the Marine Iguana males increases during the period from May to October.

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References

- Bartholomew, G.A. & Vleck, D. (1979) The relation of oxygen consumption to body size and to heating and cooling in the Galápagos marine iguana, *Amblyrhynchus cristatus*. *Journal of Comparative Physiology B* **132**, 285–288.
- Bartholomew, G.A., Bennett, A.F. & Dawson, W.R. (1976) Swimming, diving and lactate production of the marine iguana, *Amblyrhynchus cristatus*. *Copeia* **1976**, 709–720.
- Bennett, A.F., Dawson, W.R. & Bartholomew, G.A. (1975) Effects of activity and temperature on aerobic and anaerobic metabolism in the Galápagos marine iguana. *Journal of Comparative Physiology* **100**, 317–329.
- Blaxter, K. (1989) *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge.
- Christian, K.A. & Green, B. (1994) Field metabolic rates and water flux of the frilled lizard *Chlamydosaurus kingii*. *Herpetologica* **50**, 274–281.
- Christian, K., Tracy, C.R. & Porter, W.P. (1983) Seasonal shifts in body temperature and use of microhabitats by Galápagos land iguanas (*Conolophus pallidus*). *Ecology* **64**, 463–468.
- Christian, K.A., Corbett, L., Green, B. & Weavers, B. (1995) Seasonal activity and energetics of two species of varanid lizards in tropical Australia. *Oecologia* **103**, 349–357.
- Christian, K.A., Griffiths, D. & Bedford, G.S. (1996) Physiological ecology of frillneck lizards in a seasonal tropical environment. *Oecologia* **106**, 49–56.
- Christian, K.A., Baudinette, R.V. & Pamula, Y. (1997) Energetic costs of activity by lizards in the field. *Functional Ecology* **11**, 392–397.
- Colinvaux, P.A. (1984) The Galápagos climate: present and past. *Key Environments: Galápagos* (ed. R. Perry), pp. 55–69. Pergamon Press, Oxford.
- Gleeson, T.T. (1979) Foraging and transport costs in the Galápagos marine iguana, *Amblyrhynchus cristatus*. *Physiological Zoology* **52**, 549–557.
- Houvenaghel, G.T. (1978) Oceanographic conditions in the Galápagos archipelago and their relationships with life on the islands. *Upwelling Ecosystems* (eds R. Boje & P. Tomczak), pp. 181–200. Springer Verlag, Berlin.
- Laurie, W.A. (1990) Population biology of marine iguanas (*Amblyrhynchus cristatus*). I. Changes in fecundity related to a population crash. *Journal of Animal Ecology* **59**, 515–528.
- Laurie, W.A. & Brown, D. (1990) Population biology of marine iguanas (*Amblyrhynchus cristatus*). II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. *Journal of Animal Ecology* **59**, 529–544.
- Lifson, N. & McClintock, R. (1966) Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology* **12**, 46–74.
- Marken Lichtenbelt, W.D., Wesselingh, R.A., Vogel, J.T. & Albers, K.B.M. (1993) Energy budgets in free-living green iguanas in a seasonal environment. *Ecology* **74**, 1157–1172.
- Masman, D. & Klaassen, M. (1987) Energy expenditure during free flight in trained and free-living eurasian kestrels (*Falco tinnunculus*). *Auk* **104**, 603–616.
- Nagy, K.A. (1982) Energy requirements of free-living iguanid lizards. *Iguanas of the World* (eds G. M. Burghardt & A. S. Rand), pp. 49–59. Noyes Publications, Park Ridge, NJ.
- Nagy, K.A. & Costa, D.P. (1980) Water flux in animals: analysis of potential errors in the titrated water method. *American Journal of Physiology* **238**, R454–R465.
- Nagy, K.A. & Shoemaker, V.H. (1975) Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiological Zoology* **48**, 252–262.
- Nagy, K.A. & Shoemaker, V.H. (1984) Field energetics and food consumption of the Galápagos marine iguana, *Amblyrhynchus cristatus*. *Physiological Zoology* **57**, 281–290.
- Rismiller, P.D. & Heldmaier, G. (1991) Seasonal changes in daily metabolic patterns of *Lacerta viridis*. *Journal of Comparative Physiology B* **161**, 482–488.
- Schmidt-Nielsen, K. & Fänge, R. (1958) Salt glands in marine reptiles. *Nature* **182**, 783–785.
- Shoemaker, V.H. & Nagy, K.A. (1984) Osmoregulation in the Galápagos marine iguana, *Amblyrhynchus cristatus*. *Physiological Zoology* **57**, 291–300.
- Trillmich, K.G.K. (1983) The mating system of the marine iguana (*Amblyrhynchus cristatus*). *Zeitschrift für Tierpsychologie* **63**, 141–172.
- Trillmich, K.G.K. & Trillmich, F. (1986) Foraging strategies of the marine iguana *Amblyrhynchus cristatus*. *Behavioral Ecology and Sociobiology* **18**, 259–266.
- Vleck, D., Gleeson, T.T. & Bartholomew, G.A. (1981) Oxygen consumption during swimming in Galápagos marine iguanas and its ecological correlates. *Journal of Comparative Physiology* **141**, 531–536.
- White, F.N. (1973) Temperature and the Galápagos marine iguana – insights into reptilian thermoregulation. *Comparative Biochemistry and Physiology* **45A**, 503–513.
- Wikelski, M., Gall, B. & Trillmich, F. (1993) Ontogenetic changes in food intake and digestion rate of the herbivorous marine iguana (*Amblyrhynchus cristatus*). *Oecologia* **94**, 373–379.
- Wikelski, M., Carrillo, V. & Trillmich, F. (1997) Energy limits to body size in a grazing reptile, the Galápagos marine iguana. *Ecology* **78**, 2204–2217.

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